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Approaches to understanding echinoderm origins. Part 2: Questioning conceptual models

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Abstract: The two main approaches in interpreting the significance of non-radial fossil echinoderms (carpoids) have consistently produced the same two distinct clusters of results for over a century of investigation. Studies based on conceptual models imbued with Haeckelian precepts consider bilaterally symmetric or asymmetric morphologies of carpoids plesiomorphic for the phylum. These approaches do not find a place for carpoids within an existing phylogenetic framework for the phylum because it is assumed that they primitively lack pentaradiality. Emphasis on differences between these taxa and pentaradial echinoderms forces them outside of and downward from more crownward clades. It is crucial to examine the data supporting these supposed differences. Is it worth considering non-pentaradial echinoderms as members of a well-known group of echinoderms, the blastozoans, which already includes many secondarily-derived, non-pentaradial members? Followers of an empirical model think so, presenting an integration of paleontology, embryology, body wall homology, and image analysis that derives echinoderms from a bilaterian, archimeric larva, not bilateral adults. Unprecedented modification of a single mesocoel (hydrocoel) initiated the pentaradial adult echinoderm, most parsimoniously with five primary lobes in stem forms of each major clade within the phylum. The unique water vascular system led to rearrangement of adult axes that literally have no parallel with those of any other invertebrate, representing an iconic synapomorphy for the Echinodermata. There are few, if any, developmental or stratigraphic data defending carpoids as 'bilateral precursors'. Their free appendage is now shown to be an ambulacrum, undermining any supposition of a 'head', 'tail', or 'gill slits'. Pentaradiality is plesiomorphic for the phylum, obviating the requirement for a triradial intermediate (helicoplacoids) between carpoids and pentaradial forms. Carpoids, a subset of blastozoans, exploited motility as a feeding mode, leading to extraordinary adaptations that belie their interpretation as ancestral echinoderms.

Résumé : *Comprendre l'origine des échinodermes. Partie* 2 : Interroger les modèles conceptuels. Depuis plus d'un siècle, l'application de deux approches méthodologiques distinctes pour tenter d'interpréter les morphologies

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atypiques de certains échinodermes paléozoïques non-radiaires (les carpoïdes) a systématiquement produit les deux mêmes types de résultats. Largement influencées par des principes haeckéliens, les études basées sur des modèles conceptuels considèrent que les morphologies bilatérales ou asymétriques des carpoïdes sont comparables à celles des larves et donc, nécessairement plésiomorphes. D'après ce modèle, les carpoïdes n'ont jamais acquis la symétrie pentaradiaire post-métamorphique caractéristique des échinodermes. En mettant ainsi l'accent sur l'absence d'un seul caractère, ce type d'approche exclut de fait les carpoïdes des clades les plus dérivés et leur impose une position basale. Afin de déterminer la position phylogénétique des carpoïdes, il est crucial, toutefois, de tenter d'identifier de possibles synapomorphies avec d'autres échinodermes. Cette seconde approche, plus empirique, propose une interprétation alternative qui intègre différents corpus de données (paléontologiques, embryologiques, homologies de la paroi du corps). Elle considère que les échinodermes dérivent d'une larve archimérique bilatérale et non d'adultes bilatéraux. Ils se distinguent de tous les autres bilatériens par la modification, au cours du développement, d'un seul mésocèle (l'hydrocèle) à l'origine de plusieurs (généralement cinq) lobes primaires et de la morphologie (penta)radiaire de l'adulte. Le développement du système ambulacraire entraîne un réarrangement des axes de symétrie qui n'ont plus rien à voir avec ceux des autres invertébrés. Cette profonde réorganisation représente une synapormorphie fondamentale des échinodermes. Les modèles qui considèrent les carpoïdes comme des formes nécessairement primitives car bilatérales ne reposent sur aucune donnée embryologique ou stratigraphique. La présence d'un système ambulacraire chez ces formes implique que celui-ci dérive d'un rudiment et que, par conséquent, leur morphologie est incompatible avec la présence d'une "tête", d'une "queue" ou de "branchies". La symétrie cinq est plésiomorphe à l'échelle du phylum, ce qui rend inutile le recours à un hypothétique stade triradiaire (hélicoplacoïdes), intermédiaire entre carpoïdes et formes pentaradiaires. Les carpoïdes ne représentent donc pas des échinodermes ancestraux, mais probablement des blastozoaires dérivés, dont la morphologie a été modifiée par l'adoption d'un mode de vie vagile et épibenthique.

Keywords: Echinodermata ● Symmetry ● Embryology ● Carpoids ● Blastozoans ● Helicoplacoids

Introduction

As anyone who has studied a starfish, brittle star, sea urchin, sea cucumber, or sea lily rapidly comes to realize, these taxa are very unlike the vast majority of metazoans past or present. In fact, they are also all very unlike each other, which tends to make it difficult to find major features homologous across all these extant forms. Consider the myriad and sometimes bizarrely unfamiliar fossil taxa, and the problems in finding commonalities become even more challenging. Most would agree that typical salient features of the phylum include endoskeletal elements made of a unique form of calcium carbonate called stereom. The skeleton is most often found in the mesoderm of the body wall, but also in certain internal organs. However, arguably the most conspicuous characteristic of echinoderms, and the one that makes them readily recognizable to most, is the presence of a highly unusual, five-rayed symmetry known as pentaradiality. This attribute is found in all living echinoderms, at least at the early onset of development. Pentaradiality is also expressed among the stratigraphically earliest taxa, and a great many other fossils besides. Partly due to pentaradiality, echinoderms are sufficiently highly derived compared with other deuterostomes, including their sister group the hemichordates, that comparisons of body plans are fraught with different approaches in assessing homologies among the very disparate body plans within the phylum.

Most importantly, the existence of a phylum-level feature of such importance as pentaradiality has been brought into question as a characteristic of the very first echinoderms. For example, it was recently claimed by Rahman & Zamora (2024) that analyses consistently recover bilaterally symmetric forms as the earliest echinoderms. However, as pointed out by Sumrall (1997), the results of a phylogenetic analysis depend largely on how characters are selected and coded, and thus rest on assumptions made about the homologies implied by the character state assignments. Sumrall was correct to point out the pivotal nature of argumentation for or against a specific set of homology statements. Nevertheless, the discussion surrounding these character statements is sometimes not very fulsome, consisting only of lists of character states accompanied by minimal character analysis, a practice also lamented by Mooi & David (1997). The set of assumptions made by those who would regard non-radial fossils as the most stemward members of the phylum, what we call here 'conceptual models' (Lefebvre et al., 2024), represents only one

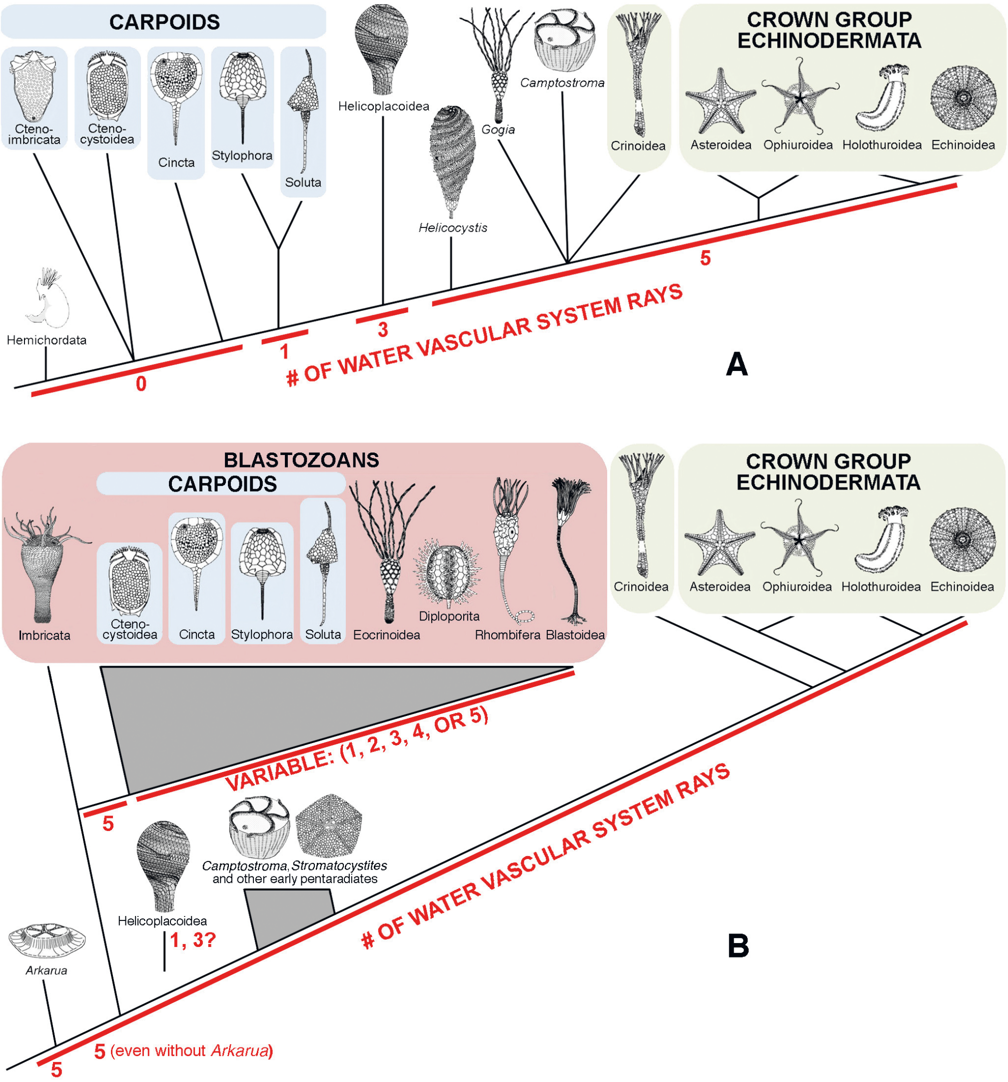


Figure 1. Comparison of tree topologies from most recent iterations of conceptual and empirical approaches to echinoderm origins. **A.** Conceptual model after Rahman & Zamora (2024), in which Ctenoimbricata, Ctenocystoidea, and Cincta are implied to lack a WVS. However, Stylophora and Soluta are now suggested to have the plesiomorphic condition of a single ray from the WVS based on the findings of Lefebvre et al. (2019). **B.** Empirical model as described herein. Pentaradiality is found to be plesiomorphic for the phylum, and taxa with fewer than five rays (carpoids and other blastozoans) are placed in the Blastozoa. The exception are helicoplacoids, which remain enigmatic due to disparate interpretations of the available material.

way of looking at the information at hand. Considering new empirical data, there is growing unease over the 'consistent' conceptual models for echinoderm origin that echoes the earlier dissatisfaction with the calcichordate theory (reviewed in Lefebvre et al., 2024).

We would further maintain that only a subset of the data has been considered in favor of a progressionist assumption that ray number increased during the evolution of the Echinodermata (Fig. 1A). Essentially, conceptual models assume the absence of a single character, pentaradial symmetry, as an indicator of plesiomorphy. The types of data that supposedly are consistent in recovering this result are worth questioning, and it is healthy for phylogenetics to do so. The perception remains that data not in agreement with the topology of the tree produced by conceptual models have to be overlooked in order for the topology to be accepted unconditionally. Consistent claims, no matter how often repeated, do not imply consensus.

The set of assumptions supporting the conceptual models summarized in Lefebvre et al. (2024) are imbued with Haeckelian principles because they assume the absence of pentaradial symmetry to recapitulate hemichordate archimery in the pre-metamorphic larval stage of echinoderms. This recapitulation forces unusual taxa that also lack pentaradiality, such as carpoids, down the phylum's phylogenetic tree. In other words, the claim is that pentaradiality is derived, because of the requirement that it be the result of teleological, step-wise addition of de novo rays during evolution of the group. We agree on many points made by those who support this conceptual model, notably concerning many of the features of the highly informative fossils so far described. However, there are valid reasons to diverge strongly on interpretations of the synapomorphies of the phylum. In other words, we need to better understand the plesiomorphic morphology represented by the first echinoderms. This is because the fossils, and especially development of, and homologies among the main parts of echinoderms suggest that similarities between outgroup bilaterians (namely, hemichordates) and non-pentaradial echinoderms are superficial, relatively easily falsified by embryology and paleontology, and not rooted in more parsimonious explanations for the unique pentaradial body plan. Consequently, it is more than equally feasible to code a dataset that does not assume that first echinoderms had a bilaterian-type anterior-posterior axis. At the very least, therefore, there are many basic questions to be asked concerning the validity of the assumptions required to push so-called bilateral carpoid echinoderms stemward in the phylogeny.

In contrast, empirical models rely on comparison of non-pentaradial early forms with a wide array of data obtained from extant and fossil echinoderms, suggesting that pentaradial symmetry was secondarily lost in such taxa, and that morphology of remaining axial skeleton documents its presence (Fig. 1B). One of the primary aims of this paper is literally to ask questions about many of these forms, and to compare interpretations upon which the conceptual and empirical models rest.

Discussion

Why are concept-based interpretations of echinoderm origins hard to test?

The situation described above exposes methodological issues with conceptual models (dipleurula, calcichordate, and ambulacrarian) that are hard to overlook, and equally hard to falsify because they are almost infinitely adaptable to contrary evidence simply by tweaking their presuppositions.

First, they are all based, at least in part, on assumptions that must be taken as correct or at least as very likely. These precepts are then taken to be validated by one or several independent observations using embryology or gene sequencing, such as: pre-metamorphic echinoderm larvae are bilaterally symmetric, or that hemichordates and echinoderms both evolved from bilaterally symmetric stem-ambulacrarians with pharyngeal openings. However, all conceptual models also rely on several untested declarations.

The first is fundamentally Haeckelian (Haeckel, 1866), and assumes that ontogeny of extant deuterostomes (chordates, echinoderms, hemichordates) recapitulates their phylogeny, thereby suggesting a robust guide to anatomy of extinct forms. Such concepts continue to resonate in even the most recent treatments of Haeckel's view of echinoderm fossils (e.g., Werneburg & Hoßfeld, 2024). This is a structural element of conceptual interpretations of carpoids, in particular (Lefebvre et al., 2024). In the dipleurula theory, bilateral symmetry of carpoids was primitive because during ontogeny of extant taxa, radially symmetric, post-metamorphic echinoderms are derived from bilaterally symmetric, pre-metamorphic larvae. The asymmetric development of gill slits during ontogeny of extant cephalochordates and tunicates was the foundation of the calcichordate theory because it was interpreted as recapitulating the transition from asymmetric cornutes (postulated pharyngeal openings restricted to one side of the theca) to supposedly bilaterally symmetric mitrates occurring much later in the fossil record (hypothetical paired internal gill slits). In the ambulacrarian theory, loss of the right hydrocoel during ontogeny of pre-metamorphic echinoderms was considered to recapitulate the implied evolutionary transition from ctenocystoids (a symmetric 'hydrovascular tentacular system') to cinctans (right branch of the hydrovascular tentacular branch shorter than the left). These arguments rest on presuppositions that hydrovascular systems were likely to have existed instead of accepting that they are water vascular (WVS) systems already known to exist in crownward echinoderms.

Second, tests of conceptual models are difficult because they assume that implied key evolutionary transitions among early deuterostomes are documented by paleontological evidence. The models do not consider other possibilities, such as that radial symmetry is secondarily lost in carpoids. The result is compulsory that such taxa had structures homologous with plesiomorphic deuterostomian features (e.g., gill slits, post-anal tail), even where evidence for existence of these structures is weak to lacking, or even shown not to exist (see below). Concomitantly, evidence for verifiable WVS structures is ignored or rejected purely because of theoretical requirements. For example, to comply with the dipleurula theory, Bather (1930) had to reject any evidence of ambulacra or the WVS in carpoids, even though he had himself earlier identified them in both cinctans and solutans (1913 & 1926). In the calcichordate theory, anatomical similarities in the stylophoran appendage with ambulacra of other echinoderm feeding arms were disregarded, because they did not comply with the adopted conceptual model that the theca was a head, and the aulacophore was a tail. The paired anterior feeding structures of cinctans and ctenocystoids could not be interpreted as ambulacral structures by Smith (2005) and Rahman & Clausen (2009) because the ambulacrarian theory required them to be homologous to the left and right hydrovascular systems of hemichordates. Although unsupported by anatomical evidence, gill slits were considered present in certain carpoid taxa even in recent publications (e.g., Rozhnov & Anekeeva, 2024). Comparative anatomy demonstrating that 'gill slits' in echinoderms are comparable with the myriad other types of respiratory structures seen in taxa widely recognized as echinoderms was set aside. New work continues to undermine the idea that 'gill slits' or other pharyngeal openings are present in carpoids (Jackson, 2024). Both the stylophoran aulacophore and the solutan homoiostele were interpreted as post-anal tails or hemichordate-like stalks because the possession of a muscular proximal region was considered incompatible with conceptual views, even though analysis of stereom microstructure in stems of pleurocystitids, a group long accepted as rhombiferan blastozoans, suggested that their proximal region also contained muscle tissue (Gorzelak & Zamora, 2016). This indicates that appendages with a muscular proximal component exist in non-stylophoran echinoderms.

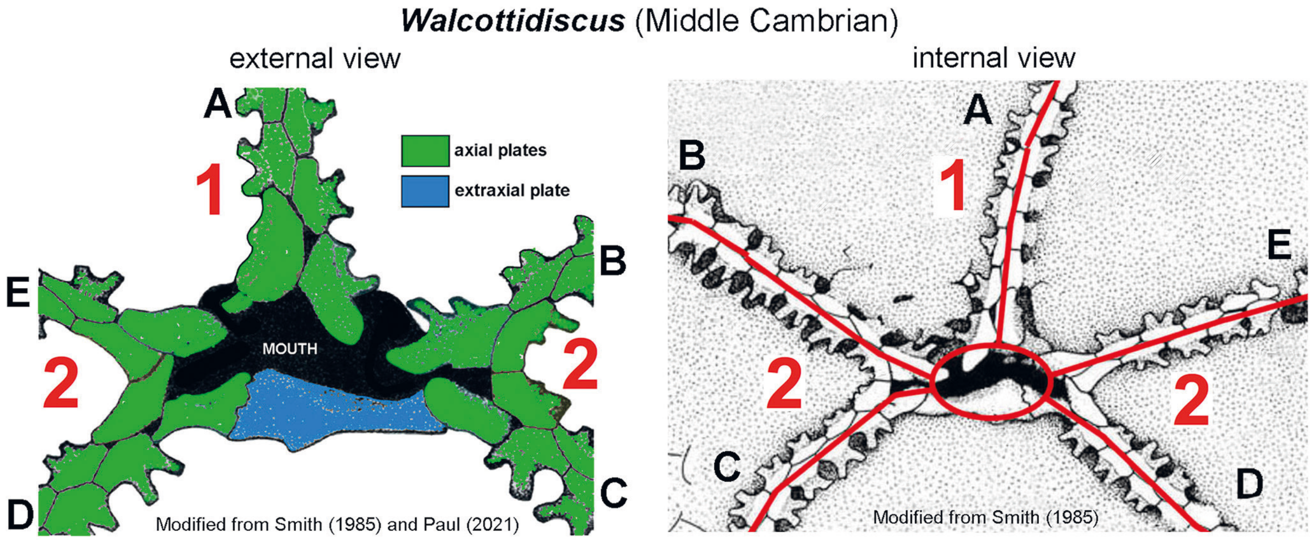
Third, conceptual interpretations of carpoids are hypothetical narratives, and thus almost impossible to test (Peterson, 1995). Testing requires independent sets of evidence obtained from different methods or techniques. Even when such independent evidence is brought to bear, concepts such as the calcichordate theory, its initial assumptions and phylogenetic implications demonstrably falsified by molecular phylogenies, persisted in a modified form, eventually giving rise to the ambulacrarian theory.

As pointed out by Rahman et al. (2009), one of the most objective ways to test the validity of conceptual models is to rely on the fortuitous discovery of exceptionally preserved soft parts in carpoids. Accordingly, a pyritized ambulacral canal and associated tube feet in the distal aulacophore of stylophorans (Lefebvre et al., 2019), reinforced by discovery of these structures in a mitrate (Boisset et al., 2024), unequivocally demonstrate that the aulacophore was a feeding appendage with clearly discernible axial components, including cover plates. As discussed in Lefebvre et al. (2024), molecular evidence indicates that echinoderms are more closely related to hemichordates than to chordates, thereby falsifying basic assumptions of the calcichordate theory. In addition, new findings among Lagerstätten in particular represent crucial sets of independent data that falsify the calcichordate theory (Lefebvre et al., 2019). These independent lines of evidence also undermine anatomical interpretations of stylophorans imposed by the ambulacrarian model. However, carpoids could still be re-interpreted as stem-group, pre-radial echinoderms with a pharynx (as in cinctans) and a single feeding arm (as in solutans). Nevertheless, there are independent reasons for questioning this interpretation (see below).

Making sense of the disparate and controversial morphologies of carpoids requires taking into account additional evidence acquired independently from other methods and techniques, so as to place them in the wider context of the diversification of earliest echinoderms. The EAT model suggests an empirical approach that integrates embryological, genetic, and morphological evidence that can illuminate paleobiology and systematic affinities of carpoids. The potential of the EAT's system of body wall determination to identify skeletal homologies in both fossil and extant echinoderms is acknowledged by diverse parties on all sides of the debate (Mooi & David, 1998; David et al., 2000; Peterson et al., 2000; Sprinkle & Guensburg, 2001; Sprinkle & Wilbur, 2005; Hotchkiss, 2012; Kammer et al., 2013; Smith & Zamora, 2013; Lefebvre et al., 2015; Paul, 2017; Guensburg et al., 2020). It is from this standpoint that more questions can be asked about echinoderm origin and its relationship to previous conceptual theories.

What can embryology tell us about origin of the echinoderm body plan?

In nearly all classic textbooks, echinoderms are generally diagnosed by three features: (1) a calcite endoskeleton with its typical stereom microstructure; (2) a water vascular system, and (3) radial symmetry usually manifested as pentaradiality in adults. In extinct taxa, all three features can be identified immediately (calcite endoskeleton, radial symmetry) or indirectly inferred from plates whose patterning is regulated by the Ocular Plate Rule (OPR), thus making their identification as echinoderms relatively straightforward. But the wide disparity among the five extant classes indicates that these diagnostic features can be dramatically altered (Mooi & David,



Modified from Smith (1985) and Paul (2021)

Modified from Smith (1985)

Figure 2. Expression of the 2-1-2 pattern in an early pentaradiate, edrioasteroid-like echinoderm. Large red numbers indicate paired and single rays in conceptual models that consider the triradial condition plesiomorphic for pentaradial echinoderms. On the right, an internal view shows how the ring canal of the WVS could easily accommodate placement of five independent radial canals. Rays are labelled according to the Carpenter system as applied by Ubaghs (1967a).

1997; Pawson, 2007). Stereom is extremely reduced among holothuroids, and in many extant taxa (e.g., irregular echinoids, holothuroids), bilateral symmetry is superimposed on and obscures the pentaradial pattern.

It is therefore worth considering in detail how the rudiment, a unique feature of echinoderm embryology, forms before examining the preconceptions inherent in conceptual models reviewed in Lefebvre et al. (2024). Rudiment formation begins with development of the left hydrocoel into a crescent-shaped structure that encircles the larval esophagus, simultaneously producing five primary lobes, evenly spaced around its perimeter (Heider, 1912; Runnström, 1918; Ubaghs, 1967a; David & Mooi, 1996 & 1998; Mooi & David, 1997 & 2008). As this torus closes to form the ring canal, it interacts with the underlying left somatocoel to produce the rudiment. Meanwhile, five primary lobes give rise to the primary tube feet of each growing ambulacral ray (Heider, 1912; Runnström, 1918; Ubaghs, 1967a). These rays lengthen and add new tube feet and axial elements during precisely controlled patterning, the OPR (David & Mooi, 1996 & 1998; Mooi & David, 1997; Mooi et al., 2005; Turner, 2024). Together, these elements comprise the main structure of the WVS.

Therefore, the most distinctive apomorphy of echinoderms is not a stereom endoskeleton or pentaradial symmetry, but dramatic modification in which rudiment formation over-writes whatever bilaterality might have existed in the early larva (Runnström, 1918; Ubaghs, 1967a; David & Mooi, 1996 & 2014; Mooi & David, 1997; Peterson et al., 2000; Arnone et al., 2015; Byrne et al., 2016). The resulting reorganization, initiated by the axial hydrocoel (left mesocoel), and superimposed on the bilaterally symmetric, extraxial larval portion, generates an entirely new body plan with a de novo axis of symmetry.

This axis is further expressed in the entrainment of the posterior somatocoels during coelomic stacking (Peterson et al., 2000), a phenomenon indicated by strong evidence from anterior-posterior patterning expressed by homeobox genes (Mooi & David, 2008; David & Mooi, 2014) and in recent work by Formery et al. (2023). This change in axis is unique, and it can be regarded as the sufficient and single most important echinoderm synapomorphy. Virtually nothing of the original, primary bilateral symmetry seen in deuterostomes, including hemichordates, is preserved in post-metamorphic echinoderms. Because post-metamorphic symmetry is not equivalent to the original larval axes, the de novo anterior-posterior axis, further reflected in the rearrangement of the coeloms via stacking, is not comparable to axes in other bilaterian metazoan (David & Mooi, 1996; Mooi & David, 1997). Crucially, this means symmetries of adult echinoderms cannot be compared to those seen in early development of sister phyla in searches for homology.

Therefore, the uniqueness of developmental patterning in echinoderms has major implications for the interpretation of fossil taxa. Rudiment formation is as clear in crinoids (Engle, 2012; Amemiya et al., 2016), a group that arose early in the history of the phylum (Guensburg et al., 2020 & 2023), as it is in the most recently evolved classes viewed as highly divergent, such as holothuroids (by virtue of their extreme paedomorphosis) and echinoids (by virtue of the degree to which extraxial region in adults is suppressed through metamorphosis).

Critical among these observations is the evagination of the growing rudiment giving rise to the axial region (David & Mooi, 1996 & 1998; Mooi & David, 1997). Skeletal elements in this rudiment-derived, axial part of the body wall can be readily and unambiguously identified in all echinoderms because their characteristic biserial plating follows the OPR (Mooi et al., 1994; David & Mooi, 1996 & 1998; Mooi & David, 1997). Therefore, body wall regions formed according to the OPR are found only in echinoderms. Concomitantly, any OPR-related skeletal pattern identified in fossil taxa is associated with an axial region derived from the rudiment (Mooi & David, 1997 & 1998; David & Mooi, 1999; David et al., 2000; Mooi et al., 2005).

The ineluctible, empirically established tenet is that any extinct echinoderm (including a carpoid), in which the existence of OPR-related ambulacral (axial) elements can be demonstrated, has necessarily undergone the aforementioned reorganization of the larva into the echinoderm-specific, novel anterior-posterior axis during ontogeny of the rudiment. Consequently, the symmetry of these fossils of adults cannot be related to the bilaterality or anterior-posterior axis of any other bilaterians, including ambulacrarians. Whether or not one relies on the EAT to interpret carpoids, these empirical outcomes have not been adequately considered by any of the conceptual models outlined above. The appeal of finding 'missing links' between bilaterians and the echinoderms has been obfuscatory, since it can be legitimately questioned whether these links should even be expected to exist, as we discuss in ensuing sections.

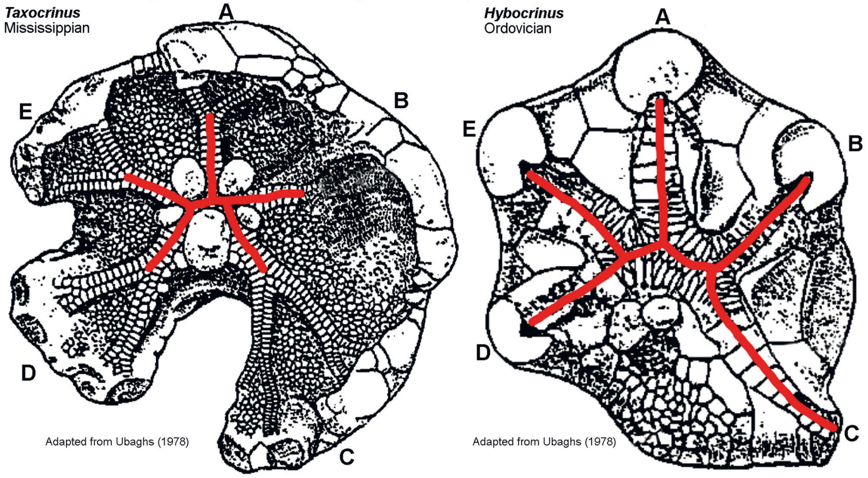
Does embryology support pentaradiality as plesiomorphic for echinoderms?

In spite of the embryological data presented above, to arrive at pentaradial echinoderm morphology, conceptual models require phylogenetic transition from uniserial or biserially symmetric fossils (e.g., carpoids) to triradial (e.g., helicoplacoids), and finally to pentaradial forms that supposedly recapitulate ontogeny of echinoderms (Walther, 1886; Haeckel, 1896a & b; Bather, 1930; Paul & Smith, 1984; Smith, 1984 & 2008; Holland, 1988; Jefferies, 1990; Domínguez, 2004; Zamora et al., 2012; Zamora & Rahman, 2014). The existence of a hypothetical triradial stage, crucial to fill the gap between carpoids and pentaradial echinoderms, relies in part on the so-called 2-1-2 ambulacral pattern apparent in many Paleozoic taxa (Fig. 2). The 2-1-2 pattern is suggested to correspond to the convergence of three main ambulacral structures (not five) at the mouth: a single ambulacrum opposite the anus, gonopore, and hydropore (Carpenter ray A), and two lateral branches, each dividing slightly distal to the mouth into two ambulacral rays (Carpenter rays B+C and D+E) (Ubaghs, 1967a; Paul, 2017). This pattern is regularly presented as evidence that pentaradial symmetry is preceded in both ontogeny and phylogeny by a triradial stage (Bather et al., 1900; Sprinkle, 1973; Bell, 1976; Paul & Smith, 1984; Smith, 1984 & 2008; Jefferies, 1990; Hotchkiss, 1998; Sumrall & Waters, 2012; Kammer et al., 2013; Paul, 2017; Paul & Hotchkiss, 2020). However, this assumption is almost never accompanied by attempts to reconcile the implied evolutionary steps with known steps in the development of the rudiment.

Plesiomorphic embryological patterns of many phyla are inferred from extant taxa and ancestors held in common with sister taxa. However, and in spite of evidence to the contrary, the ad hoc argument is often brought forward that processes observed among extant forms operated differently in early echinoderms (e.g., Paul, 2017). If this is true, then it is logical to ask if actuopaleontology in this particular case is of any use at all. Crinoids have the most plesiomorphic morphology of any extant class, based on expressions of axial, perforate, and imperforate extraxial regions that are remarkably similar to those of earliest echinoderms (Guensburg et al., 2023). Among both fossil and extant crinoids (Ubaghs, 1978), there are supposed 2-1-2 examples (Fig. 3). These expressions are identical to those frequently described for other Paleozoic taxa (e.g., Saulsbury, 2020). However, during ontogeny, no modern crinoid expresses even a hint of three rays, two of which later bifurcate, in the essential pentaradiality expressed by the rudiment (Engle, 2012; Amemiya et al., 2016) (Fig. 3). The pseudo-triradial 2-1-2 pattern is therefore secondary to the fully pentaradial patterning of five simultaneously expressed primary lobes, each of which gives rise to a primary tube foot that in turn lengthens to make five radial canals. At no point in development of extant taxa in which this aspect has been examined, even of crinoids, is there an ontogenetic stage with three primary lobes, let alone only one or two.

Considering that observation of ontogenetic patterns among extant forms is commonly used to assess those of even the earliest of fossils, we ask why this axiom has been so differently applied to the

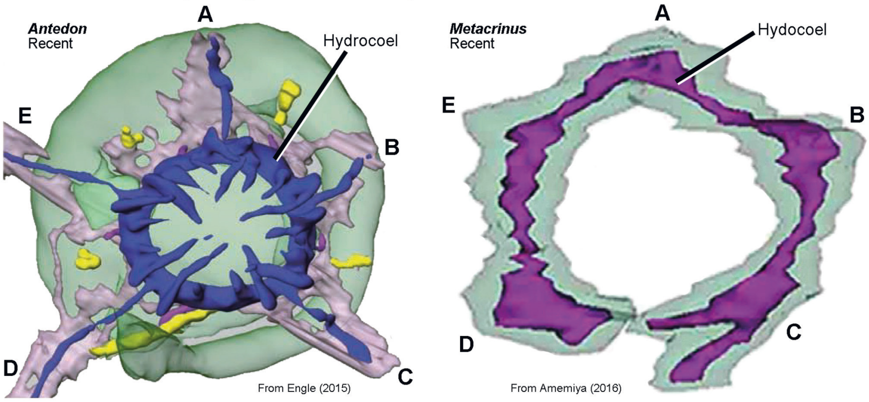
Expression of 2-1-2 patterns (red) in fossil crinoids



Adapted from Ubaghs (1978)

Adapted from Ubaghs (1978)

Early stages in development of crinoid rudiment



From Engle (2015)

From Amemiya (2016)

Figure 3. Expression of the 2-1-2 pattern in ambulacra of fossil crinoids, but not in early development. Ambulacra in two examples of fossil crinoids are marked in red. Rays are labelled according to the Carpenter system as applied by Ubaghs (1967a).

Echinodermata. As already pointed out by Ubaghs (1967a) and Stephenson (1979), there are no ontogenetic data indicating that pentaradial symmetry of post-metamorphic echinoderms derives from a triradial stage. Likewise, there is no embryological argument supporting the view that the propensity to produce ambulacral rays was expressed any differently in the earliest echinoderms (Mooi & David, 1998).

Is the 2-1-2 pattern in early pentaradial echinoderms a 'red herring'?

A so-called 2-1-2 ambulacral pattern observed in extant as well as many Paleozoic crinoids is widely distributed at phylum scale, and is often suggested to distinguish forms with that pattern 'pseudo fivefold symmetry' (Rahman & Zamora, 2024) from those with perfect pentaradial symmetry among asterozoans and echinozoans 'true fivefold symmetry' (Rahman & Zamora, 2024). However, in early pentaradial taxa, this conclusion is drawn solely from cover plates that obscure the peristome below, preventing observations of the arrangements of the first axial floor plates adjacent to the mouth. Remarkably, in earliest echinoderms such as *Stromatocystites* or *Walcottidiscus* (Smith, 1985; Paul, 2017 & 2021) in which we can see the mouth frame, particularly from the interior, the first ambulacrals do not actually express a 2-1-2 pattern (Fig. 2). In all five ambulacra, both members of the first pair of ambulacral floor plates are in contact with the mouth, or nearly so, and the supposed branches forming common BC and DE rays do not exist. Each ray is independent. Elongation of the mouth between the BC and DE rays (the CD interray), which can lead one to think that independence is not the case, is a product of inserting a single extraxial plate bearing the hydropore/gonopore into the CD interray next to the mouth (Fig. 2, blue plate). Envisioned without this plate, which is clearly a perforate extraxial element,

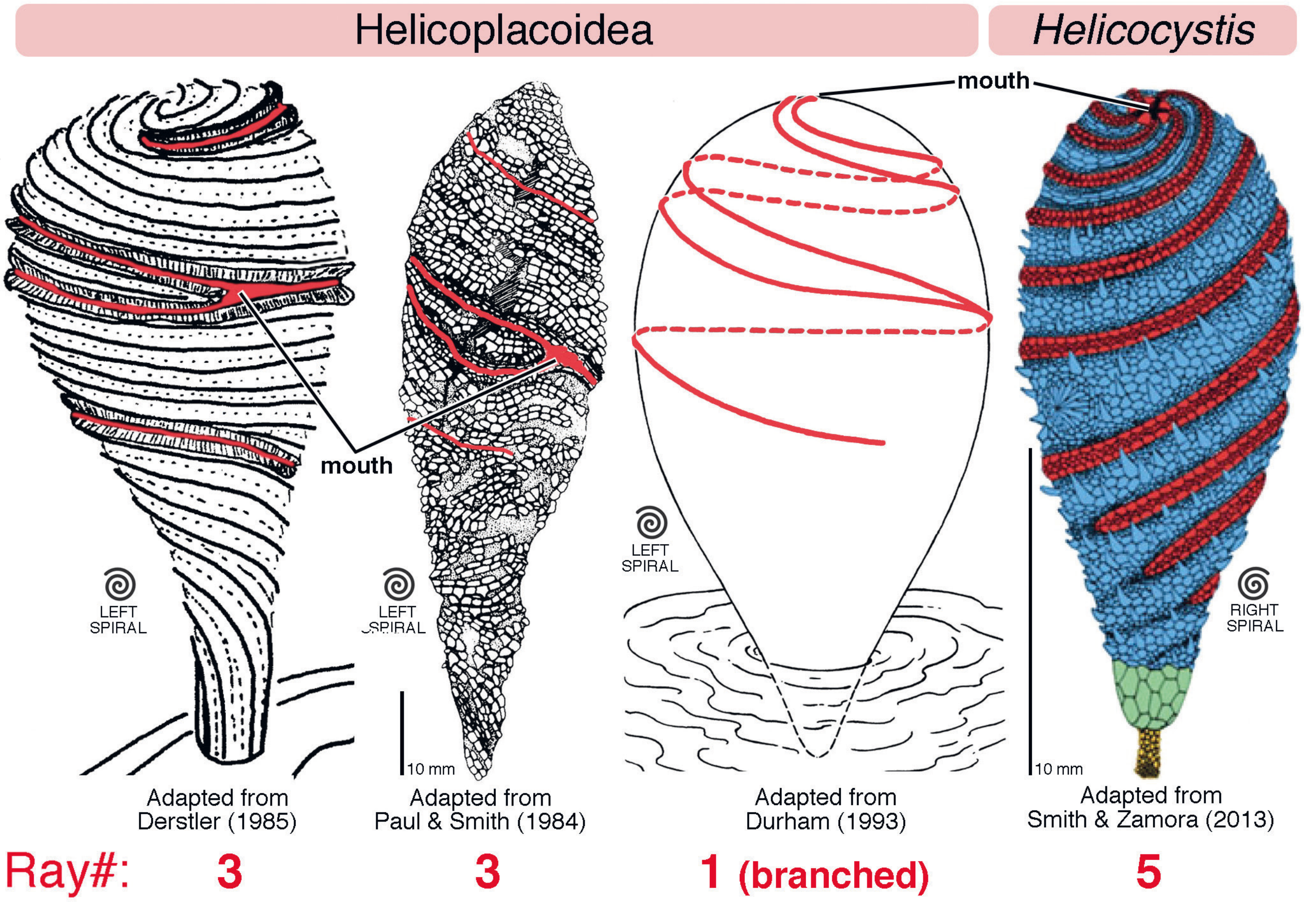


Figure 4. Comparison of reconstructions in different works on helicoplacoids and *Helicocystis*. Ambulacral pathways marked in red.

the five ambulacra would form near-perfect pentaradial symmetry consisting of the oldest axial elements next to the mouth, with successively younger elements radiating independently according to the OPR. Therefore, even in apparent 2-1-2 structures, we find little by which to separate 'pseudo fivefold symmetry' from 'true fivefold symmetry' (Rahman & Zamora, 2024). The supposed dissimilarities do not hold up during analysis using diverse data such as topology, configuration of first axial floor plates, and embryology that supercede superficial differences.

Thus, there is no a priori reason to think that in any echinoderm, the ring canal in a 'triradial configuration', made in the rudiment from the hydrocoel, gives rise to three primary lobes, two of which later bifurcate to make five in total. Given the evidence at hand, it is more parsimonious to suggest that non-pentaradial forms suppress full development of primary lobes typical of the plesiomorphic morphology, much as is seen throughout the blastozoans and among certain crinoids (see below). Moreover, without the interpolated perforate extraxial plate, the mouth frame is pentaradial, and the water ring is a perfect torus, just as it is in crinoids that also express the 2-1-2 pattern (Fig. 3). This was realized in the depiction of the water ring (Breimer & Macurda, 1972: text-fig. 48) in blastozoans otherwise well-known for their 2-1-2 pattern (Paul, 2021).

The 2-1-2 pattern should be manifested only by axial determinants of pentaradiality, the floor plates themselves. Because the pattern is shown in a subset of axial elements, the 2-1-2 pattern is only about plates, not conserved developmental patterns. Furthermore, the series of small cover plates over these parts of the ambulacra of early echinoderms can be positively misleading in reinforcing the suggestion that the BC and DE rays bifurcate. For example, the ontogeny of edrioasteroids shown in Sprinkle & Bell (1978) illustrates what is occurring in patterning of cover plates, not the floor plates. In addition, investigators are predisposed to see a 'bilateral' axis from the A ray through the CD interray because of the way that these are universally illustrated, with the periproct at the lower, 'posterior' part of the animal, and the two 'bifurcating' rays on each side. The placement of the periproct in early pentaradial echinoderms is not a marker for an anterior-posterior axis (Peterson et al., 2000). The de novo echinoderm anterior-posterior axis is not the same axis as that described by Li et al. (2020), strongly undermining the purported significance of their findings.

In summary, there is no evidence to suggest that the skeletal structures exhibiting the 2-1-2 pattern in earliest fossil echinoderms reflect the ontogeny or even the form of the water vascular system itself, but there is evidence to suggest that it does not. The 2-1-2 pattern is secondary, superimposed on a pentaradial plan, and not a plesiomorphic echo of the origins of pentaradiality. The 2-1-2 pattern fails to provide any support for the existence of a hypothetical, triradial ancestral condition, and we can answer in the affirmative that it is indeed a red herring.

Are helicoplacoids triradial intermediates?

Helicoplacoids have long been touted as the most convincing paleontological evidence for plesiomorphic triradial symmetry in echinoderms (Paul & Smith, 1984; Smith, 1984, 1988 & 2008; Holland, 1988; Jefferies, 1990; Domínguez, 2004; Bottjer et al., 2006; Zamora et al., 2012; Smith & Zamora, 2013; Zamora & Rahman, 2014; Lin et al., 2015). This view was supported by the early stratigraphic occurrence of helicoplacoids (Cambrian Series 2, Stage 3) and their reported unusual morphology, supposedly evincing triradiality. Derstler (1981) was the first to suggest that helicoplacoids had a mouth on the side from which three rays radiate to spiral around the body (Fig. 4). Unfortunately, the specimen used to show this is apparently missing (TG, personal observation).

On the basis of analysis of only a handful of specimens chosen from among hundreds that exist, Paul & Smith (1984) contradicted Durham & Caster's (1963) and Durham's (1967) placement of the peristomial area at the apical pole of helicoplacoids. Paul & Smith (1984: 400) stated that they "believe that the mouth lay laterally at the confluence of the ambulacral branches", without presenting unequivocal evidence. The belief became a fact in subsequent conceptual models of echinoderm evolution (Fig. 4). Although this interpretation was originally suggested by Derstler (1981 & 1985) and later restated by Wilbur (2005), incontrovertible evidence for the existence of a mouth frame at the lateral triple junction of the ambulacra remains elusive. There is no published image showing a mouth frame on the side of a helicoplacoid, only images that show variously preserved cover plates which, as stated above, tell us little about floor plate expressions. Nevertheless, the interpretation of helicoplacoids as triradial became mainstream, in spite of available evidence to the contrary.

Durham (1993) presented an unparalleled, detailed description of helicoplacoid morphology based on dozens of specimens representing several different taxa, including the same specimen used by Paul & Smith (1984) to illustrate the 'triradial' nature of helicoplacoids. Durham (1993: 595) found that "...during burial and fossilization plates from the back side have been thrust into a position between the frontal columns. These allochthonous plates were utilized in their [Paul & Smith's] reconstruction of the plating across an ambulacrum and adjacent interambulacrum... Thus, their [Paul & Smith's] reconstruction is invalid. Further, in the area identified as the mouth there are only scattered small plates from the ambulacrum. There is no suggestion of a mouth in this area on this or any other specimen." Instead, Durham found evidence that not only was the mouth situated at the apical pole of a helical body, but that it had a single ambulacrum with a branch at the point at which Paul & Smith (1984) believed the mouth to be (Fig. 4). With the exception of Wilbur (2005), whose evidence relies on equivocal assignments of certain plates to a kind of primary mouth cover plate series at this junction, little evidence has been provided to contradict, or to falsify Durham & Caster's (1963) original, or Durham's (1993) further supported placement of the mouth at the apical pole. A reduced mouth frame would be hard to detect in the apical pole region, but it would not only be a natural consequence of the reduction in ray number, it would explain the lack of unambiguous evidence for a mouth frame, or a mouth iteself, at the supposed lateral origin point of three rays. Branching ambulacra are not unknown among early forms in many echinoderm clades, suggesting there is no a priori reason to rule this out in helicoplacoids (Fig. 4).

By ignoring Durham's (1993) work, even to refute it fully, and uncritically accepting the triradial model, conceptual models seized upon helicoplacoids as a convenient, early, triradial intermediate 'leading' to more crownward, pentaradial forms (Paul & Smith, 1984; Smith, 1984, 1988 & 2008; Holland, 1988; Jefferies, 1990; Domínguez, 2004; Bottjer et al., 2006; Zamora et al., 2012; Smith & Zamora, 2013; Zamora & Rahman, 2014; Paul & Hotchkiss, 2020; Rahman & Zamora, 2024).

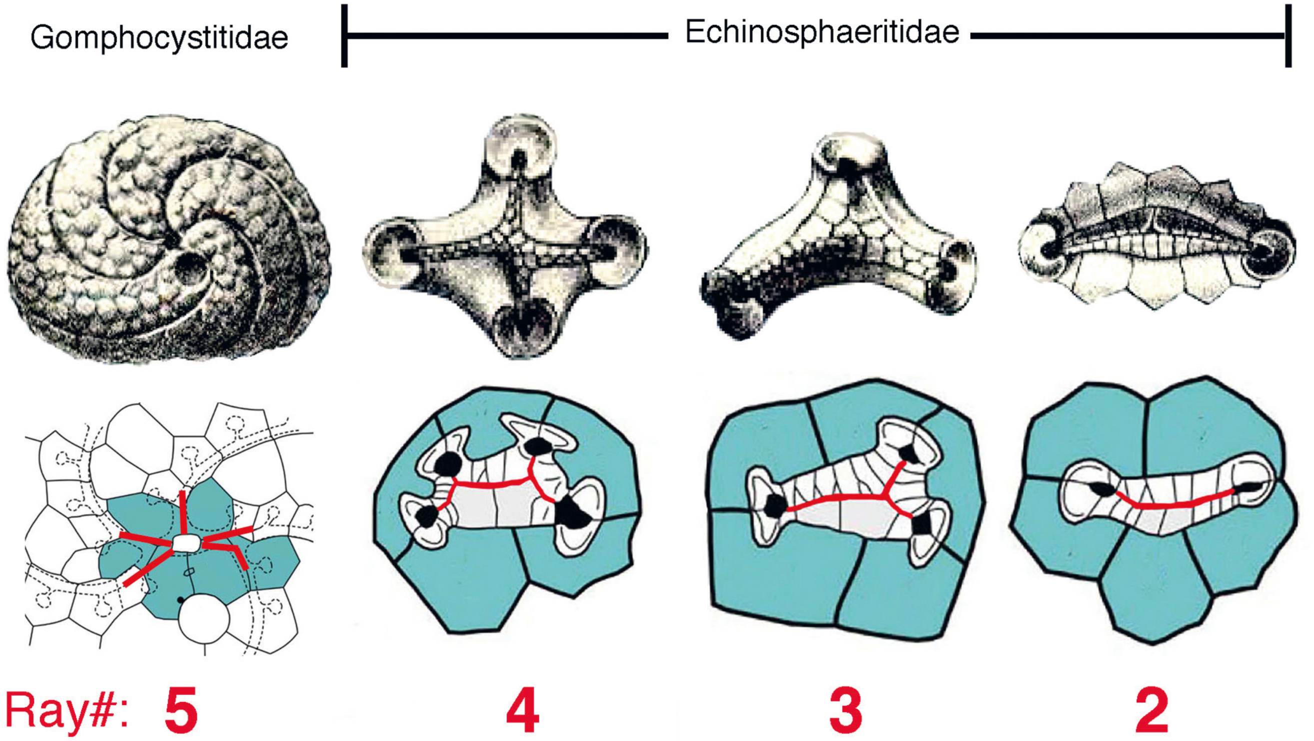


Figure 5. Oral areas of gomphocystitid and echinosphaeritid blastozoans expressing different ray numbers. Upper row of figures shows fossils with cover plates in place, lower row shows plate pattern in wall of theca (circumoral plates in turquoise), cover plates removed. Ambulacral pathways marked in red.

Swimming against this tide, several authors suggested instead that the atypical morphology of helicoplacoids was derived, because it lacked plesiomorphic features widespread in most other early echinoderms (e.g., epispires) (Ubaghs, 1971 & 1975; Mooi & David, 1998; Sprinkle & Wilbur, 2005). Wilbur (2005) explicitly promoted the idea that helicoplacoids did indeed have the mouth on the side of the body, but that triradiality was actually derived from a pentaradial ancestor though the loss of two rays.

It is not unusual for members of pentaradial groups to exhibit reductions in ray number at least to three rays (Fig. 5). Both crinoids and blastozoans provide examples of triradiality derived from pentaradial ancestors. For example, forms younger than helicoplacoids, such as the diploporitan *Triamara*, the rhombiferans *Caryocrinites*, *Hemicosmites*, *Tyrridiocystis*, and *Echinosphaerites*, and the hybocrinoids *Tripatocrinus* and *Cornucrinus* have triradial members, all unquestionably with pentaradial ancestors (Paul, 1988; Sheffield & Sumrall, 2019). Therefore, even if we accept that helicoplacoids were triradial, there is no reason to adopt, uncritically, the idea that this signifies a plesiomorphic symmetry for the phylum that necessarily predates pentaradiality, particularly as pentaradiate echinoderms are known in equally early strata (Zhao et al., 2022).

Is Helicocystis *a missing link?*

The description of *Helicocystis* in slightly younger deposits (lowermost Miaolingian) from Morocco (Smith & Zamora, 2013) has been suggested to support helicoplacoids as a triradial intermediate, since *Helicocystis* itself was viewed as the first pentaradial echinoderm (Smith & Zamora, 2013; Rahman & Zamora, 2024) (Fig. 1A). In turn, *Helicocystis* is supposed to be a morphologically intermediate 'missing link' between the precursor helicoplacoids and earliest pentaradial taxa, such as *Camptostroma* and *Stromatocystites*, but which are actually stratigraphically older forms (Zamora et al., 2015, and see below). *Helicocystis* consists of a short, polyplated stem-like appendage topped by a spindle-shaped body (Fig. 4). The body was made of two distinct parts: (1) an elongate, fusiform upper portion possessing five spirally arranged ambulacral rays with polyplated interambulacral areas containing the anus, hydropore and gonopore; and (2) a short, cone-shaped, basal portion showing distinct, tesselate plating lacking any evidence of coiling (Smith & Zamora, 2013).

Helicocystis is known from few specimens, and fundamental questions remain concerning the interpretation of this difficult fossil. A proposed anatomical difference from helicoplacoids is that the mouth is at the upper pole of its theca, and the periproct on the side (Fig. 4). The large, disorganized, tesselate plates at the base of *Helicocystis* brings it into the disparate landscape of early-middle Cambrian pentaradial echinoderms. Paul (2021: 44) stated that the "hypothesis that the pentaradiate *Helicocystis* is derived from the triradiate *Helicoplacus* explains many additional observations for which there is no alternative explanation". Instead, the fossil seems only to raise more questions that, when answered, undermine the initial suggestions for its significance.

The helicity of the helicoplacoids and *Helicocystis* calls into question the purported morphological similarity between them. In order to make the former into the latter, the mouth has to be twisted to the aboral end of the theca, which is, ironically, where Durham (1993) considered the helicoplacoid mouth to be. At the same time, two new rays have to appear, presumably as additional primary lobes in the rudiment just as seen in all forms crownward to *Helicocystis* in the echinoderm tree. No evidence has been presented as to whether the movement of the mouth to the pole preceded or followed the appearance of two additional, de novo rays. This causes problems concerning another important point. Assuming that some form of torsion could push the mouth from the side, dragging the already twisted ambulacra with it, the unexplained fact remains that *Helicocystis* possessed right-handed coiling of the body, whereas helicoplacoids had a left-handed twist (Fig. 4). This has been shown consistently in reconstructions, though seldom discussed in terms of its implications for the position of either helicoplacoids or *Helicocystis* in echinoderm phylogeny. The spirality in these two forms is unlikely to be homologous, thereby undermining initial reasons to compare these two forms in the first place. If there is no special feature by which to base this comparison, making helicoplacoids into precursors of *Helicocystis* is forced, and not based on any special relationship between the two taxa. Given how different these two forms actually are, including direction of spirality, the number of changes needed to transform one morphology into the other invites us to consider other alternatives.

It has even been argued on the basis of very poorly preserved, cherry-picked specimens from among hundreds of specimens, that gogiids retained plesiomorphic helicity inherited from triradial forebears (Lin et al., 2015). The so-called helical anatomy of gogiids was described as confined to the peduncle region (plesiomorphic stem), a situation not seen in helicoplacoids in which the ambulacra themselves are helical.

Work is ongoing to apply the EAT to the unusual morphology of *Helicocystis*. However, it seems clear that the radii emerging from the upper pole represent axial region, and interradial areas are perforate extraxial, containing the anus, gonopore and hydropore. The aboral portion, consisting of lower part of the body capsule and stem-like appendage, corresponds to imperforate extraxial region. In turn, this would imply that the spirally coiled upper part is homologous to the perforate extraxial, oral surface of edrioasteroid-like taxa. The lower part, plus the stem-like appendage, would be equivalent to the imperforate extraxial region of taxa such as *Camptostroma* or *Stromatocystites*, a comparison made already by Smith & Zamora (2013: fig. 5).

It is interesting to note that more crownward 'spiral' cystoids such as *Gomphocystis* are left-handed spirals, not the right-handed spiral of the 'ancestral' *Helicocystis*. However, if we ignore the chirality issue and assume spiral morphology to be homologous between helicoplacoids and *Helicocystis*, then the conceptual ambulacrarian hypothesis indicates spiral morphology to be plesiomorphic for the entire clade of pentaradial forms. The loss of this feature seems not to have been addressed directly in publications espousing conceptual models to build phylogenetic character sets (e.g., Smith & Zamora, 2013; Rahman & Zamora, 2024). Moreover, it is important to point out that the Helicoplacoidea comprises several taxa. No works have addressed the question of whether this is a monophyletic assemblage, or if *Helicocystis* is supposed to share common ancestry with only a single member of the group. In other words, it remains possible that helicoplacoids represent a monophyletic, highly specialized branch of echinoderms that have nothing at all to do with *Helicocystis* or the rest of the pentaradial echinoderms (Mooi & David, 1998).

Are carpoids pre-radial echinoderms?

Crinoids and blastozoans both contain forms with fewer than five rays (Fig. 5). Nevertheless, there has been no perceived need to fit any of these, or the even more reduced and strange two- or one-rayed blastozoans, into the stem of the phylum. This raises the question as to why this forced placement was deemed necessary in the case of carpoids. Instead, this was performed through a priori assumptions concerning tentacular vascular systems and the dismissal of ambulacral structures as tails. Requirements of theory-based interpretations of carpoids did not fully consider opposing empirical evidence from the fossil record, embryology, and homologies of body wall regions that support more parsimonious explanations. In addition, as suggested above, the Haeckelian evolutionary scenario suggesting that pentaradial echinoderms are derived from a helicoplacoid-like triradial ancestor is not confirmed by embryological or paleontological data (Ubaghs, 1967a, 1971 & 1975; Stephenson, 1979; Mooi & David, 1998; Sprinkle & Wilbur, 2005).

To answer the titular question, we turn to the fossils themselves for evidence of relationships to already known forms. Specifically, we focus on the blastozoan clade. We first note here that in crinoids, axial and extraxial systems and their attendant coeloms worked together to produce 'true arms' (Guensburg & Sprinkle, 2009; Guensburg et al., 2010, 2020 & 2023). Late in their evolution, crinoids abandoned calcification of superfluous floor plates, although signal of their existence persists in the embryology and topology and of the coeloms and the WVS in every part of a crinoid arm, including the pinnules. Unlike crinoids, blastozoans did not use extensions of the central coelom and accompanying stereom to support feeding structures. The latter arise as 'free' axial region in the form of brachioles, which are unique to the Blastozoa (David et al., 2000; Guensburg & Sprinkle, 2009; Guensburg et al., 2010, 2020 & 2023).

In blastozoans such as rhombiferans and diploporitans, the proximal 'circumoral' plates only weakly evince governance by the OPR, if they do so at all. The plesiomorphic condition might, or might not be the seven circumorals depicted by Paul (2021), but these are not circumoral, first-formed axial floor plates that express Lovén's Rule. Instead, we have the illuminating possibility that on the theca itself, blastozoan 'floor plates' are perforate extraxial in origin, and assume the role of supporting the water vascular system along with the tube feet and the cover plates. The soft tissues of axial body wall would not be observed, as this would not be preserved, leaving the cover plates to appear as though they were directly attached to the perforate extraxial thecal plates. With this observation, the usual expression of Lovén's Rule seen across other echinoderm groups (David et al., 1995) would not be expected, as evidence for Lovén's Rule and the OPR is not necessarily expected when plates from adjacent interradii form the 'paired first ambulacrals' instead of axial floor plates (Paul & Hotchkiss, 2020; Paul, 2021). It is possible that some form of Lovén's Rule could be manifested in 'terminal branching' of the WVS (Paul & Hotchkiss, 2020), but this is not a requirement.

The considerable variation in expression of thecal plating across the Blastozoa is a product of the fact that these plates are likely perforate extraxial body wall that do not grow according to any ontogenetic ordering process (i.e., not in accord with the OPR). In addition, the implicit suggestion by Paul & Hotchkiss (2020) and Paul (2021) that brachioles are formed as if they were tube feet, or even that they might be precursors of tube feet themselves (Paul & Smith, 1984) does not follow from our observations of blastozoan fossils, including the earliest known members of the clade, the imbricates. For example, the idea that brachioles are somehow equivalent to tube feet is not congruent with the work of Breimer & Macurda (1972: text-fig. 48), in which tube feet are mapped onto plates below the cover plate series, notably around the mouth, but also in the brachioles themselves. In addition, in *Gogia*, preliminary re-examinations of intact oral regions show what appears to be an irregular 'oral frame' (Sprinkle & Wilbur, 2012). Pentaradiality seen in cover plates of the oral region does not extend to the frame beneath, in which the plates form an ovoid construct with monoserial elements lacking the zig-zag perradius typical of floor plate series formed in accord with the OPR. In these fossils, brachioles are otherwise typical for blastozoans, with cover plates attached on either side of the channel along which the WVS runs. The aberrant structure of the oral frame strongly suggests that it is not derived from axial region, but is most likely perforate extraxial in origin, as is the rest of the theca, and that it is the extraxial body wall that supports the brachioles.

This suggestion carries deep implications for understanding blastozoans, as well as the carpoids. Firstly, there are two autapomorphies for the blastozoans: (1) lack of expression of paired, calcified floor plates on the theca; (2) the expression of brachioles as floor plates plus cover plates as extensions from the theca that do not include any coelomic derivatives other than the WVS (David et al., 2000; Guensburg & Sprinkle, 2009; Guensburg et al., 2010 & 2020). It is possible that all taxa with brachioles lacked calcified floor plates. Moreover, it is clear that the first blastozoans were pentaradial (Paul & Smith, 1984; Nardin et al., 2017; Nohejlová et al., 2019). Work is in progress on fossils of plesiomorphic blastozoans such as the imbricates *Lepidocystis* and *Kinzercystis*, as well as early 'eocrinoids' such as gogiids, to determine the point at which the aforementioned synapomorphies appeared during diversification of the blastozoans.

Without the expression of calcified floor plates, lability in ray number would be a consequence of relaxed phylogenetic constraints imposed by pentaradial plate formation in accordance with the OPR. Concomitant recumbency of the WVS over variably expressed

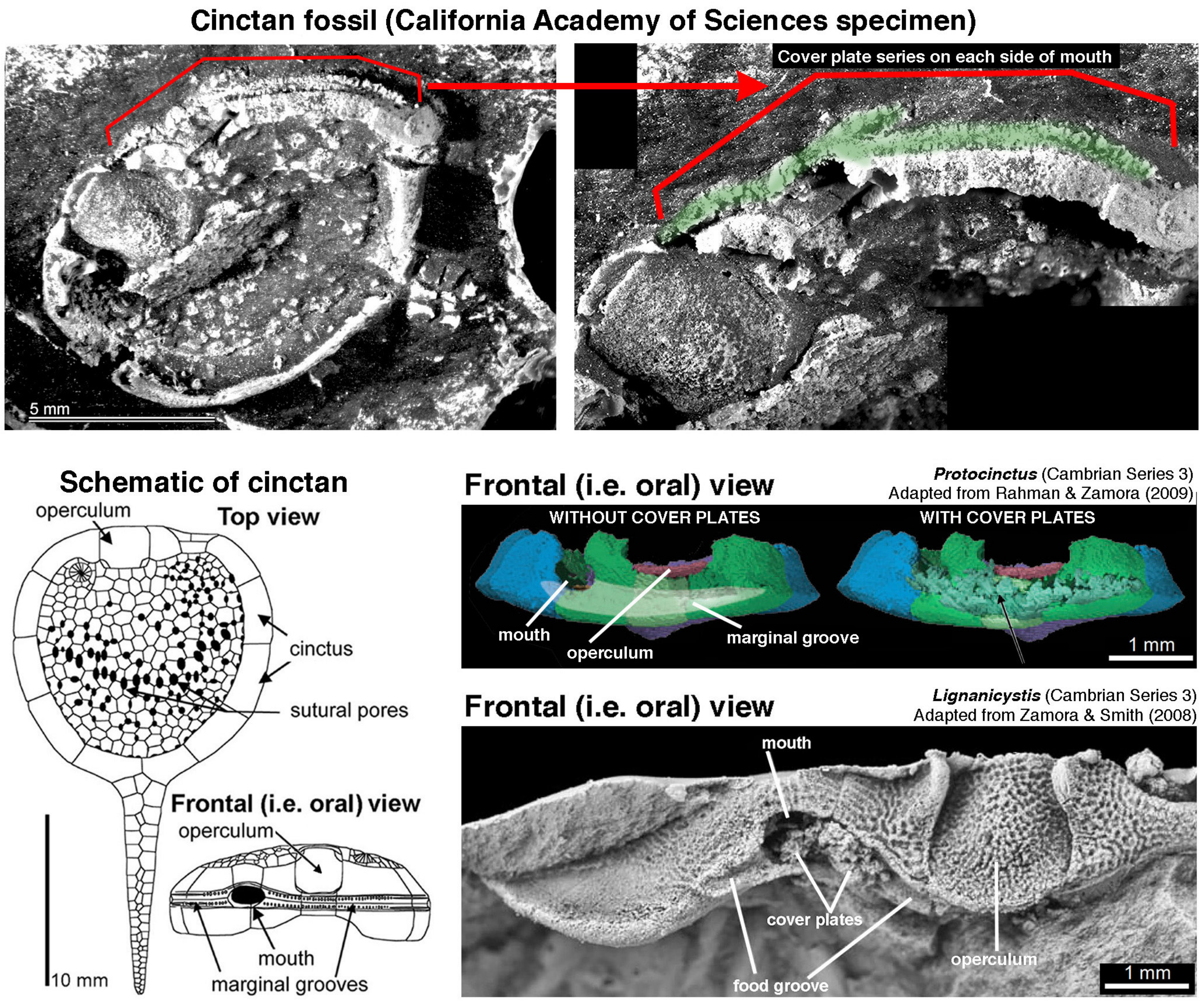


Figure 6. Ambulacral regions of cinctans. Upper figures show latex pulls of entire (left), and detail (right) of cover plates along cinctus proximal to the operculum (see schematic, lower left). Images on lower right show frontal views of a stemward cinctan (*Protocinctus*) and more crownward form (*Lignanicystis*) as depicted in the literature.

extraxial body wall helps to explain the variation in expression of ray number in the blastozoans, which includes multiple, convergent expressions of four-, three-, and even two-rayed forms such as that seen within a single family, the Echinosphaeritidae (Paul, 2017) (Fig. 5). Two-rayed blastozoans also include *Dibrachicystis* and pleurocystitids, and there are even one-rayed forms (e.g. *Hillocystis*). In no other echinoderm group is this type of variation expressed to such a degree.

These observations beg the question as to why none of these taxa have been considered part of the conceptual model for origins of the phylum. Some of these forms are arguably as bizarre and unfamiliar as the carpoids and helicoplacoids that are held up as stages in a teleological progression towards pentaradiality. In fact, virtually all the departures from pentaradiality within the blastozoans have been regarded as reductions in ray number, not precursors of pentaradial taxa also assigned to the Blastozoa.

The purposeful exclusion of carpoids from any relation to blastozoans in conceptual echinoderm phylogenies (Rahman & Clausen, 2009; Rahman & Zamora, 2009 & 2024; Zamora et al., 2012; Smith & Zamora, 2013; Zamora & Rahman, 2014) exemplifies a careful choice of what taxa to consider for evidence of bilateral ancestry. In these phylogenies, blastozoan departures from pentaradiality are not assessed for their relevance to the question. Nor are reasons for their exclusion from the character analyses presented in attempts to convince other workers that expressions similar between carpoids and some blastozoans have nothing to do with one another. Carpoids are clearly bizarre, but there are compelling reasons to compare them with blastozoans in the context of empirical models. This comparison gives us reasons to evaluate carpoids as blastozoans, and not indicative of early, non-pentaradial echinoderms.

Can carpoids be considered blastozoans?

Conceptual models focused early on taxa that best fit the model for first echinoderms predicted to resemble 'next steps' above the node shared with hemichordates. Followers of the calcichordate hypothesis found what they needed among the solutans and stylophorans (cornutes and mitrates). Jefferies (1967) was explicit in declaring cornute and mitrate stylophorans were like 'tadpoles', with a head (theca) containing gill slits and other vertebrate features and a muscular tail (aulacophore) bearing a notochord. We have already noted the multiple evolutionary losses required by this suggestion (Lefebvre et al., 2024), and the ultimate falling out of favor of the calcichordate scenario. However, later proponents of these forms as pre-radial echinoderms instead of stem chordates nevertheless continued to follow the general concept that stylophorans had a head and a tail (Smith, 2005 & 2008; inter alia).

Recent studies have since falsified this view of stylophorans (Lefebvre et al., 2019; Boisset et al., 2024) by showing conclusively that the aulacophore contains tube feet connected to a branch of the WVS traveling up the center of a series of stereom ossicles, and protected by corresponding cover plates. In spite of this, the conceptual model continues to consider stylophorans compatible with the idea that they originated below the node containing pentaradial taxa (Rahman & Zamora, 2024). Instead of a tail, the aulacophore had now to be considered a precursor to the multiple rays seen within its sister group, including the blastozoans, and the head became a plated theca, in order to retain consistency with the idea that the ctenocystoids and cinctans were pre-radial, leading to yet another permutation of the basic precursor calcichordate model.

David et al. (2000) felt that the aulacophore could be a crinoid arm, even without clear evidence that it contained the WVS and tube feet later demonstrated by Lefebvre et al. (2019). Although data from the latter study were definitive in rejecting the tadpole morphology, they were not used to place stylophorans in close relationship to any other echinoderm group. The implication that they might be more like crinoids than other forms could not be refuted, but it is now clear that the aulacophore is completely unlike a crinoid arm. For example, although the WVS lies along a monoseries of brachial-like plates, this series is not accompanied by any other somatocoelar derivative, neither left nor right. Both of these coeloms are found along the arms of crinoids (David et al., 2000; Guensburg & Sprinkle, 2009; Guensburg et al., 2010 & 2020). The monoserial ossicles of stylophorans are also found in the brachioles of some blastozoan taxa, just as biserial brachiolar series are found among crinoids (Sprinkle, 1973).

In turn, the existence of the monoseries does not undermine favorable comparison of the stylophoran aulacophore with a brachiole. In addition, the placement of a single primary cover plate on the edge of each floor plate is a common expression among blastozoans. The explanation that best fits the available data is that the aulacophore is a brachiole made of axial elements, albeit a highly modified one. The presence of axial region in stylophorans indicates the presence of a rudiment, and that the morphology of stylophorans is post-metamorphic. Their single ambulacral ray represents a reduction in the expression of the primary lobes of the left hydrocoel, a pattern not unique to stylophorans, as it occurred independently in several other uniradial blastozoans such as *Fusicystis* and *Hillocystis* (Jell, 1983; Zuykov et al., 2008). Stylophorans are most parsimoniously placed in the blastozoan clade (Fig. 1B).

Another carpoid group, the solutans, have also been interpreted as tadpole-like forms, with the stalk (homoiostele) representing a post-anal tail, and the main body a head. However, the 'feeding appendage' on the 'head' is constructed of axial skeletal elements (floor plates with cover plates), and represents a free ambulacral structure (Parsley, 1997; David et al., 2000; Peterson et al., 2000; Sprinkle & Guensburg, 2004; Nardin et al., 2009; Lefebvre et al., 2012 & 2013; Rahman & Lintz, 2012; Noailles et al., 2014; Lefebvre & Lerosey-Aubril, 2018). The mouth was located at the base of this appendage (Bather, 1913; Caster, 1967; Ubaghs, 1969; Kolata et al., 1977; Jefferies, 1990; Daley, 1995; David et al., 2000; Smith, 2005; Rahman & Lintz, 2012; Noailles et al., 2014). In addition, Daley (1996) reported evidence for a WVS and associated tube feet in the feeding arm of *Coleicarpus*. This is compatible with evidence for these same structures in the brachiole of stylophorans. Therefore, the appendage of solutans and the brachioles of blastozoans are identical in construction. In fact, if one were to envisage an early blastozoan in which four of the rays were not expressed, it would look very much like a solutan.

This leaves for consideration two other carpoid groups, the cinctans and the ctenocystoids. Among the strangest of all echinoderm taxa, and as noted above, these are consistently placed most stemward in phylogenies based on conceptual models largely because they are not considered to have ambulacra at all (Rahman & Clausen, 2009; Rahman & Zamora, 2009 & 2024; Zamora et al., 2012; Smith & Zamora, 2013; Zamora & Rahman, 2014). However, David et al. (2000) considered that the presence of several openings within the body and/or through the upper surface of a cinctan theca, such as sutural pores (epispires), identify thecal plates as part of the perforate extraxial body wall. The cinctan homostele was therefore a stalk-like extension of the marginal system of perforate extraxial plates, and not homologous to stems of other echinoderms (e.g., blastozoans, crinoids, *Helicocystis*), all of which are made only of imperforate extraxial elements (Mooi & David, 1997; David et al., 2000; Sprinkle & Guensburg, 2001; Guensburg & Sprinkle, 2007; Nardin et al., 2009 & 2017; Lefebvre et al., 2015). The homostele is autapomorphic for cinctans (e.g., Ubaghs, 1967c; Jefferies, 1990; David et al., 2000).

In early cinctans (e.g., *Asturicystis*, *Sotocinctus*, *Trochocystoides*), the two anterior marginal grooves converging towards the mouth are each protected by opposing sheets of small plates, one on each side of the marginal groove (Friedrich, 1993; Sdzuy, 1993; Smith & Zamora, 2009). These are almost identical to the cover plate series of other echinoderms (Ubaghs, 1967c; David et al., 2000; Rozhnov, 2006). Moreover, these sheets are like axial constructs of other echinoderms in expressing patterns consistent with the OPR (Fig. 6). Even among diploporitans, when present (e.g. in some specimens of *Protocrinites*) they indicate a condition very similar to that in cinctans. This observation supports their interpretation as cover plates over a WVS in which the floor plates are not expressed. This expression could represent a recumbent brachiole, or part of the WVS normally found on the theca in other blastozoans, and in complete accord with the findings described above for loss of axial skeletal elements on the theca of blastozoans. This is further supported by the clearly perforate extraxial nature of plates supporting not just a single brachiole, but sometimes several brachioles, as in reconstructions of the previously enigmatic *Cymbionites* and *Peridionites* (Jell & Sprinkle, 2021).

Several authors (Smith, 2005; Rahman & Zamora, 2009; inter alia) considered cinctan food grooves to be unrelated to echinoderm ambulacral structures because the sheets of small cover plates attached directly to the edges of thecal marginals. However, as documented by Guensburg & Sprinkle (2001, 2003, 2007 & 2009) and Guensburg et al. (2020), floor plates are known to be absent in other types of echinoderms such as all post-Floian, crownward crinoids even though they were clearly present as calcified ambulacral plates in some of the earliest known crinoids (e.g., *Apektocrinus*, *Athenacrinus*, *Titanocrinus*). In modern crinoids, the axial region is not represented by actual plates, but by shelves of soft tissue supporting the WVS. However, the lack of calcified floor plates has not posed a barrier to assignment of crownward crinoids to the Echinodermata. It is more parsimonious to consider that the two grooves leading to the mouth of cinctans and protected by ambulacral cover plates are two ambulacral channels, incised on extraxial elements (David et al., 2000) (Fig. 6).

Since Gislén (1930), much has been made concerning the fact that in cinctans, one food groove was larger longer than the other (Smith, 2005; Rahman & Zamora, 2009; Smith & Zamora, 2009; Zamora et al., 2012). Although one can assume that the two grooves were originally of different lengths, the variable extension of these grooves could simply depend on whether ambulacral structures were partially erect as brachioles not yet discovered, or largely recumbent over the theca (Ubaghs, 1967c). Comparisons with early blastozoans suggest that they also have free and/or more or less recumbent ambulacral structures (Sumrall, 1997; Parsley, 1999; David et al., 2000). The unequal length of the two grooves could be explained by displacement of the mouth to the right, or simply by varying the length of the recumbent versus free portions of the ambulacrum. For example, cinctans have been reported to the authors that appear to have two free portions of ambulacra (brachioles) still attached to the theca (O. Fatka, personal communication, 2005).

As a result, cinctans can be characterized as having two ambulacra lying over a subset of thecal plates extending aborally from either side of the mouth, much as seen frequently among blastozoans with two rays, such as some rhombiferans (Callocystitidae, Echinosphaeritidae [Kesling, 1967; Paul, 2017]), diploporitans (Dactylocystidae, Gomphocystidae, Protocrinitidae [Régnell, 1945; Kesling, 1967; Bockelie, 1984; Paul, 2017]), and some paracrinoids (*Malocystites* [Parsley & Mintz, 1975]). Consideration of any of these taxa as anything other than blastozoans that lack floor plates has not been presented, thereby weakening arguments that cinctans cannot be typical echinoderms because they lack floor plates. As for stylophorans and solutans, the presence of ambulacral structures in cinctans connotes axial elements from the rudiment that underwent the early larval ontogenetic trajectory typical of echinoderms. Cinctans would

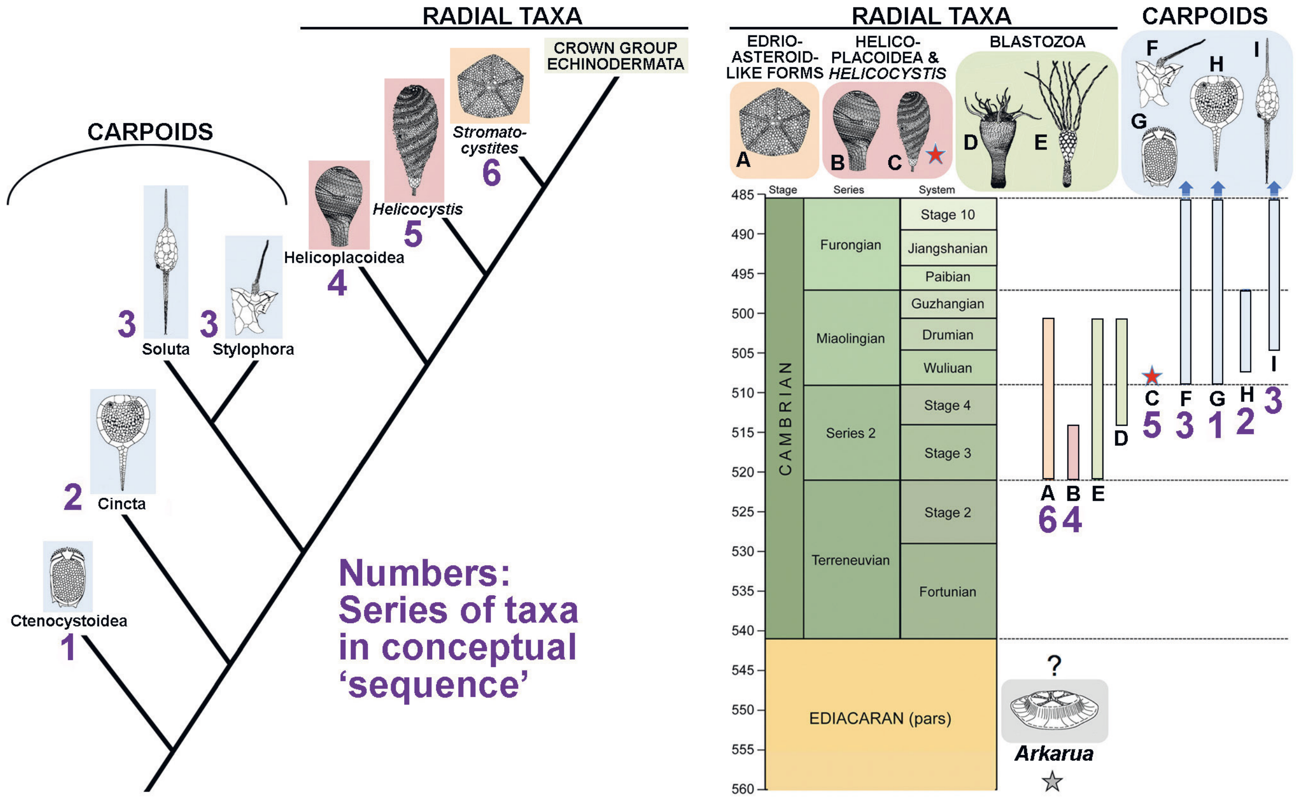


Figure 7. Disagreement between echinoderm relationships indicated by recent iteration of conceptual models (Rahman & Zamora, 2024) and the presently known stratigraphic distributions of stemward echinoderm groups. Sequence of purple numbers and black lettering in the tree at left correspond to those for taxa in the stratigraphic column at right.

therefore correspond to a clade of highly specialized, early blastozoans derived from a pentaradial ancestor.

Ctenocystoids are among the most difficult of carpoids to understand because of their atypical morphology, notably the 'ctenidium' (Robison & Sprinkle, 1969; Ubaghs, 1971, 1975 & 1987; Sprinkle & Robison, 1978; Fatka & Kordule, 1985; Jell et al., 1985; Ubaghs & Robison, 1988; Dzik & Orlowski, 1995; David et al., 2000; Domínguez, 2004; Smith, 2005; Zamora et al., 2013). Recently described ctenocystoids (e.g., *Courtessolea*, *Ctenoimbricata*, *Jugoszowia*) demonstrate more disparity than previously understood (Domínguez, 2004; Zamora et al., 2012; Smith et al., 2013). In most taxa, the theca is delimited by a marginal frame made of one or two elements separating the upper and lower surfaces. However, ctenocystoids such as *Jugoszowia* lack a marginal frame. Their theca is made entirely of numerous, disorganized, spiny plates (Smith et al., 2013; Zamora et al., 2013). This difference was sufficient to recognize them as being outside the main clade of ctenocystoids (Fig. 1A). Although body openings such as epispires seem to be lacking, the position of the anus and the lack of differentiation between upper and lower surfaces suggest the theca is made of perforate extraxial plates, much as in cinctans.

The ctenidium is a bilaterally symmetric, comb-like structure at one end of the body. In anterior view, the teeth of the comb look like two open 'jaws' above and below two marginal grooves, one on either side of the mouth. The upper part of the ctenidium is compared favorably to a series of primary cover plates (named 'laterals' in ctenocystoids), with two sets of 'medials' that express a denticulate morphology strikingly similar to the adradial elements of several other early echinoderms with multi-tiered sets of cover plates, such as *Helicoplacus* (Wilbur, 2006), *Kailidiscus* (Zhao et al., 2010), and many early crinoids (e.g., *Apektocrinus*, *Titanocrinus*; Guensburg et al., 2020). In addition, the multi-tiered plate pattern in the upper part of the ctenidium in some ctenocystoids is constructed similarly to sheets of ambulacral cover plates. The configuration of ctenidials in ctenocystoids is compatible with their interpretation as modified axial cover plates. Therefore, the two underlying lateral grooves borne by anterior marginals below the ctenidials represent the paths of two ambulacral canals on the external wall of the theca. Albeit modified, this topology is otherwise much like that seen in cinctans, in which the axial region and its accompanying WVS was supported by extraxial plates. As discussed for cinctans, this strongly suggests blastozoan affinities for ctenocystoids (David et al., 2000).

What about Arkarua*?*

Biomineralization of a calcite endoskeleton was acquired by echinoderms during Cambrian Stage 3 (~ 521-514 Ma), likely because of shifts in ocean geochemistry (Kouchinsky et al., 2012). Echinoderms are already diverse and widely distributed across the globe by that time (e.g., Ubaghs, 1967a, 1971 & 1975), indicating that the origination of the phylum took place earlier, perhaps even before the acquisition of the calcite endoskeleton (Zamora & Rahman, 2014). This interpretation is in line with molecular clock analyses, all of which imply that echinoderms and hemichordates diverged from ambulacrarians in the Ediacaran (~ 635-541 Ma) (Peterson et al., 2008; Erwin et al., 2011).

Arkarua is a Precambrian fossil described as a kind of echinoderm by Gehling (1987). Although the material is relatively poorly preserved, the reconstructed morphology of *Arkarua* provided by Gehling is strikingly similar to that of 'edrioasteroid-like taxa' sensu Mooi & David (1997) from Cambrian Series 2, with five rays converging towards a mouth in the center of a disc-like body (Fig. 1B). The presence of five putative rays on the upper surface of *Arkarua* is compatible with its interpretation as an early echinoderm that had not yet acquired stereom elements (Gehling, 1987; Smith, 1990; Smith & Jell, 1990; Mooi & David, 1997 & 1998; David et al., 2000). Consequently, it is compelling enough to warrant consideration in all discussions of echinoderm origins. Primarily, this is because of the fact that if *Arkarua* was an echinoderm, it possessed a rudiment-derived, axial region associated with a water vascular system (Mooi & David, 1997).

The possibility that *Arkarua* represents the plesiomorphic morphology for echinoderms is damaging to conceptual models in which first echinoderms were pre-radial. Consequently, its affinities are hotly debated in order to defend these models, in which non-pentaradial forms have yet to be found in strata below Stage 3 of the Cambrian. For example, Zamora & Rahman (2014) and Rahman & Zamora (2024) suggested that the ambulacral pattern of *Arkarua* does not express the 2-1-2 arrangement observed in early edrioasteroid-like taxa. Instead, they expressed the opinion that the arrangement in *Arkarua* closely resembles the 'true fivefold symmetry' of forms such as asterozoans and echinozoans. Therefore, they contrasted this with what they feel is the much later appearance of 'pseudo fivefold symmetry' associated with the 2-1-2 pattern. We have already found this objection wanting on the basis of several arguments (see "Is the 2-1-2 pattern in early pentaradial echinoderms a red herring?").

If it is significant at all, the lack of 2-1-2 expression in *Arkarua* is in favor of it being an early pentaradial echinoderm, as we have already indicated that 2-1-2 expressions are manifested by plates in the body wall, not by patterning of the WVS early in ontogeny. Since *Arkarua* lacked stereom, it is logical to assume that it would not express a modified pentaradiality manifested only in plate pattern.

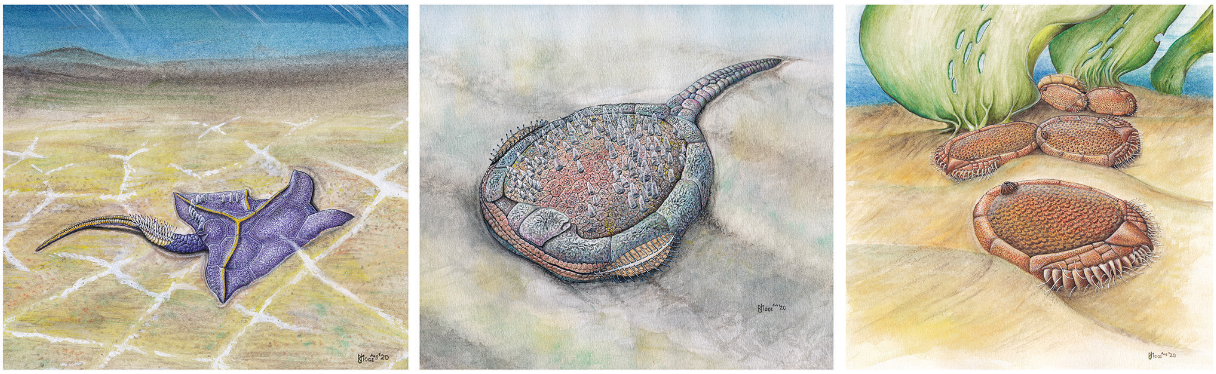
Is Arkarua *crucial to empirical models in which pentaradiality is plesiomorphic?*

Although they were already relatively diverse taxonomically, earliest calcite-plated echinoderms (Cambrian Series 2, ~521–509 Ma) can provide data concerning potential symplesiomorphies among stemward forms at the scale of the phylum. Available paleontological evidence suggests that echinoderms exhibited three main morphotypes at this time: edrioasteroid-like taxa, blastozoans, and helicoplacoids (Ubaghs, 1971 & 1975; Derstler, 1981; Paul & Smith, 1984; Smith, 1988; Sprinkle, 1992; Lefebvre & Fatka, 2003; Kouchinsky et al., 2012; Smith et al., 2013; Zamora et al., 2013; Zamora & Rahman, 2014).

The upper (oral) surface of edrioasteroid-like forms contains both axial and extraxial skeletal elements, and the five ambulacra are made entirely of axial elements, including biserial floor plates and cover plates. The presence of the periproct, numerous pores (e.g. epispires), and other body openings (e.g., gonopore and hydropore) strongly indicates that the oral interradii represent perforate extraxial region. The aboralmost region can be identified as imperforate extraxial body wall (David & Mooi, 1999; Mooi & David, 1997 & 1998). During Cambrian Series 2, blastozoans were represented by both imbricates (*Kinzercystis*, *Lepidocystis*) and gogiids such as *Alanisicystis*, *Balangicystis*, *Gogia*, and *Guizhoueocrinus* (Sprinkle, 1973; Paul & Smith, 1984; Ubaghs & Vizcaïno, 1990; Zhao et al., 1994 & 2007; Parsley, 2009 & 2012). Integration of *Felbabkacystis* into phylogenetic work has confirmed that gogiids are derived from imbricate-like ancestors (Lefebvre et al., 2015; Nardin et al.,

Solutan: *Coleicarpus* (Cambrian Series 3)

Mitrate: *Chinianocarpos* (Lower Ordovician)



Cornute*: Ceratocystis* (Cambrian Series 3)

Cinctan: *Trochocystites* (Cambrian Series 3)

Ctenocystoid*: Courtessolea* (Cambrian Series 3)

Figure 8. Paleoart reconstructing carpoids in life position. Morphology and habit follow the empirical models described herein (artwork by RM).

2017). Presence of brachioles notwithstanding, morphology of imbricates is very similar to that of coeval edrioasteroid-like taxa (David & Mooi, 1999; Sumrall et al., 2001). Otherwise, the main difference between these two morphologies lies in the elongation of the aboral region into a stalk-like appendage (David & Mooi, 1999; David et al., 2000; Lefebvre et al., 2015). As discussed above, the unique morphology of helicoplacoids is largely autapomorphic and likely derived from a pentaradial, edrioasteroid-like ancestor, as surmised by Mooi & David (1998) and Sprinkle & Wilbur (2005).

Morphotypes from Cambrian Series 2 indicate that the stratigraphically earliest stereom-bearing representatives of the phylum had significant features in common, including: (1) an oral surface in which five ambulacral rays converged towards a central mouth (axial region); (2) generally isotropically plated interradial areas containing body openings in addition to the mouth (perforate extraxial body wall); (3) a generally isotropically plated aboral surface that not only closed the coelom aborally, but provided attachment to the substrate (imperforate extraxial body wall). These commonalities delineate a general morphology consistent with that of edrioasteroid-like taxa (e.g., *Stromatocystites*). These forms represent earliest echinoderms among which stem taxa of other morphotypes can be found (Mooi & David, 1997 & 1998; David & Mooi, 1999; David et al., 2000; Sumrall et al., 2001; Mooi et al., 2005; Zamora et al., 2015).

What stratigraphic challenges exist for conceptual theories?

In spite of intensive work for the last two or three decades that yielded important new data on the morphology and biodiversity of earliest echinoderms, the fossil record of carpoids has so far failed to fill the stratigraphic gap between their earliest occurrences and those of oldest pentaradial echinoderms (Dzik & Orlowski, 1995; Sumrall & Sprinkle, 1999; Domínguez, 2004; Clausen & Smith, 2005; Rahman & Zamora, 2009; Rahman et al., 2010; Zamora, 2010; Zamora et al., 2012; Smith et al., 2013). Extensive searches through formations that predate the Miaolingian that normally contain many echinoderm fossils, including isolated stereom elements (Kouchinsky et al., 2012; Zamora et al., 2012), have revealed no remains identified even as parts of carpoids, a group in which individual plates are arguably among the easiest to recognize. Recent efforts to identify carpoid elements from earlier in the Miaolingian are equivocal, and have not significantly altered concepts of their stratigraphic range, contrary to statements to the contrary (Kouchinsky et al., 2022). The signal for distinctive carpoid fossils is demonstrably absent from Cambrian Series 2 (Fig. 7). Although there is no paleontological evidence suggesting that cinctans, ctenocystoids and stylophorans were present before the Wuliuan (early Miaolingian, ~ 509-504.5 Ma) (David et al., 2000; Zamora et al., 2013; Zamora & Rahman, 2014) or solutans before the Drumian (Wheeler Formation, middle Miaolingian, ~ 504.5-500.5 Ma) (Ubaghs & Robison, 1988; Daley, 1996; Lefebvre & Lerosey-Aubril, 2018), conceptual models requiring the existence of carpoids as earliest fossil echinoderms continue to fall back on imperfection of the fossil record to explain the gap. This insistence ignores ample evidence that pentaradial echinoderms were already diversified into major, disparate clades such as blastozoans in the form of imbricates and eocrinoids (Ubaghs, 1953, 1960 & 1967b) in particular, and edrioasteroid-like taxa such as stromatocystitids (Zamora et al., 2015).

As pointed out by Zamora & Rahman (2014), the Cambrian fossil record is indeed far short of complete. Nevertheless, first appearance data for taxa other than carpoids are also incongruent with conceptual models (Fig. 7). For example, *Helicocystis*, a supposed precursor to pentaradial echinoderms in the conceptual model, is known from a single occurrence at the base of the Miaolingian in Morocco. This stratigraphic position is well above occurrences of pentaradial taxa such as the edrioasteroid-like forms noted above (Fig. 7). The situation is exacerbated by the supposition that helicoplacoids represent triradial precursors of the pentaradial *Helicocystis* itself, because the oldest levels with echinoderm remains (the Issafen Formation in Morocco, which is Cambrian Stage 3), is the same age as formations bearing helicoplacoids. At this time, there are already pentaradial lepidocystids (early pentaradial blastozoans) and gogiids (more derived blastozoans). Along with the already wide, nearly cosmopolitan paleobiogeographic distribution of early forms in Cambrian Stage 3, these observations suggest that the diversification of the phylum occurred earlier among as yet unknown taxa, likely similar to edrioasteroid-like forms noted above. It is possible these earliest forms were poorly calcified, as exemplified by the lightly skeletonized edrioasteroid-like pentaradiate, *Yorkicystis*, from the Cambrian Stage 4 Kinzers Formation (Zamora et al., 2022). This might also suggest that *Yorkicystis* does not represent secondary reduction of calcification.

However, if carpoids were actually stem-group echinoderms, then they should have already diversified much earlier than pentaradial forms - at least before Cambrian Stage 3, if not during the Ediacaran (Fig. 7). In particular, the conceptual ambulacrarian scenario continues to require long ghost lineages. It is well known that stratigraphic data are logically unable to test phylogenetic relationships fully due to the essential differences in the nature of these two datasets. However, absolute ages can still be used to point out problems with the robustness of various nodes in topologies that are not consistent with these ages. If the challenges are consistently illuminating the same issues, or concentrated effort is not revealing any additional fossils to fill in ghost lineages of forms predicted to be there, then it becomes increasingly necessary that the topology be re-examined through alternative character analyses. In other words, because the first carpoid fossils appear so late in the fossil record, their stratigraphic occurrence does not enhance confidence that they were pre-radial echinoderms.

Why are there carpoids?

The earliest records of calcite-plated echinoderms (Cambrian Stages 3 and 4) coincide with diversification of infaunal taxa and marked increase in depth and complexity in bioturbation (Mángano & Buatois, 2014 & 2017; Buatois et al., 2014). Before this 'Cambrian revolution', earliest echinoderms of Series 2 lived on soft substrates, attaching to any available benthic hard structures (skeletal fragments, other organisms) (Sprinkle & Guensburg, 1997; Guensburg & Sprinkle, 2000; Sprinkle & Wilbur, 2005; Zamora et al., 2017; Novack-Gottshall et al., 2024). It is possible that some of these early echinoderms also attached to matgrounds (Bottjer et al., 2000; Lefebvre & Fatka, 2003; Parsley & Prokop, 2004; Dornbos, 2006; Kloss et al., 2015), this mode of life is rare in the Cambrian. In any case, fossils indicate that all Cambrian Series 2 echinoderms were sessile, attaching by their aboral surface (e.g., *Stromatocystites*) or by a holdfast at the end of an aboral peduncle (e.g., *Gogia*, *Kinzercystis*, *Lepidocystis*).

The appearance of carpoids during the Miaolingian signifies a marked increase in echinoderm biodiversity, and coincides with the exploitation of new resources (Sprinkle, 1992; Sprinkle & Guensburg, 1997;

Guensburg & Sprinkle, 2000; Lefebvre & Fatka, 2003; Nardin et al., 2009). All carpoid classes eventually acquired flattened thecae, frequently with large, blade-like structures (e.g., cinctan homostele; stylophoran spine-like projections) that enhanced stability on soft substrates (Fig. 8). Their bilaterally symmetric thecae typify vagile 'snowshoe' strategists (Thayer, 1975). Diversification of carpoids can be considered a major ecological transition from originally sessile, radial, suspension-feeders (edrioasteroid-like taxa, helicoplacoids, stemward blastozoans) to vagile, non-radial, suspension and/or detritus feeders (Sprinkle, 1992; Sprinkle & Guensburg, 1997; Dzik, 1999; Guensburg & Sprinkle, 2000).

Solutans such as *Coleicarpus* illustrate key innovations during this transition, being morphologically similar to a gogiid with a reduced number of brachioles, an inflated polyplated theca without epispires, a serially plated feeding appendage, and a distal holdfast at the end of a stalk for permanent attachment on hard substrates lying on the surrounding soft bottom (Fig. 8). A mobile, epibenthic mode of life was later acquired by modification of the stalk into a complex homoiostele with a differentiated, flexible, muscular, proximal region, and a rigid, distal part (e.g. *Castericystis*). The theca of crownward solutans is also generally flattened and asymmetric (e.g. *Girvanicystis*).

Seldom considered to be involved in the origins of the phylum itself, pleurocystitid rhombiferans are instead considered an example of a later, remarkable convergence with solutans resulting from the adoption of a similar, unattached, vagile mode of life (Parsley, 1972; Ubaghs, 1981). Differences in plating between the solutan homoiostele and the pleurocystitid stalk are often relied upon to dismiss homology of these two structures (e.g., Smith, 2005 & 2008). However, these two appendages are in fact homologous, because they both evolved from a gogiid-like, imperforate extraxial peduncle. The stalk of pleurocystitids is made of ring-like columnals because glyptocystitids likely inherited it from crownward gogiids such as *Akadocrinus* that possessed a holomeric stalk.

A stylophoran from the lowermost Wuliuan 'Brèche à Micmacca Member' of Morocco is atypical for that class (Smith et al., 2013: fig. 3e). This taxon has an elongate, moderately inflated, polyplated theca lacking any trace of the stylophoran marginal frame typical of later forms. Crownward taxa are characterized by a flattened, asymmetrical ('boot-shaped') theca with a well-defined, stiffened marginal frame and spike-like posterior extensions, as seen in *Ceratocystis* (Ubaghs, 1967d) (Fig. 8). This morphology is well-suited to a vagile, epibenthic mode of life on soft substrates (Parsley, 1988; Woods & Jefferies, 1992; Lefebvre, 2003 & 2007; Lefebvre et al., 2006). The form of the new Brèche à Micmacca stylophoran indicates that it was plesiomorphic, and that more crownward morphologies were a secondary adaptation to the snowshoe strategy. Moreover, there is evidence suggesting that locomotion of stylophorans was accomplished by movements of the aulacophore (Lefebvre, 2003; Rahman et al., 2009), with the aulacophore in the lead, 'pulling' the theca behind it. Seen in this light, various spike-like protrusions on the bottom of the aulacophore would greatly facilitate 'forward' motion by reducing energy expenditures due to backslipping. The large, articulated, spine-like structures on the opposite end of the animal could have served as counter-weights that would not only prevent backslipping, but enhance the effectiveness of hypertrophied musculature in the proximal aulacophore during the power stroke.

Oldest known, but as yet undescribed ctenocystoids also occur in the Moroccan Brèche à Micmacca Member (lowermost Wuliuan) (Smith et al., 2013: fig. 4f). These are similar to *Jugoszowia* (Wuliuan, Poland), with a conspicuous ctenidium anteriorly, but lacking a marginal frame (Domínguez, 2004), much as noted above for earliest stylophorans. As in stylophorans, morphological features found in more advanced ctenocystoids were likely acquired secondarily as adaptations to a free-living, epibenthic mode of life on soft substrates, such as differentiated lower and upper thecal surfaces and a rigidifying marginal frame. Being small animals living underwater, where overall weight is much less a consideration, locomotion would easily have been achieved through actions of tube feet extending beyond the ctenidium of the ctenocystoids depicted in figure 8.

Earliest cinctans already express all apomorphies of the class, and no forms transitional from other echinoderm groups have yet been found (Ubaghs, 1967c, 1971 & 1975; Friedrich, 1993; Rahman & Zamora, 2009; Smith & Zamora, 2009). Cinctan multi-tiered cover plate sheets suggest affinities with early (imbricate) blastozoans. The reduction in ray number, flattened theca, strong ring of marginal plates, and differentiated upper (convex) and lower (planar) thecal surfaces suggest motility, with the spike-like homostele functioning much like the functionally rearward-facing spikes and articulated spine-like structures of crownward solutans. Moreover, the boot-shaped theca of some cinctans represents an adapatation convergent with that of other snowshoe strategists such as stylophorans. As for ctenocystoids, locomotion would have been accomplished through use of tube feet at the functional front of the animal

(Fig. 8), though some flexure of the homostele cannot be ruled out.

Arguably the most remarkable feature of the changes among these otherwise disparate carpoid taxa is their similarity in response to the availability of new resources and niches that could be exploited at the time of their origination. This explains the reasons that carpoids appeared from within the blastozoans, among which other forms (e.g., pleurocystitids), also evolved in order to adopt these new lifestyles.

Conclusions

It is a common occurrence in studies of forms with strongly expressed autapomorphies that the degree of evolutionary change among these taxa makes them difficult to place among those in which such 'bizarre' morphologies have not obscured phylogenetic signal. This is especially true for fossils, for which molecular evidence cannot be of help and the possibilities are ripe for 'shoehorning' morphologies into conceptual scenarios relying on morphological transitions that cannot be tested. In conceptual models, 'pre-radial' echinoderms 'fall out of the tree' due to the absence of a single, phylum-level autapomorphy - radiality itself. It should come as no surprise that these forms can superficially resemble morphologies that another group, the bilaterians, had already evolved.

Empirical models of echinoderm evolution integrate embryology, development, and morphology of both extant and fossil forms to arrive at the following main points:

(1) The pentaradial form of adult echinoderms, based on the rudiment-derived water vascular system, is patterned after the unique expression of single body cavity, the left mesocoel, as a five-lobed hydrocoel. The hydrocoel is the necessary and sufficient answer to the question, "Why are there echinoderms?" The morphology of edrioasteroid-like taxa (e.g., *Stromatocystites*) very likely approximates the plesiomorphic condition of the earliest, stereom-plated echinoderms.

(2) So-called 'pre-radial' fossils of adults cannot shed light on the origins of echinoderms — they had radial rudiments just like other members of the phylum. Even as diverse as they might be, carpoids can be viewed parsimoniously as having descended from pentaradial ancestors. Carpoid morphologies were acquired from members of the Blastozoa, a clade well-recognized as a significant part of the echinoderm biota during the Cambrian, and that already possessed a pantheon of taxa with reduced numbers of rays.

(3) The fossils themselves show that there is no need to presuppose a 'head' or 'tail' in any carpoid. The so-called 'tadpole morphology' is not supported by fossil evidence, which instead demonstrates the existence of a fully functioning water vascular system in the 'tail', and that the 'head' is actually a theca constructed in the same way as in other taxa, notably blastozoans.

(4) During the Cambrian substrate revolution, some blastozoans diversified into newly available ecological niches and arrived, almost simultaneously, at convergent solutions to the new conditions they encountered, notably modifications to permit motility. The feeding appendage of stylophorans (aulacophore) possesses an overall topology identical to that of the blastozoan brachiole, from which it is derived. However, the aulacophore is itself highly derived, with morphologies specifically adapted to its function as both a locomotory and feeding ray. Solutans evolved from a *Gogia*-like ancestor by retention of a single brachiole that did not become the primary locomotory organ, as it did for stylophorans. Instead, the original blastozoan stalk was retained for that function. Cinctans and ctenocystoids represent two clades of early blastozoans retaining an ambulacrum on each side of the mouth, with tube feet in the associated WVS acting as both feeding and locomotory organs.

(5) Helicoplacoids are poorly understood and therefore subject to multiple reconstructions, so it is not tenable to single them out as triradial, teleologically-required intermediates between single-rayed and pentaradial echinoderms. The evidence for a lateral position of the mouth, along with implied triradiality, is weak at best, and significantly undermined by empirical findings to the contrary. Instead, those are findings provide evidence that their unusual ambulacral configuration actually represents a derived condition, albeit an early one. Helicoplacoids constitute a weak peg upon which to hang heavy implications.

Non-pentaradial echinoderms among blastozoans are consistent with a grander view, namely that they evince responses to lifestyles without having anything to do with ambulacrarian ancestry. They accomplished these adaptations in the same way that all organisms evolve, by adapting the morphologies that they inherited from their ancestors. In this case, they acquired these features from pentaradial forms that otherwise lacked the enlarged tube feet and highly differentiated ambulacra that characterize the body wall construction of extant mobile taxa such as echinozoans and asterozoans.

The hydrocoel represents a key innovation that became the primary way with which the first echinoderms interfaced with their environment. Looked at objectively, without the lens of familiarity, modern vagile forms arguably represent the phylum's most eccentric departures from these earliest forms. The so-called 'eleutherozoans' adopted yet another, very different approach to motility. Unlike carpoids, modern eleutherozoans literally 'flipped over', with the mouth now directly aimed at benthic food sources. Dramatic expressions of metamorphosis resulted in the loss of large amounts of the body wall no longer needed for attachment, concomitantly enhancing the participation of the axial region in construction of the body wall. These changes also facilitated amplified roles for the tube feet in behaviors such as feeding, locomotion, and gathering information about the environment. Echinoderms achieved this by relying on a unique piece of anatomy available to them for these purposes, the water vascular system itself.

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