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Approaches to understanding echinoderm origins. Part 1: Conceptual and empirical models

Bertrand LEFEBVRE[1], Rich MOOI[2], Thomas E. GUENSBURG[3],
Christophe DUPICHAUD[1] and Martina NOHEJLOVÁ[4]
[(1)] Université Claude Bernard Lyon 1, ENSL, CNRS, LGL-TPE, F-69622, Villeurbanne, France
[(2)] Department of Invertebrate Zoology & Geology, California Academy of Sciences,
San Francisco, California, USA
[(3)] Department of Geology, Field Museum, 1400 S. DuSable Lake Shore Drive,
Chicago, Illinois 60605, USA
[(4)] Czech Geological Survey, Klárov 3, Praha 1, 118 21, Czech Republic
Corresponding author: bertrand.lefebvre@univ-lyon1.fr

Abstract: Echinoderms are so highly derived compared with other deuterostomes, including their sister group, hemichordates, that comparisons of body plans are sometimes accompanied by points of view enjoying varying levels of morphological, paleontological, and especially, embryological support. No echinoderm taxon has been the subject of more contentious debate than the carpoids, a disparate assemblage of non-pentaradial, flattened echinoderms that includes the Cincta, Ctenocystoidea, Soluta, and Stylophora. Because of their unusual morphologies, the phylogenetic position and significance of carpoids concerning the origins of the Echinodermata are still being evaluated. A detailed review of carpoid research over the past century and a half reveals that the debate largely results from methodological issues employing two basic, but very different models. Conceptual models, usually imbued with Haeckelian principles, consider the absence of a single character (pentaradial symmetry) as a recapitulation of the pre-metamorphic larval stage of echinoderms, forcing unusual taxa that also lack pentaradiality down the phylum's phylogenetic tree. Such scenarios assume that first echinoderms had a bilaterian-type anterior-posterior axis. Empirical models rely on comparison of non-pentaradial early forms with a wide array of data obtained from extant and fossil echinoderms. These data support a view in which larval morphologies of echinoderms are not represented in the fossil record of echinoderms, and that pentaradial symmetry was secondarily lost in carpoids, just as it was in many other coeval types of echinoderms.

Résumé : *Comprendre les origines des échinodermes. Partie 1 : Modèles conceptuels et empiriques.* Les échinodermes sont tellement dérivés par rapport aux autres deutérostomes, y compris leur groupe frère, les hémichordés, que la comparaison de leurs plans d'organisation nécessite la prise en compte de données à la fois morphologiques, paléontologiques et embryologiques. Les carpoïdes (Cincta, Ctenocystoidea, Soluta et Stylophora) représentent probablement les échinodermes dont l'interprétation et la position phylogénétique ont été les plus débattues, en raison de leurs morphologies non pentaradiaires et aplaties. L'examen détaillé des

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recherches sur les carpoïdes au cours du siècle et demi écoulé révèle que le débat est lié en grande partie à des questions méthodologiques faisant appel à deux grands types de modèles. Les modèles conceptuels, généralement imprégnés de principes haeckéliens, considèrent l'absence d'un caractère unique (la symétrie pentaradiaire) comme une récapitulation du stade larvaire pré-métamorphique des échinodermes : par conséquent, tous les taxons non-radiaires apparaissent nécessairement en position basale, au sein du phylum. De tels scénarios supposent que les premiers échinodermes avaient un axe antéro-postérieur de type bilatéral. Les modèles empiriques reposent sur la comparaison des carpoïdes avec un large éventail de données obtenues à partir d'autres échinodermes actuels et fossiles. D'après ceux-ci, les morphologies larvaires des échinodermes ne sont pas représentées dans les archives fossiles et la symétrie pentaradiaire a été perdue secondairement chez les carpoïdes, comme c'est le cas chez de nombreux autres groupes d'échinodermes.

Keywords. Echinodermata ● Conceptual ● Empirical ● Phylogeny ● Paleontology ● Embryology

Introduction

"And when you gaze long into an abyss the abyss also gazes into you."

Friedrich Nietzsche, *Beyond Good and Evil*

Over the last 150 years, the question of the origin of the Echinodermata has rested on a deep, occasionally abstruse literature involving paleontological, embryological, and morphological data. The overall strangeness of the phylum itself has opened many avenues for interpretation of these data. It is not surprising that a review of the field reveals a tapestry of interwoven concepts. However, the threads in this tapestry do not always come together to form a harmonious picture with consensus of meaning. Therefore, it is of great value to review the various approaches taken and determine how they originated, evolved, and diverged.

Central to these issues is the phylogenetic position of various taxa now grouped under the term 'carpoid' (Fig. 1). As originally described by Jaekel (1901), the class Carpoidea constitutes echinoderms with few (generally two) ambulacral structures loosely articulated with the theca. Jaekel divided carpoids into two orders, Heterostelea and Eustelea (Jaekel, 1901; Zittel, 1903). Heterosteleans were characterized by a flattened theca and a biserial (at least proximally) appendage. Eusteleans possessed a more globose theca and a holomeric stem (e.g., pleurocystitids). This taxonomic scheme was critically reviewed by Bather (1913), who suggested removal of eusteleans from carpoids, but acknowledged Heterostelea as a valid group, which thus became synonymous with Carpoidea. Following Bather's (1913) critique, Jaekel (1918) revised the systematics of carpoids. Again, eusteleans were excluded, and his former heterosteleans were subdivided into four orders: Cincta, Cornuta, Mitrata, and Soluta.

The term Homalozoa (from the Greek όμαλός, flat, and ζωον, animal) was originally coined by Whitehouse (1941) for a subphylum of Paleozoic echinoderms uniting two of the most enigmatic and controversial groups of Paleozoic fossils: carpoids and machaeridians (Fell, 1965; Ubaghs, 1968a). Machaeridians were eventually confirmed as armoured annelids (Vinther et al., 2008). Consequently, 'homalozoan' represents an unofficial, objective junior synonym of the term carpoid.

The systematics of the Carpoidea was further elaborated by Gill & Caster (1960), who subdivided it into two subclasses based on features of their appendage: Homostelea (longitudinally undifferentiated stele: Cincta and Digitata) and Homoiostelea (appendage with distinct proximal and distal regions: Cornuta, Mitrata and Soluta). Cornutes and mitrates were placed in the same suborder, Stylophora (Gill & Caster, 1960). In the *Treatise on Invertebrate Paleontology*, this scheme was modified by Ubaghs (1968a), who assigned *Rhipidocystis* to eocrinoids. Homostelea (Cincta), Homoiostelea (Soluta) and Stylophora (Cornuta and Mitrata) were elevated to class level (Caster, 1968; Ubaghs, 1968b & c). As a consequence, homosteleans and homoiosteleans represent junior synonyms of cinctans and solutans, respectively (Schroeder, 1973; Termier & Termier, 1973; Caster, 1983; Friedrich, 1993; Lefebvre et al., 2012). Since the description of a fourth class, Ctenocystoidea (Robison & Sprinkle, 1969; Sprinkle & Robison, 1978), the systematics of carpoids remained almost unchanged in the last 50 years.

Carpoids already represent some of the most unfamiliar and enigmatic of echinoderms, and the burden of their nomenclature should not add

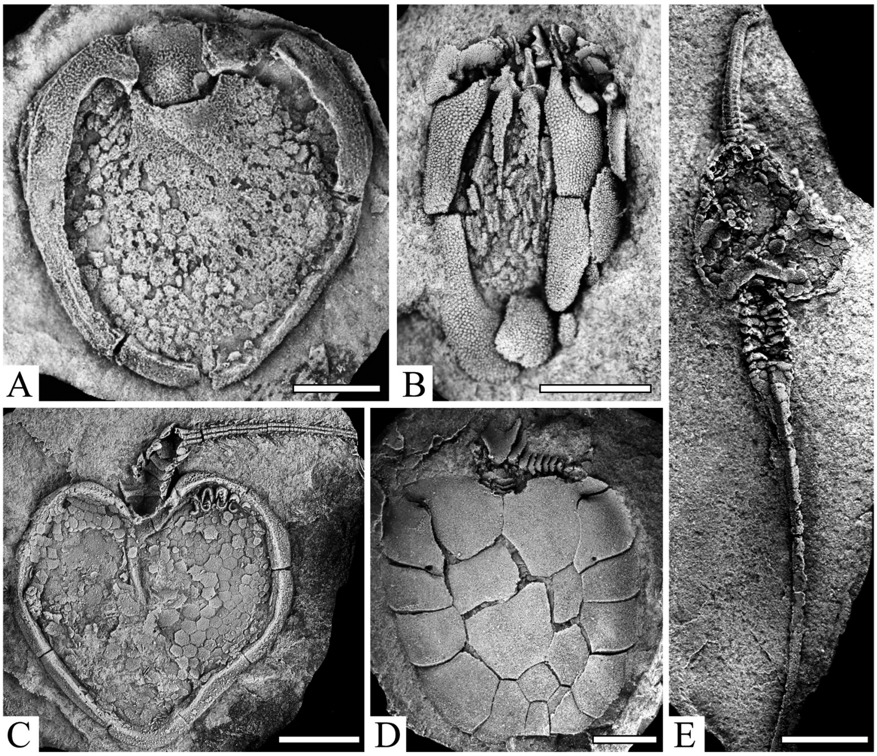

Figure 1. Morphological diversity in carpoid echinoderms. **A.** *Trochocystites bohemicus* (Cincta), upper aspect of lectotype showing sutural pores and articulated cinctus with mouth and operculum, appendage (homostele) not preserved (National Museum, Prague, Czech Republic: NMP.L 9060); Drumian (Cambrian Series 3), Czech Republic. **B.** *Etoctenocystis bohemica* (Ctenocystoidea), lower aspect of slightly disarticulated theca with well-preserved ctenoid organ (Czech Geological Survey, Prague, Czech Republic: CGS.VK 387b); Drumian (Cambrian Series 3), Czech Republic. **C.** *Phyllocystis blayaci* (Cornuta, Stylophora), upper aspect of lectotype with sutural pores (cothurnopores) in right anterior corner of theca and fully articulated aulacophore with proximal rings and distal region (stylocone, ossicles and widely open cover plates) (Montpellier University, Montpellier, France: UM.ACI 640); late Tremadocian (Lower Ordovician), France. **D.** *Mitrocystites mitra* (Mitrata, Stylophora), lower aspect of slightly disarticulated theca and partial aulacophore in lateral view (proximal rings, stylocone and ossicles) (Natural History Museum, London, BMNHUK.E 16062); Darriwilian (Middle Ordovician), Czech Republic. **E.** *Dendrocystites barrandei* (Soluta), well-preserved specimen in upper (aboral) view with complete brachiole, slightly disarticulated theca, and stem-like appendage (homoiostele) (Musée des Confluences, Lyon, France: ML 20 269425); early Katian (Upper Ordovician), Morocco. Scale bars: 1 mm (B), 5 mm (A, C, D), 10 mm (E).

more obfuscation. Referring to this assemblage is problematic as there are no broadly accepted analyses supporting its monophyly. Nevertheless, a term of convenience is required when referring to them as a group. Both 'carpoid' and 'homalozoan' have entered the literature almost interchangeably, but we need to select one for consistency. We have settled on 'carpoid', though in an unofficial, non-statutory sense, because this name is closest to the meaning that fits our discussions, and because it focuses attention on the historical significance of the grouping. Because of almost universally accepted evidence that each of the constituent classes of carpoids forms a clade, we use the formal nomenclature of Soluta, Stylophora, Cincta, and Ctenocystoidea.

Cinctans (Fig. 1A) are characterized by a flattened theca with a thick marginal frame (cinctus). A large anterior medial plate (operculum) articulates with this frame. Right of the operculum, the mouth opens laterally through the cinctus. The mouth is accompanied by one or more sometimes unequal, lateral grooves. At the end of the theca opposite the operculum, the marginal frame forms a short, posterior, stem-like expansion or 'homostele' (Ubaghs, 1971 & 1975; Termier & Termier, 1973; Friedrich, 1993; Rahman & Zamora, 2009; Smith & Zamora, 2009; inter alia).

Ctenocystoids (Fig. 1B) are recognized by a unique ctenoid apparatus (ctenidium), a complex anterior structure formed by two opposite (upper and lower) series of plates. The ctenidium covers the mouth and, on each side of the mouth, a short lateral groove (Ubaghs, 1975 & 1987; Ubaghs & Robison, 1988; Domínguez, 2004; Rahman & Clausen, 2009; inter alia).

Stylophorans (Fig. 1C, D) are bipartite, with an appendage (aulacophore) extending from a flattened

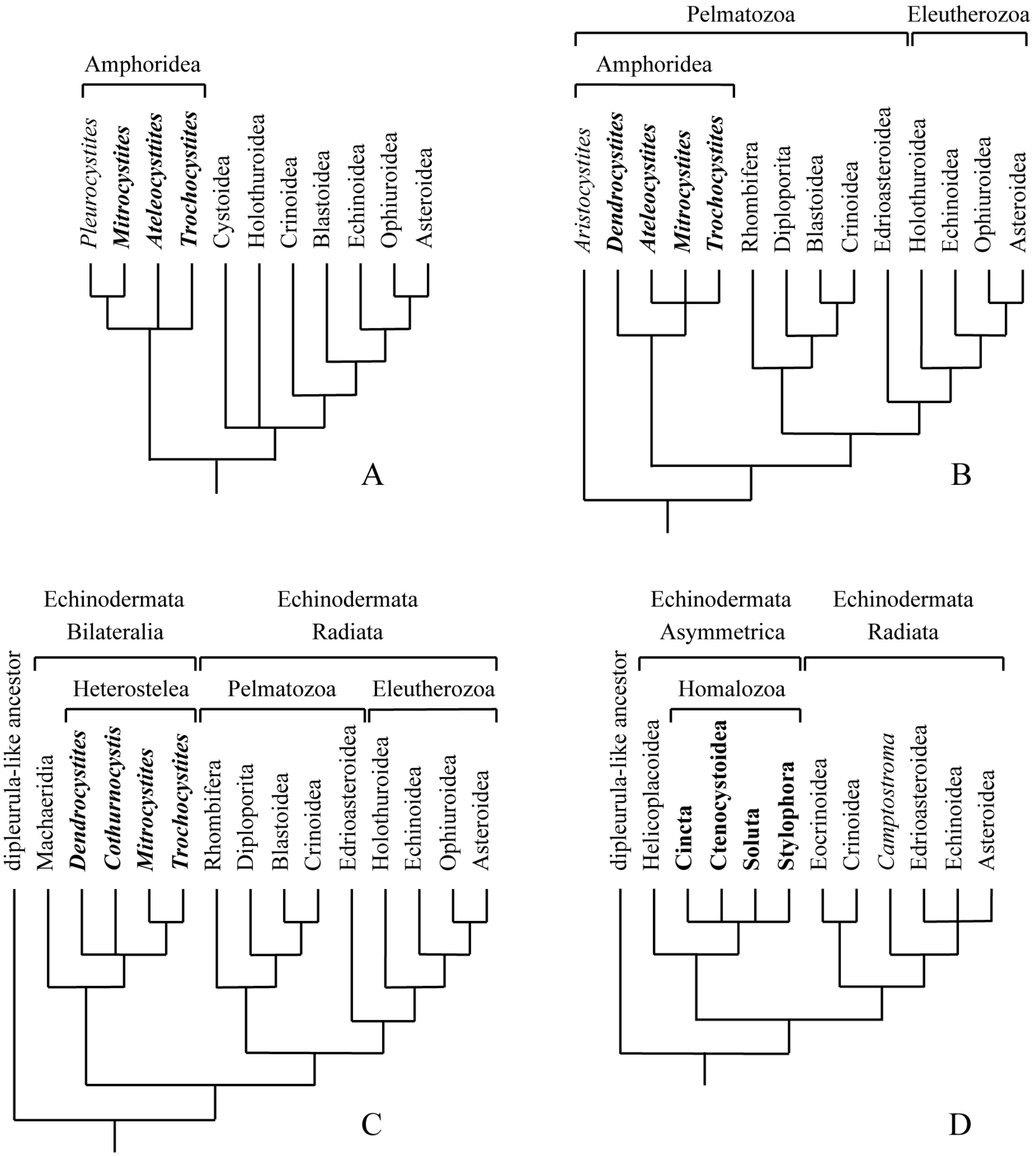

Figure 2. Phylogenies of fossil and extant echinoderms based on conceptual models. **A.** Phylogeny adapted from Haeckel (1896a & b). All known genera of carpoids and *Pleurocystites* are placed within the order Amphoralia (class Amphoridea). They are interpreted as bilaterally symmetric early echinoderms morphologically close to the hypothetical dipleurula-like ancestor. **B.** Phylogeny adapted from Bather (1899) and Bather et al. (1900). All known genera of carpoids are assigned to the class Amphoridea. Within amphorids, stemless taxa (e.g. *Aristocystites*) are considered as more stemward and morphologically closer to the hypothetical dipleurula-like ancestor. **C.** Phylogeny adapted from Bather (1930). Carpoids (heterosteleans) and machaeridians are interpreted as the earliest representatives of the phylum Echinodermata, corresponding to early, bilaterally symmetrical forms (Echinoderma bilateralia), that have not acquired the pentaradial symmetry of other taxa (Echinoderma radiata). **D.** Phylogeny adapted from Ubaghs (1971 & 1975). Carpoids (homalozoans) and helicoplacoids are interpreted as a grade of unrelated, early echinoderms that have not acquired the pentaradial symmetry typical of other taxa (Echinodermata radiata).

to globose theca. The aulacophore has a short, broad, flexible proximal region made of a small series of telescopic rings and a narrower, much longer distal part built of two opposite, longitudinal sets of small plates articulated with a single series of larger underlying ossicles (Ubaghs, 1975 & 1981; Parsley, 1988 & 1991; Kolata et al., 1991; Ruta, 1999; Lefebvre, 2003; Lefebvre et al., 2022; inter alia). New data from these fossils demonstrate that the distal aulacophore carried a single ambulacral ray leading to a proximal mouth (Lefebvre et al., 2019; Saleh et al., 2023).

Solutans (Fig. 1E) have two distinct appendages attached to a globose to somewhat flattened, polyplated theca. The shorter appendage is usually identified as a free, erect ambulacrum consisting of one or two series of floor plates, and two series of cover plates. The longer appendage (homoiostele) is a stem-like structure used by earliest known solutans for permanent attachment, but as a locomotory device in later taxa (Ubaghs & Robison, 1988; Jefferies, 1990; Daley, 1995 & 1996; Noailles et al., 2014; Lefebvre & Lerosey-Aubril, 2018; Dupichaud et al., 2023; inter alia).

The paleobiology and phylogenetic position of the various carpoid classes remain highly controversial issues. Pivotal to this ongoing scientific discussion is significance (ecological versus phylogenetic) given the lack of a single character, radial symmetry, in carpoids. Consequently, understanding asymmetric morphologies of carpoids requires determination of whether the absence of pentamery in these fossils is original or secondary.

This stimulating debate reveals the development through time of two distinct, but complementary, scientific approaches. The first, which could be described as a series of theory-based, or 'top-down' conceptual models, is based on a priori theoretical concepts applied to the morphology of fossils while comparing them to hemichordate morphology. The second approach, which can be described as consisting of empirical, or 'bottom-up' models, uses data from sets of observations from both fossil and extant forms, embryology, and character analyses derived from observation to assess homologies of body wall regions. Both models attempt to place not just carpoids, but all echinoderms in a coherent and integrative framework by asking, "Do carpoids represent an assemblage of early, pre-radial echinoderms, or do they correspond to various taxa that lost pentaradiality?"

Before we can answer this question, as well as many others posed in an accompanying work (Mooi et al., 2024), it will be necessary to examine the scientific roots of some of these concepts in order to understand better how we have landed in this landscape of greatly differing interpretations of echinoderm origins.

Conceptual models of echinoderm origins

The dipleurula model

One of the first conceptual models for echinoderm origins was the dipleurula theory, which grew out of careful descriptions of echinoderm larvae by Müller (1848, 1850 & 1853). In this framework, four main larval types were suggested for extant taxa: auricularia, bipinnaria, echinopluteus, and ophiopluteus. In turn, during the mid-19th century it was implied that these larval morphologies could be derived from an originally bilateral precursor, the dipleurula, which was similar to the tornaria larva of hemichordates. Walther (1886), following Haeckel's (1866) biogenetic 'law' that ontogeny recapitulates phylogeny, applied this concept in his search for a dipleurula-like ancestor for the Echinodermata. Walther (1886) suggested that forms such as the mitrate stylophoran *Ateleocystites* or related forms represented an ideal candidate for an ancestral, dipleurula-like echinoderm.

Walther's (1886) work was seized upon by Haeckel (1896a & b), who applied the biogenetic law and observed that during development of extant echinoderms, bilaterally symmetric larvae preceded the pentaradial morphology of the adults. Therefore, Haeckel concluded that during echinoderm phylogeny, pentaradial taxa were necessarily derived from Paleozoic forms that seemed to have bilateral symmetry resembling that of the hypothetical dipleurula: the Anomalocystidae (taxa known today as carpoids and pleurocystitid blastozoans) (Fig. 2A). Moreover, after unsuccessful attempts to find typical ambulacral structures associated with the water vascular system (WVS) in these fossils, Haeckel (1896a & b) considered that these animals had unfossilized tentacles and lacked a WVS entirely. He claimed that diversity among carpoids and pleurocystitids indicated an evolutionary transition from primitive bilateral taxa with two tentacles ('Anomalocystidae') to more derived, radial forms with three ('Eocystida') and finally, five tentacles (holothurians). This teleological description of progressive 'improvement' was entrenched in a mechanistic understanding of evolutionary change at the time (Greene, 1986), and not in Darwinian concepts of stochasticity. Nevertheless, even at this point, non-pentaradial forms were considered echinoderms, but pre-radial taxa lacking a WVS (Fig. 2A).

In contrast, Bather (1913 & 1926) considered that the bilateral symmetry of carpoids was a derived character, unrelated to that of the dipleurula. This interpretation was based on his conclusion that solutans had a single ambulacrum, and that forms such as cinctans had two. Presciently, Bather indicated that carpoids clearly possessed ambulacral structures, necessitating their derivation from pentaradial precursors directly attached by their theca to the substrate. However, he continued to view these forms as lacking a WVS, decoupling the concept of ambulacra from this system. In his view, pentaradiality was primitive in echinoderms and developed from a hypothetical dipleurula-like ancestor attached to the sea floor (Fig. 2B; Bather, 1899 & 1913; Bather et al., 1900). Coincidentally, Bather (1913 & 1926) was the first to suggest that the numerous and sometimes elaborate pore structures (cothurnopores, lamellipores) found among cornute stylophorans were respiratory apertures leading to an internal pharynx, but at the same time emphasizing that these pore structures could not be homologous to the pharyngeal clefts of chordates.

Bather (1930) completely changed his mind after reading Withers (1926), who described machaeridians as echinoderms, deciding that machaeridians were worm-like early echinoderms. Therefore, machaeridians were pre-radial forms derived from a dipleurula-like ancestor, more or less as Walther (1886) and Haeckel (1896a & b) had suggested (Fig. 2C). Bather (1930) hypothesized that if such a form attached itself to the sea floor by its ventral surface, this fixed stage could have evolved into a primitive carpoid. To make this claim, Bather relied on the biserial structure of the cinctan homostele and the proximal appendages of both solutans (homoiostele) and stylophorans (aulacophore). He also had to abandon the idea that there were ambulacral structures in carpoids, even though he had previously described them in both cinctans and solutans (Bather et al., 1900; Bather, 1913). Because ambulacral structures had to be deemed absent in all carpoids, they were forced into an extinct early branch of pre-radial echinoderms lacking a WVS: the Echinoderma bilateralia (Fig. 2C; Bather, 1930).

Bather (1930) then hypothesized a scenario for the origin of echinoderms that apparently still influences ensuing generations of researchers. This scenario assumed that carpoids were bilaterally symmetric, dipleurula-like forms that had not yet acquired the typical radial symmetry of echinoderms (Gislén, 1930; Thoral, 1935; Chauvel, 1941; Whitehouse, 1941; Jefferies, 1967 & 1986; Nichols, 1967; Ubaghs, 1968a, 1971 & 1975; Philip, 1979; Holland, 1988; Parsley, 1988; Domínguez, 2004; Smith, 2005 & 2008; Zamora et al., 2012; Zamora & Rahman, 2014). Some of the early versions of these ideas diverge considerably from accepted modern interpretations. For example, Whitehouse (1941) supposed that enigmatic, cone-shaped fossils found in early Cambrian rocks (Cambrian Series 2) of Australia were laterally compressed (*Peridionites*), or globose (*Cymbionites*) thecae of a new, early subphylum of echinoderms (Haplozoa). For Whitehouse, haplozoans represented a grade of unattached and possibly swimming echinoderms illustrating a key transition from pre-metamorphic, bilaterally symmetric, dipleurula-like *Peridionites* to post-metamorphic, radial *Cymbionites*. Whitehouse (1941) erected yet another subphylum, Homalozoa, to contain flattened, unattached, bilaterally symmetric taxa such as carpoids. These were considered to be derived from a mobile, epibenthic *Peridionites*-like ancestor, whereas pentaradial echinoderms were to have originated from a permanently attached *Cymbionites*-like form.

Whitehouse's interpretation of *Cymbionites* and *Peridionites* (1941) was reviewed by Gislén (1947), Schmidt (1951), and Ubaghs (1968d), who felt that these were parts of eocrinoids. Smith (1982) and Jell & Sprinkle (2021) definitively established that these fossils were indeed stemward examples of two distinct species of epispire-bearing eocrinoids.

Fell (1965) revived the term 'Homalozoa', which was also adopted by Ubaghs (1968a). Ubaghs (1968a, 1971 & 1975) also considered carpoids and helicoplacoids as pre-radial echinoderms, possibly derived from a dipleurula-like ancestor (Fig. 2D). However, in numerous works, Ubaghs (1961b, 1963, 1968a, b & c, 1969, 1971, 1975, 1979, 1981, 1983, 1987, 1991, 1994 & 1998) confirmed the presence of ambulacral structures in both cinctans and solutans. Most importantly, for the first time, he showed that the stylophoran appendage (aulacophore) was not a stem, but an ambulacral feeding structure. This interpretation has been followed by Durham (1971), Nichols (1972), Ubaghs & Robison (1985 & 1988), Sprinkle (1983 & 1992), Parsley (1988, 1991 & 1997), Haude (1995), Sumrall (1997), Lefebvre & Vizcaïno (1999), Ruta (1999), David et al. (2000), Guensburg & Sprinkle (2000), Martí Mus (2002), Valentine (2004), and Lefebvre et al. (2019 & 2022), among others. Although Ubaghs (1968a, 1971 & 1975) felt that there were enough similarities between the hemichordate tornaria and the echinoderm dipleurula to suggest common ancestry, he emphasized that forms providing evidence for earliest stages of echinoderm evolution would not likely be represented in the fossil record.

In summary, the dipleurula theory implied that the ontogeny of extant echinoderm taxa was Haeckelian and followed the biogenetic law. Ubaghs (1968a, 1971 & 1975) accepted this, but with caveats. The scenario makes predictions, particularly that: (1) a bilaterally symmetric dipleurula-like ancestor of echinoderms was attached to the sea floor on its right side; (2) this led to the resorption of the right mesocoel and progressive transition from biradial (e.g., carpoids) to triradial, and finally to pentaradial body plans. Ubaghs (1968a, 1971 & 1975) did not formally reject this idea, but presciently pointed out several inconsistencies with both embryological and paleontological evidence. For example, Ubaghs (1968a) argued that the existence of a putative intermediate, triradial stage had no embryological support (see also Stephenson, 1979). Moreover, Ubaghs (1968a, 1971 & 1975) stressed that the dipleurula theory lacked corroboration from fossils themselves because all Cambrian, putative pre-radial echinoderms (carpoids and helicoplacoids) were vagile and emerged on the scene with already highly specialized morphologies. For Ubaghs, if echinoderms were derived from a fixed, dipleurula-like ancestor, then the transition would likely have occurred much earlier, in Precambrian times, leaving no trace in the fossil record.

The calcichordate theory

In the early 20th century, data on deuterostome embryology confirmed affinities between the hemichordate tornaria and the echinoderm dipleurula, while introducing the possibility that echinoderms and chordates could both have evolved from a pterobranch-like ancestor (Heider, 1912; Grobben, 1924; Garstang, 1928). In the process, attention turned to the asymmetric, flattened carpoids frequently considered as pre-radial echinoderms (Walther, 1886; Haeckel, 1896a & b; Bather, 1930). However, this time they were revisited in the wider context of deuterostome phylogeny (Fig. 3). Matsumoto (1929) briefly suggested that the bipartite morphology of carpoids could be homologous with that of tunicate larvae - that is, tadpole-like, with a head and a tail. Therefore, carpoids should be removed from the Echinodermata and considered to be earliest urochordates. Gislén (1930) was probably the first to suggest an apparent trend among cinctans characterized by the progressive reduction of their ambulacral grooves on anterior marginals, a phenomenon also exploited by Rahman & Zamora (2009) and Smith & Zamora (2009). This pattern, coincident with the apparent absence of ambulacral structures associated with the main thecal orifice of stylophorans, led Gislén (1930) to suggest that the WVS was reduced and eventually lost in carpoids as it was being replaced by a different feeding strategy. He interpreted the pore structures of cornutes (e.g., lamellipores) as literal branchial slits, comparing their placement on one side of the upper thecal surface to asymmetries in the early ontogeny of cephalochordates and tunicates, in which gill slits appear earlier on the left than on the right. Gislén (1930) also suggested that the long appendage of carpoids contained a nerve cord extending from a ganglion, indicating that the appendage was like the tail of appendicularian tunicates. Gislén (1930) maintained that the similarities in position and asymmetry he saw in carpoids, chordates, and hemichordates were more likely primitive features among all deuterostomes, rather than indicative of a scenario in which a carpoid-like ancestor gave rise to cephalochordates or tunicates, an idea set aside by later authors. For example, Dehm (1934) suggested that the transition from asymmetric early carpoids such as cinctans to more bilaterally symmetric ones such as the mitrate *Rhenocystis*, resulted from the acquisition of a swimming mode of life. This implied that cephalochordates could be derived from a cornute-like ancestor, because they shared comparable asymmetries such as left gill slits. Gregory (1935) pointed out similarities in shape between mitrates and early vertebrates (agnathans), suggesting that Gislén (1930) had found the key to understanding origins of vertebrates. Affinities between mitrates and ostracoderms were also suggested by Caster (1952) and Caster & Eaton (1956).

The most famous outcome of Gislén's (1930) interpretation of carpoids was the detailed evolutionary scenario elaborated in the many works by Jefferies (1967, 1968, 1973, 1979, 1981, 1986, 1988, 1990, 1991, 1994 & 1997). Jefferies based his hypothesis on the assumption that hemichordates were stemward to the clade uniting echinoderms and chordates, leading him to postulate that the fossil record should produce taxa documenting key evolutionary transitions among the three deuterostome phyla (Jefferies, 1967 & 1968). Citing work by Bather (1930), Gislén (1930), Gregory (1935), and Romer (1967 & 1972), Jefferies (1967 & 1990) pointed to the four classes of carpoids, redescribing them as plesiomorphic, calcite-plated deuterostomes that never acquired the pentaradiality of echinoderms. He built a hypothetical scenario for how both echinoderms and chordates originated from a bilaterally symmetric, *Cephalodiscus*-like ancestor permanently attached to the sea floor by a stalk (Fig. 3A). According to Jefferies (1967 & 1969), some of these hypothetical, stalked, early hemichordates adopted a vagile, epibenthic habit, eventually acquiring an asymmetric 'flatfish' morphology. Lying on their right side, these deuterostomes lost all coeloms and associated structures originally located on this side, including the right gill slits and right hydrovascular tentacle (dexiothetism of Jefferies, 1967, 1990 & 1997). This narrative, or parts thereof, was further employed in work by Jefferies & Prokop (1972), Paul (1977 & 1990), Jefferies & Lewis (1978) Cripps (1989, 1990 & 1991), Daley (1992, 1995 & 1996), Cripps & Daley (1994), Gee (1996), Gil Cid et al. (1996), Jefferies et al. (1996), Rozhnov & Jefferies (1996), Ruta (1997), Ruta & Theron (1997), Jefferies & Jacobson (1998), Ruta & Bartels (1998), Conway Morris (2000), Domínguez et al. (2002), and Domínguez (2004).

Jefferies (1967, 1990 & 1997) further indicated that this soft-bodied, asymmetric, flattened deuterostome then acquired a calcite-based mesodermal skeleton synapomorphic between both chordates and echinoderms. The resulting morphology was identical to that of solutans, who had a single left feeding arm, left 'gill slits' and a hemichordate-like stalk, making these forms into early, calcite-plated dexiothete deuterostomes belonging to the stem group of both echinoderms and chordates (Fig. 3A; Jefferies, 1990 & 1997; Paul, 1990; Daley, 1992, 1995 & 1996; Rozhnov & Jefferies, 1996; Jefferies & Jacobson, 1998). In turn, this provided the scope for a narrative in which evolutionary pathways led either to the chordates or to the echinoderms.

Under this rubric, cornutes were interpreted as stem-group chordates by Jefferies (1967), who assigned them, along with mitrates, to a new subphylum, Calcichordata, a junior synonym of the Stylophora. Calcichordates were stereom-plated, tadpole-like earliest chordates, with a head (theca) and a muscular tail (aulacophore) containing a notochord. This scenario required that during the solutan-cornute transition the (left) hydrovascular system (the feeding arm) was lost. Mitrates, on the other hand, had to be more derived members of the stem groups of the three chordate clades, including cephalochordates, urochordates, and craniates (including vertebrates) (Fig. 3A).

Remarkably, this required that the echinoderm-like endoskeleton of calcichordates was lost three times. Moreover, the cornute-mitrate transition was interpreted as leading to the duplication of most internal structures (see e.g., Jefferies, 1967, 1968 & 1973; Jefferies & Lewis, 1978; Cripps, 1991). This hypothesized internal anatomy of stylophorans and left-right asymmetries forced Jefferies (1967) to consider that the concave thecal surface was ventral in cornutes but dorsal in mitrates (e.g., Jefferies, 1973, 1986, 1990 & 1997; Jefferies & Lewis, 1978; Cripps, 1991; Jefferies et al., 1996; Jefferies & Jacobson, 1998). Undaunted, followers of the calcichordate hypothesis embraced the consequence of this reorientation. This included the fact that the distal aulacophore consisted of one series of ventral ossicles and two series of dorsal plates in cornutes, but of uniserial dorsal ossicles and two sets of ventral plates in mitrates. The explanation provided was that the distal part of the appendage was lost during the cornute-mitrate transition, and that a new one re-evolved in the earliest mitrates (Jefferies & Prokop, 1972; Jefferies, 1973, 1986, 1990 & 1997; Jefferies & Lewis, 1978; Cripps, 1991).

Jefferies (1990, 1991, 1994 & 1997), Jefferies et al. (1996), and Domínguez (1999 & 2004) then interpreted cinctans as stem-group echinoderms derived from a solutan-like ancestor, a transition characterized by the duplication of the single solutan feeding arm into two lateral ambulacral structures (Fig. 3A). This rendered cinctans the earliest pre-radial echinoderms retaining plesiomorphic deuterostome features lost in more derived taxa. In this case, the large opening (porta) protected by the operculum was the outlet valve (gill slit) of a large intrathecal pharynx (Jefferies, 1990, 1991 & 1997; Friedrich, 1993 & 1995; Jefferies et al., 1996; Domínguez, 1999).

Ctenocystoids were interpreted as early, pre-radial, stem-group echinoderms derived from a cinctan-like ancestor that shared with more derived echinoderms the loss of the hemichordate-like stalk (Fig. 3A; Jefferies, 1994; Jefferies et al., 1996; Domínguez, 1999 & 2004). As did previous authors (Haeckel, 1896a & b; Bather, 1930; Paul & Smith, 1984; Smith, 1988), Jefferies (1990) considered the bilaterally symmetric cinctans and ctenocystoids precursors to triradial taxa (helicoplacoids) that in turn gave rise to pentaradial forms (Fig. 3A; Jefferies, 1991, 1994 & 1997; Jefferies et al., 1996; Domínguez, 1999 & 2004).

In the past two decades, abundant molecular evidence supporting a tree in which echinoderms were more closely related to hemichordates than to chordates began to falsify the basic assumptions of the calcichordate theory (Bromham & Degnan, 1999; Cameron et al., 2000; Peterson & Eernisse, 2001; Furlong & Holland, 2002). Nevertheless, this new phylogenetic evidence was integrated by Jefferies (2001a & b), without impact on the theory itself (Fig. 3C; Shu et al., 2001; Domínguez et al., 2002; Domínguez, 2004; Holland, 2005; Domínguez & Jefferies, 2006a & b; Tatarinov, 2011). The hypothetical pterobranch-like ancestor was modified into a stem-group deuterostome morphologically close to *Cephalodiscus*, but now with the assumption that it possessed an echinoderm-like stereom skeleton. Stereom then became a synapomorphy of all deuterostomes, with subsequent loss no fewer than four times independently (in hemichordates, cephalochordates, tunicates and craniates), but retained only in echinoderms (Jefferies, 2001a & b). Solutans could no longer be considered stem-group dexiothetes (echinoderms +

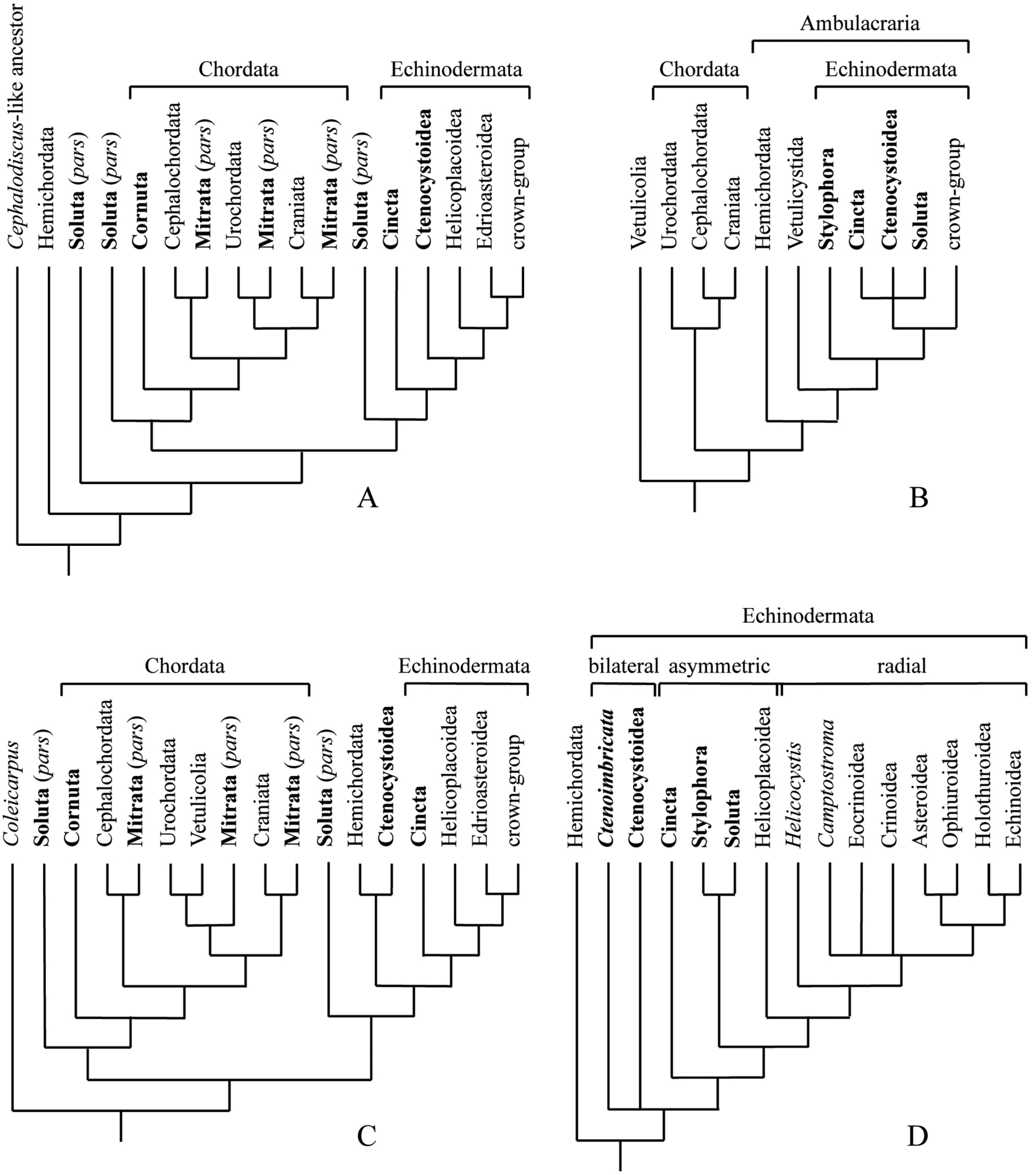

Figure 3. Phylogenies of fossil and extant deuterostomes based on conceptual models. **A.** Phylogeny adapted from Jefferies (1967, 1969, 1986, 1990 & 1991) and Jefferies et al. (1996). Cornutes and mitrates (calcichordates) are considered as stem-group chordates; cinctans and ctenocystoids are interpreted as bilaterally symmetrical, early, pre-radial echinoderms; solutans are identified as early deuterostomes belonging to the stem-groups of both chordates and echinoderms. **B.** Phylogeny adapted from Gee (2001a & 2006), Conway Morris (2003), Shu et al. (2004), and Shu (2005). Carpoids are interpreted as early, pre-radial echinoderms, morphologically close to hemichordates, vetulicolians, and vetulicystids. **C.** Phylogeny adapted from Jefferies (2001a & b) and Domínguez & Jefferies (2006a). In this revised phylogeny, hemichordates (and not chordates) are the sister-group of echinoderms. Cornutes and mitrates (calcichordates) are still considered stem-group chordates, and cinctans as stem-group echinoderms. However, the early solutan *Coleicarpus* is reinterpreted as an early deuterostome belonging to the stem-group of both ambulacrarians and chordates, whereas ctenocystoids are assigned to the hemichordate stem-group. **D.** Phylogeny adapted from Smith (2005 & 2008), Bottjer et al. (2006), Rahman & Clausen (2009), Zamora et al. (2012), Zamora & Rahman (2014), and Rahman & Zamora (2024). Carpoids are interpreted as a paraphyletic assemblage of hemichordate-like, pre-radial echinoderms.

chordates), but became stem-group deuterostomes (ambulacrarians + chordates) (Fig. 3C). In a significant modification of the calcichordate theory, ctenocystoids were incorporated into the hemichordate stem group (Domínguez & Jefferies, 2006a & b), with other carpoids in their previously interpreted positions: cinctans as pre-radial, stem-group echinoderms, cornutes as stem-group chordates, and mitrates as members of stem groups of the three chordate lineages (Fig. 3C; Jefferies, 2001a & b; Domínguez & Jefferies, 2006a).

The ambulacrarian theory

That echinoderms and hemichordates were sister groups had been suspected through studies of the tornaria and dipleurula (Metschnikoff, 1881; Heider, 1912; Grobben, 1924; Ubaghs, 1968a). The development of molecular phylogenetics strongly supported a tree in which chordates were the sister group of ambulacrarians (echinoderms + hemichordates) (Bromham & Degnan, 1999; Cameron et al., 2000; Peterson & Eernisse, 2001; Furlong & Holland, 2002; Winchell et al., 2002). It followed that early echinoderms such as the carpoids needed new scrutiny in order to reconcile the dipleurula and calcichordate conceptual models (Fig. 3B; Gee, 2001a & 2006; Winchell et al., 2002; Conway Morris, 2003; Shu et al., 2004; Northcutt, 2005; Shu, 2005; Smith, 2005, 2008; Bottjer et al., 2006; Swalla & Smith, 2008; Zamora et al., 2012; Zamora & Rahman, 2014).

Again, observation of bilateral symmetry in extant chordates, hemichordates and pre-metamorphic larval stages of echinoderms emboldened thinking that bilateral symmetry was a plesiomorphic feature in all deuterostomes (e.g., Shu et al., 2004; Shu, 2005; Smith, 2005 & 2008; Zamora et al., 2012). Therefore, post-metamorphic pentaradiality of extant echinoderms was pronounced an autapomorphy of extant forms (Shu et al., 2004; Shu, 2005; Smith, 2005 & 2008; Bottjer et al., 2006; Zamora et al., 2012), and possesion of a 'hydrovascular tentacular system' derived from the mesocoel was declared a synapomorphy for ambulacrarians (Shu et al., 2004; Smith, 2005 & 2008). This side-stepped the problem that in adult hemichordates, this tentacular system is paired and derived from both the left and right mesocoels, whereas in post-metamorphic extant echinoderms, the ambulacral system is already pentaradial and derived exclusively from the left mesocoel, called the hydrocoel for that reason. That both extant hemichordates and chordates have pharyngeal openings and a 'true tail' indicated their symplesiomorphy among deuterostomes. Their absence in crownward echinoderms was explained by secondary loss (Shu et al., 2004; Shu, 2005; Smith, 2005 & 2008; Bottjer et al., 2006; Zamora et al., 2012). Since stereom is exclusive to echinoderms, it was more parsimonious to interpret it as an echinoderm autapomorphy, rather than a deuterostome symplesiomorphy requiring the four independent losses in chordates and hemichordates indicated above (Gee, 2001a & 2006; Conway Morris, 2003; Shu et al., 2004; Northcutt, 2005; Shu, 2005; Smith, 2005 & 2008; Bottjer et al., 2006; Caron et al., 2010; Vinther et al., 2011; Zamora et al., 2012).

It was proposed that extant echinoderms differed from their last common ambulacrarian ancestor with hemichordates by the loss of several characters (bilateral symmetry in adults, post-anal tail, pharyngeal openings), coupled with the acquisition of several autapomorphic features (stereom, adult pentaradiality associated with an unpaired hydrovascular system). Several works insisted that all evolutionary changes between stem-group ambulacrarians and extant echinoderms could be identified among fossils (Gee, 2001a & 2006; Winchell et al., 2002; Conway Morris, 2003; Northcutt, 2005; Shu et al., 2004 & 2005; Smith, 2005 & 2008; Bottjer et al., 2006; Swalla & Smith, 2008; Rahman & Clausen, 2009; Caron et al., 2010; Zamora et al., 2012; Smith & Zamora, 2013; Zamora & Rahman, 2014; Nanglu et al., 2022; Rahman & Zamora, 2024). Carpoids were again considered the best candidates in the hunt for corroborating evidence (Gee, 2001a & 2006). The conceptual framework of the authors listed above required that carpoids be a disparate assemblage of early, pre-radial echinoderms retaining plesiomorphic deuterostome and/or ambulacrarian features (gill slits, post-anal tail, bilateral symmetry) lost in more derived members of the phylum (Fig. 3B). An enigmatic group of Cambrian putative deuterostomes, the vetulicolians (Shu et al., 2001), was seized upon by Conway Morris (2003) as strong evidence supporting the interpretation of stylophorans as early, pre-radial, stem-group echinoderms (Fig. 3B; Shu et al., 2004; Shu, 2005; Vinther et al., 2011; Ou et al., 2012). The two parts of the vetulicolian body were generally interpreted as a post-anal tail and a large head containing both a putative pharynx and pharyngeal openings. Supposed affinities of vetulicolians with stem-group ambulacrarians largely relied on the comparison of their tadpole-like organization with the supposedly similar bipartite body of stylophorans, in this context considered stem-group echinoderms (Conway Morris, 2003; Shu et al., 2004; Shu, 2005; Vinther et al., 2011; Ou et al., 2012). Interpretation of anatomical characters preserved in vetulicolians remained equivocal, even questioning their deuterostome affinities (Butterfield, 2003;

Aldridge et al., 2007; Chen, 2009). Reinterpretation of vetulicolians as stem-group tunicates (Gee, 2001b; Garcia-Bellido et al., 2014) falsifies homology between their tadpole-like morphology and bipartite body of stylophorans (McMenamin, 2019).

The proposition that carpoids represent pre-radial stem-group echinoderms preserving evolutionary steps between stem-group ambulacrarians and extant crown-group echinoderms (Fig. 3D) continued to find favor in the literature (Clausen & Smith, 2005; Smith, 2005 & 2008; Bottjer et al., 2006; Swalla & Smith, 2008; Zamora & Smith, 2008; Rahman & Clausen, 2009; Rahman & Zamora, 2009 & 2024; Smith & Zamora, 2009 & 2013; Zamora et al., 2012; Zamora & Rahman, 2014). In all cases, however, this position requires a priori assumptions to deal with the disparate, asymmetric morphologies of three carpoid classes (cinctans, solutans and stylophorans). Ctenocystoids were later added to this conceptual model by Rahman & Clausen (2009), Rahman & Zamora (2009 & 2024), Zamora et al. (2012), Smith & Zamora (2013), Zamora & Rahman (2014), and Rahman & Zamora (2024).

Smith (2005), in identifying the two polyplated structures extended laterally on each side of the mouth of cinctans as extensions of an ambulacrarian-like 'hydrovascular system', rejected them as ambulacral rays due to their lack of floor plates. Smith (2005) followed Gislén (1930) in assessment of the unequal length of the two anterior marginal grooves associated with these extensions (the right one being shorter than the left). Smith ascribed this as Haeckelian recapitulation of both the ontogeny of extant echinoderms (pre-metamorphic loss of the right mesocoel) and the transition from stem-group ambulacrarians with a paired hydrovascular system to crown-group echinoderms that retained an unpaired structure, the hydrocoel. Cinctans by this interpretation, therefore, were pre-radial stem-group echinoderms retaining ambulacrarian plesiomorphic features (paired hydrovascular system, pharynx) (Fig. 3D). The porta (anterior orifice with an operculum) was considered as an atrial opening (Jefferies, 1990; Friedrich, 1993). The posterior stem (homostele) was interpreted as a cinctan autapomorphy (Smith, 2005). In addition, the bilaterally symmetric ctenoid apparatus of ctenocystoids was considered a feeding structure characterized by a paired, ambulacrarian-like hydrovascular system (Rahman & Clausen, 2009). As Smith (2005) suggested for cinctans, the idea that these were modified ambulacra was rejected as not being like 'standard' ambulacra (no floor plates, food grooves borne by anterior marginals). Rahman & Clausen (2009), Zamora et al. (2012), Zamora & Rahman (2014) considered the two 'tentacular systems' of ctenocystoids to be symmetric precursors of their asymmetric counterparts in cinctans. This was again presented as Haeckelian recapitulatory evidence that ctenocystoids shared plesiomorphic configuration of equal left and right tentacular systems with the hypothetical ambulacrarian ancestor (Fig. 3D). Cinctans were necessarily more derived, because the asymmetry fit conceptualized reduction of the right tentacular system (Rahman & Clausen, 2009; Caron et al., 2010; Zamora et al., 2012; Smith & Zamora, 2013; Zamora & Rahman, 2014; Rahman & Zamora, 2024).

Smith (2005 & 2008), Caron et al. (2010), Smith & Zamora (2013), Zamora & Rahman (2014), and Rahman & Zamora (2024) considered solutans to be derived from a cinctan-like common ancestor that evolved a free erect ambulacrum from the left hydrovascular system (Fig. 3D). This in turn necessitated complete loss of the right tentacular system already noted to be reduced in cinctans, and the modification of the left one into a feeding arm. Unable to find the gill slits in solutans described by Jefferies (1990), Smith (2005) and Bottjer et al. (2006) concluded that they were originally absent in these carpoids. Moreover, the morphology of the solutan homoiostele was incompatible with that of blastozoan or crinoid stems, because its distal region was biserial (not holomeric or pentameric). The large, flexible proximal region was declared to contain powerful muscles, indicating that the homoiostele was instead homologous to a hemichordate-like (pterobranch) stem (Smith, 2005 & 2008). The observation that one of the earliest known solutans (*Castericystis*) had juveniles attached to the stalk of larger (adult?) individuals (Daley, 1996; Lefebvre & Lerosey-Aubril, 2018), was used as evidence that early solutans were colonial and budding, like pterobranchs (Smith, 2008).

As previously argued by many authors (Bather, 1930; Jefferies, 1967; Philip, 1979; Kolata et al., 1991), Smith (2005 & 2008), Clausen & Smith, (2005), Zamora & Smith (2008), and Rahman et al. (2009) considered the stylophoran aulacophore and the solutan homoiostele to be strongly muscled proximally, with a stiffer distal region that could be employed in locomotion. This necessitated the rejection of Ubaghs' (1961b & 1968b) interpretation that the aulacophore was a feeding arm, because solutans had now to be considered to have both an indisputable feeding appendage plus an aulacophore-like homoiostele, in turn forcing the conclusion that the stylophoran appendage was a muscular, hemichordate-like stalk. This assumption further implied that stylophorans completely lacked ambulacral or even ambulacrarian-like WVS structures, suggesting that the stylophoran theca contained a large pharynx with gill slits represented by pore structures seen in some cornutes (Bottjer et al., 2006; Smith, 2008; Zamora & Smith, 2008; Rahman et al., 2009; Caron et al., 2010). In this view, all mitrates had to possess paired internal gill slits, based on the interpretation of digitate internal structures in two taxa (*Jaekelocarpus* and *Lagynocystis*) (Jefferies, 1973 & 1986; Domínguez et al., 2002; Bottjer et al., 2006). Therefore, stylophorans were regarded as stem-group, pre-radial forms retaining plesiomorphic ambulacrarian characters (hemichordate-like tail, pharynx) lost in crown-group echinoderms (Fig. 3D; Smith, 2005 & 2008).

To summarize these complicated issues, it helps to realize that to accommodate these theory-driven assumptions, the four carpoid classes had to be integrated with some other early taxa (*Camptostroma*, *Gogia*, *Helicocystis*, helicoplacoids, *Lepidocystis*) in trees implied to support the initial stages of echinoderm diversification from a stem ambulacrarian-like ancestor (Smith, 2005 & 2008; Bottjer et al., 2006; Smith & Zamora, 2013; Zamora et al., 2012; Zamora & Rahman, 2014; Rahman & Zamora, 2024). To do so, the scenario relied on symmetry of postulated hydrovascular structures in the various fossil taxa, and identified two major subdivisions within echinoderms that precisely coincided with Bather's (1930) classification of the phylum into Echinoderma bilateralia (carpoids) and Echinoderma radiata (all other taxa) (Fig. 3D). Carpoids had to be interpreted as pre-radial, stem-group echinoderms because of their bilaterally symmetric (ctenocystoids) or asymmetric morphologies (cinctans, solutans, stylophorans). Ctenocystoids were viewed as the earliest because of bilateral symmetry supposedly inherited from a stem ambulacrarian-like ancestor with left and right hydrovascular systems (Fig. 3D). Asymmetry in the three other carpoid clades had to result from the reduction (cinctans) or loss (solutans, stylophorans) of this hypothesized right tentacular system. Even though they retained a deeply plesiomorphic hemichordate-like tail, solutans were considered the most derived carpoids because they lacked any evidence of pharyngeal gill slits.

In turn, the transition from a solutan-like ancestor to a radial echinoderm was characterized by loss of the presumed hemichordate-like stalk, and sudden, enigmatic appearance of two additional ambulacral rays to produce the earliest echinoderms. The latter were then assumed to have transitioned to triradiality (Smith, 2005 & 2008; Zamora et al., 2012; Smith & Zamora, 2013; Zamora & Rahman, 2014; Rahman & Zamora, 2024). As already suggested in many earlier works (e.g., Haeckel, 1896a; Bather et al., 1900; Foerste, 1914; Haugh, 1973; Sprinkle, 1973; Bell, 1976; Paul & Smith, 1984; Jefferies, 1990; Hotchkiss, 1998), pentaradiality of the majority of earliest echinoderms (e.g., *Camptostroma*, gogiids, *Helicocystis*, *Lepidocystis*, *Stromatocystites*) was interpreted by Smith (2008) to be derived from a triradial, helicoplacoid-like ancestor, in part due to modification of the so-called 2-1-2 configuration of rays in such pentaradial forms. We will be probing this in more detail below, along with many other complicated postulates presented above.

Empirical models of echinoderm origins

Early observations supporting affinities of carpoids with typical echinoderms

The very first descriptions of carpoids were essentially empirical, lacking discussion of the pivotal position with which these animals are now imbued by conceptual models. Attempts to understand them were based on comparisons with other Paleozoic echinoderms known at that time. Carpoids were characterized by a stem-like appendage and affiliated with pelmatozoans, themselves diagnosed as all forms permanently attached to the sea floor via stems or by the theca. Among pelmatozoans, carpoids were allocated to the Cystoidea, with which they shared an irregularly plated theca and the lack of branched arms (Billings, 1858; Hall, 1859; De Koninck, 1869; Prado et al., 1860; Woodward, 1871; Meek, 1872; Barrande, 1887; Miller, 1889; Neumayr, 1889; Bell, 1891; Bernard, 1895; Pompeckj, 1896; Zittel, 1900). New discoveries attempted to recognize unique carpoid features by placing them into distinct families such as Anomalocystidae (Meek, 1872; Woodward, 1880; Miller, 1889; Miller & Gurley, 1894; Zittel, 1900) or Pleurocystidae (Bernard, 1895), which grouped stemmed cystoids diagnosed by a flattened theca bearing dissimilar plate patterns on its opposing sides.

Jaekel elaborated upon this apparent uniqueness by describing a distinct class, Carpoidea (Fig. 4A & B), to hold pelmatozoans with a flattened theca, a non-holomeric appendage and no pore structures (Jaekel, 1901 & 1918; Zittel, 1903; Schuchert, 1904; Dehm, 1932; Hecker, 1940 & 1964; Régnell, 1945; Termier & Termier, 1947 & 1973; Caster, 1952; Gill & Caster, 1960; Ubaghs, 1961a & b, 1963). Pleurocystitids, in spite of their similar-looking flattened theca, were separated from carpoids and assigned to dichoporite cystoids, since they also had rhombs and a holomeric stem. Jaekel (1918) suggested that carpoids were derived from crinoid-like ancestors, but possibly related to holothuroids or to 'thecoids' (edrioasteroids) (Fig. 4B). The asymmetric morphology of carpoids was deemed a consequence of their unattached, free-living, 'flat-fish' mode of life on the sea floor. This interpretation, shared by several later authors (Spencer, 1938; Delpey, 1941; Termier & Termier, 1973; Sprinkle, 1983 & 1992; Dzik, 1999; David et al., 2000), relied on the fact that pentaradial symmetry is lost independently in a myriad diversity of fossil and extant echinoderms over the past half billion years (e.g., *Dibrachicystis*, *Hillocystis*, *Monobrachiocrinus*, pleurocystitids, irregular echinoids).

After Jaekel's (1918) revision of the systematics of Pelmatozoa, only a few attempts were subsequently made to interpret carpoids using similar empirical methodology relying on detailed morphological comparison with other echinoderms (Spencer, 1938; Cabibel et al., 1959; Haugh & Bell, 1980a & b). This marked a shift from fossil-based, empirical approaches to a more theory-laden approach, as lamented by Stephenson (1979: 47) who advised instead that: "echinoderm phylogenies should be constructed empirically without pre-conceived ideas about the primitive symmetry of echinoderms". However, interest in empirical models and their application for the interpretation of carpoids did eventually appear (Sumrall, 1997; David & Mooi, 1999; Dzik, 1999; David et al., 2000; Mooi, 2001; Sprinkle & Guensburg, 2001; Sumrall et al., 2001; Lefebvre, 2003; Lefebvre et al., 2019; Guensburg et al., 2020).

Spencer (1938) rejected traditional classification of echinoderms into eleutherozoans (free-living) and pelmatozoans (attached), rightly pointing out the dangers of basing classifications on behaviors that can be adopted independently. He distinguished two groups: Dactylozoa that possessed brachioles and fed using ciliary currents (blastoids, cystoids, edrioasteroids), and Podozoa that possessed arms and used tube feet for feeding (crinoids, asterozoans, echinozoans). For Spencer, carpoids constituted a polyphyletic assemblage of echinoderms that secondarily lost radial symmetry, with some of them identified as dactylozoans (solutans) and others as podozoans (cinctans and stylophorans).

In reviewing Cambrian echinoderms from the Montagne Noire, Cabibel et al. (1959) suggested that cinctans were derived from a *Stromatocystites*- or *Cambraster*-like ancestor. Their work largely relied on an analogy with post-Paleozoic echinoids, in which transition from pentaradial (regular sea urchins) to almost bilaterally symmetric morphologies (irregular echinoids) was well-documented. From this, they argued that more elongate and symmetric outlines in cinctans were related to the adoption of a vagile mode of life.

Haugh & Bell (1980a & b) echoed Spencer (1938) in pointing out that echinoderm systematics should not rely on superficial similarities that often resulted from adaptations to similar modes of life. Detailed comparisons among exceptionally preserved soft parts in various Paleozoic blastoids, camerate crinoids, diploporitans, edrioasteroids, and rhombiferans (Breimer & Macurda, 1972; Haugh, 1973, 1975a & b; Haugh & Bell, 1980a), as well as with extant taxa, suggested a coelom-based classification with three main subdivisions (Fig. 4C), or subphyla: I (crinoids, edrioasteroids and related forms, and helicoplacoids); II (blastoids, diploporitans, eocrinoids, parablastoids, paracrinoids, and rhombiferans); and III (asteroids, echinoids, holothuroids, and ophiuroids). Soft parts were unknown for carpoids, but they were assigned to subphylum II with blastozoans (Haugh & Bell, 1980a & b) through deduction of relationships between soft anatomy and skeletal features observed in other Paleozoic fossils (Fig. 4C).

Empirical phylogenetic approaches dealing with fossil symmetries

Formal analyses of character distributions using cladistics have changed the landscape of studies on echinoderm origins (Fortey & Jefferies, 1982; Smith, 1984; David, 1993; Mooi, 2001). Phylogenetics of extant groups relies on embryology, soft tissues, skeletal morphology, and molecular analyses (Smith, 1992; Wada & Satoh, 1994; Littlewood, 1995; Littlewood et al., 1997; Janies, 2001; Kondo & Akasaka, 2012; David & Mooi, 2014; Byrne et al., 2016). However, there remain many significant extinct taxa to integrate, and there are both advantages and disadvantages to including fossils in these analyses. The common set of data, with only a few exceptions, is reduced to skeletal morphology. However, echinoderm skeletons are character rich, and in many cases, the fossils are the only windows we have to place extant taxa in the rich history afforded by a record stretching back over half a billion years.

In spite of the inclusion of other fossil forms, carpoids did not make their way into the earliest morphological phylogenetic analysis of the phylum (Smith, 1984). However, representatives of the four carpoid classes were included in phylum-scale phylogenies of Sumrall (1997) and Sumrall et al. (2001). These analyses (Fig. 4E) attempted to avoid assumptions that affect character selection and coding by testing with criteria identified by Patterson (1982): similarity, conjunction, and congruence. For example, the aulacophore of stylophorans was coded as a feeding arm due to similarity in structure to feeding appendages of other echinoderms (Sumrall, 1997). Likewise, tests of similarity and congruence were also used to reject the hypothesis that thecal flattening was homologous across taxa. Sumrall's (1997) analysis recovered two clades: eleutherozoans (asteroids, echinoids, ophiuroids, and holothuroids), and dorsistomatans, i.e. echinoderms with an upward-facing mouth (edrioasteroids, blastozoans, and crinoids) (Fig. 4E). These were placed crownward of *Camptostroma*- or *Lepidocystis*-like ancestors. Carpoids were nested as within early dorsistomatans, closely related to cyclocystoids and *Lichenoides* (Fig. 4E).

The asymmetric body organization of the earliest carpoids was investigated by Dzik (1999) via comparison with other Cambrian echinoderms, who reported that the biseries of alternating, hinged plates along the distal part of the stylophoran appendage were comparable to cover plates in brachioles of gogiids. Applying the criteria of similarity and congruence, Dzik deduced that the aulacophore was uniserial, crinoid-like arm, but that the polyplated, disorganized morphology of the stem-like appendage of the earliest solutan (*Coleicarpus*) was homologous with the stem of gogiids. Therefore, solutans were derived from a *Gogia*-like ancestor and carpoids were regarded as a polyphyletic assemblage of relatively derived pelmatozoans (solutans and stylophorans), possibly related to helicoplacoids or ctenocystoids (Fig. 4D). Dzik (1999) also pointed out that fossil radial taxa (*Camptostroma*, gogiids, helicoplacoids, *Kinzercystis*, *Lepidocystis*) appeared earlier (Cambrian Series 2) than carpoids (Miaolingian [Smith et al., 2013; Zamora et al., 2013]), supporting the view that carpoids descended from radial ancestors while losing pentaradiality due to their vagile, epibenthic habit (Dzik, 1999).

Echinoderm embryology, origins, and the Extraxial-Axial Theory

The Extraxial-Axial Theory (EAT) has been used to explore the origins of the echinoderms and position of carpoids in some empirically-driven phylogenetic schemes (Mooi & David, 1998; David & Mooi, 1999; David et al., 2000; Peterson et al., 2000; Sprinkle & Guensburg, 2001; Lefebvre, 2003; Lefebvre & Fatka, 2003; Nardin et al., 2009; Lefebvre et al., 2013 & 2019; Guensburg et al., 2020). The EAT is an empirical model developed using data from both fossil and extant echinoderms, notably echinoids and edrioasteroid-like taxa (David & Néraudeau, 1994; Mooi et al., 1994). The theory integrates embryology, morphology, and paleontology (Fig. 5). The EAT shows that all skeletal elements in the axial part of an echinoderm originated through a distinct biserial addition pattern at the end of a growing ray (Jackson, 1912; David & Néraudeau, 1994; Mooi et al., 1994). The term 'ocular plate rule' (OPR) was coined for this patterning (Mooi et al., 1994). The OPR is diagnostic of axial body wall and skeletal elements that are closely associated with the WVS. Generalizing from extant forms to all fossil taxa, echinoderms are characterized by five growth zones, each consisting of two main columns of plates variously known as ambulacra, floor plates and other specialized elements (such as cover plates) formed in accordance with the OPR (Mooi et al., 2005; Mooi & David, 2008).

In contrast, extraxial body wall regions included stereom plates that did not follow any specified ontogenetic patterning, such as the OPR. Examination of a wide variety of echinoderms throughout their evolutionary history suggests that the extraxial body wall is divided into a perforate region containing the anus, gonopore, hydropore, epispires, and other apertures, and an aboral, imperforate portion that could be variously modified into attachment structures, but contains no apertures (Mooi et al., 1994 & 2005; Mooi & David, 2008). Comparison of the morphology of early pentaradial echinoderms (e.g., *Stromatocystites*; Fig. 5G & H) with extant echinoderms explains many empirical observations, such as that the interambulacrum of echinoids is not homologous with the interradii of stemward echinoderms (Mooi et al., 1994), that holothuroids are strongly paedomorphic (Mooi & David, 1997; David & Mooi, 1998), and that 'true' arms are a specific, unique type of body wall extension (David & Mooi, 1998; Mooi et al., 2005; Guensburg et al., 2010 & 2020). In addition, it was observed that axial regions are seldom, if ever, in contact with imperforate extraxial body wall, as the perforate extraxial is always expressed as an intervening region. The corollary is that the imperforate extraxial body wall could be absent, but the perforate extraxial always exists to some degree, and always in contact with the axial region.

The EAT was tested with developmental criteria (David & Mooi, 1996 & 1998; Mooi & David, 1997) as well as those outlined by Patterson (1982). Independent evidence from homeobox expression patterns confirmed the existence of two main regions, not only in the body wall, but also in internal anatomy of all extant echinoderms (David & Mooi, 1996, 1998 & 2014; Mooi & David, 1997 & 2008; Peterson et al., 2000; Mooi et al., 2005). This revealed a crucial, ontogeny-based observation concerning the relationship between rudiment formation and metamorphosis (Fig.

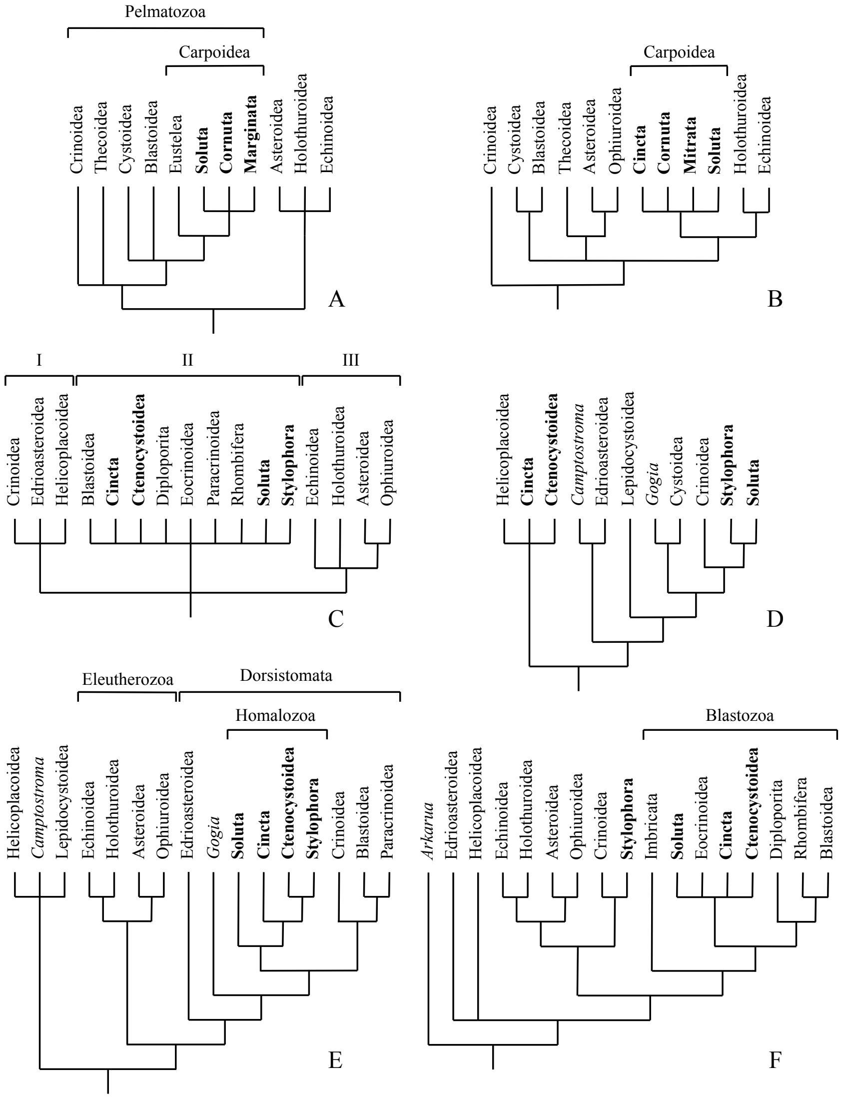

Figure 4. Phylogenies of fossil and extant echinoderms based on empirical models. **A.** Phylogeny adapted from Jaekel (1901), with carpoids as a clade of pelmatozoans. The carpoid order Eustelea contains several Ordovician genera now assigned to Paracrinoidea (e.g. *Amygdalocystites*, *Canadocystis*, *Comarocystites*, *Malocystites*). **B.** Phylogeny adapted from Jaekel (1918), with carpoids as a relatively derived clade of pelmatozoans. The class Carpoidea is divided into four orders, each of which continues to be recognized as a natural grouping: Cincta, Cornuta, Mitrata and Soluta. **C.** Phylogeny adapted from Haugh & Bell (1980a & b). The identification of three distinct subphyla is based on exceptionally preserved soft parts in several fossil taxa. All carpoids are assigned to subphylum II, which also includes all classes generally assigned to Blastozoa. **D.** Phylogeny adapted from Dzik (1999), with carpoids as a polyphyletic group. Ctenocystoids and possibly cinctans are interpreted as relatively early basal branches in the echinoderm tree, whereas solutans and stylophorans are considered as more derived and closely related to crinoids. **E.** Phylogeny adapted from Sumrall (1997), with all carpoids grouped within the same clade (Homalozoa), within dorsistomatans (echinoderms with an upward-facing mouth). **F.** Phylogeny adapted from David et al. (2000). Carpoids are polyphyletic: stylophorans are interpreted as the sister-group of the crinoids, whereas cinctans, ctenocystoids and solutans are allied with blastozoans.

5A-C). The rudiment forms during early development of the echinoderm larva through elaboration of the left mesocoel into the hydrocoel via outward growth of primary lobes around a hydrocoel-derived torus encircling the esophagus (Fig. 5B). As the hydrocoel forms this torus, it entrains more posterior somatocoels to form the rudiment itself (Fig. 5C). The rudiment is a completely de novo construct with no counterpart either in the earlier part of embryological development, or in any other phylum.

It is important to note that this is not related to metamorphosis, because after the appearance of the rudiment, modification or resorption of the non-rudiment portion of the larva is a separate process that can occur to varying degrees, resulting in an imago. The crucial element of this embryological patterning is the unique nature of the hydrocoel, not processes involved in metamorphosis, such as loss or appearance of structures related to survival of the larva. The importance of this distinction clarifies terminology, and underscores a seldom-appreciated fact that it is rudiment formation, not metamorphosis, that harbors evidence for the origin of pentaradiality in all echinoderms, including carpoids, in which pentaradiality is secondarily suppressed to result in only one or two rays.

The axial region is associated with the hydrocoel, which dominates rudiment formation (Fig. 5A-C). In contrast, the extraxial portion is closely associated with left and right somatocoels of the most posterior part of the archimery inherited from the larval body (David & Mooi, 1996 & 1998; Mooi & David, 1997). Evolutionary events altering the relative expression of the axial versus extraxial regions in adults result in vastly different degrees to which axial structures derived from the rudiment dominate the adult morphology. For example, the morphology of adult echinoids represents an extreme in which drastic metamorphosis results in near-total dominance of the axial region at the cost of near-total resorption of the larval body (David & Mooi, 1996 & 1998; Mooi & David, 1997). At the opposite end of the spectrum, crinoids undergo minimal metamorphosis because the adult body is made mostly of extraxial region plesiomorphically retained from the larva (Engle, 2012). Holothuroids also undergo minimal metamorphosis, but in this case because the axial region is paedomorphically restricted to the oral tentacles at one end of the body, with nearly all the larval body persisting in the adult. This indicates that holothuroids are essentially giant larvae (David & Mooi, 1996 & 1998; Mooi & David, 1997).

Embryological data show that in all extant echinoderms, pentaradiality in adults is superimposed onto larval development by the outward growth of the five primary hydrocoelar lobes in the rudiment (Fig. 5A-C). Pentaradiality is associated only with the rudiment-derived, axial region, with degree of prominence in adult morphology largely dependent on the degree to which metamorphosis suppresses into adulthood expression of the non-rudiment part of the larval body (David & Mooi, 1996 & 1998; Mooi & David, 1997). This balance between rudiment-derived (axial) and larval-inherited (extraxial) regions could be placed in a broad phylogenetic context. During their history, echinoderms displayed evolutionary novelties that altered this balance in specific ways (Mooi & David, 1997 & 1998). Early pentaradial forms such as *Camptostroma*, *Stromatocystites*, blastozoans, or crinoids were extraxial-dominated, retaining large proportions of perforate and imperforate extraxial region. In contrast, more crownward forms such as echinozoans and asterozoans were axial-dominated. This implied that earlier echinoderms experienced almost no metamorphosis, resulting in more restricted expression of rudiment-derived axial region in adults. Consequently, in early echinoderms there is far less expression of pentaradiality in the extraxial regions outside the axial rays (Mooi & David, 1997 & 1998; David & Mooi, 1998).

The very disparate morphologies of Paleozoic echinoderms were investigated through the EAT, including early pentaradial, edrioasteroid-like forms (Mooi & David, 1998), blastozoans (David & Mooi, 1999; David et al., 2000; Sprinkle & Guensburg, 2001; Nardin et al., 2009 & 2017; Lefebvre et al., 2015), stylophorans (Mooi & David, 1998; David & Mooi, 1999; David et al., 2000; Lefebvre, 2003; Lefebvre et al., 2019 & 2022; Saleh et al., 2023), cinctans, ctenocystoids, and solutans (David et al., 2000; Peterson et al., 2000; Sprinkle & Guensburg, 2001; Nardin et al., 2009), somasteroids and other early asterozoans (Mooi & David, 2000), helicoplacoids (Sprinkle & Wilbur, 2005), and early crinoids (Guensburg et al., 2020). Soft parts and ontogeny are virtually unknown in Paleozoic echinoderms, but empirically observed contributions of body wall components can be estimated from their skeletal morphology. Rudiment-derived axial elements can be identified through their expression of the OPR, as well as their close association with the mouth and the water vascular system. Extraxial elements from the larval body often display, at least plesiomorphically, an isotropic pattern. Among fossils, perforate extraxial region consistently contains the anus, gonopore, and hydropore, as well as various other types of pore structures such as diplopores, humatirhombs, pectinirhombs, or epispires (Fig. 5G). The imperforate extraxial region forms the aboralmost part of the body wall, lacks apertures, and is sometimes modified into an attachment pad or peduncle (Fig. 5H; Mooi & David, 1998; David & Mooi, 1999; David et al., 2000).

The empirically derived precepts of the EAT fuse modern biological and paleontological data to provide a toolkit in identifying two main types of feeding appendages in Paleozoic echinoderms (Mooi & David, 1998; David & Mooi, 1999; David et al., 2000). (1) Brachioles, or 'axial arms', are feeding appendages consisting entirely of axial elements (biserial floor plates plus cover plates), representing free, erect ambulacra associated only with the hydrocoel (Fig. 5D; David & Mooi, 1999; David et al., 2000; Mooi et al., 2005; Guensburg & Sprinkle, 2007; Guensburg et al., 2010 & 2020). These structures, identified only in blastozoans, are derived features supporting monophyly of that group (Sprinkle, 1973; David & Mooi,

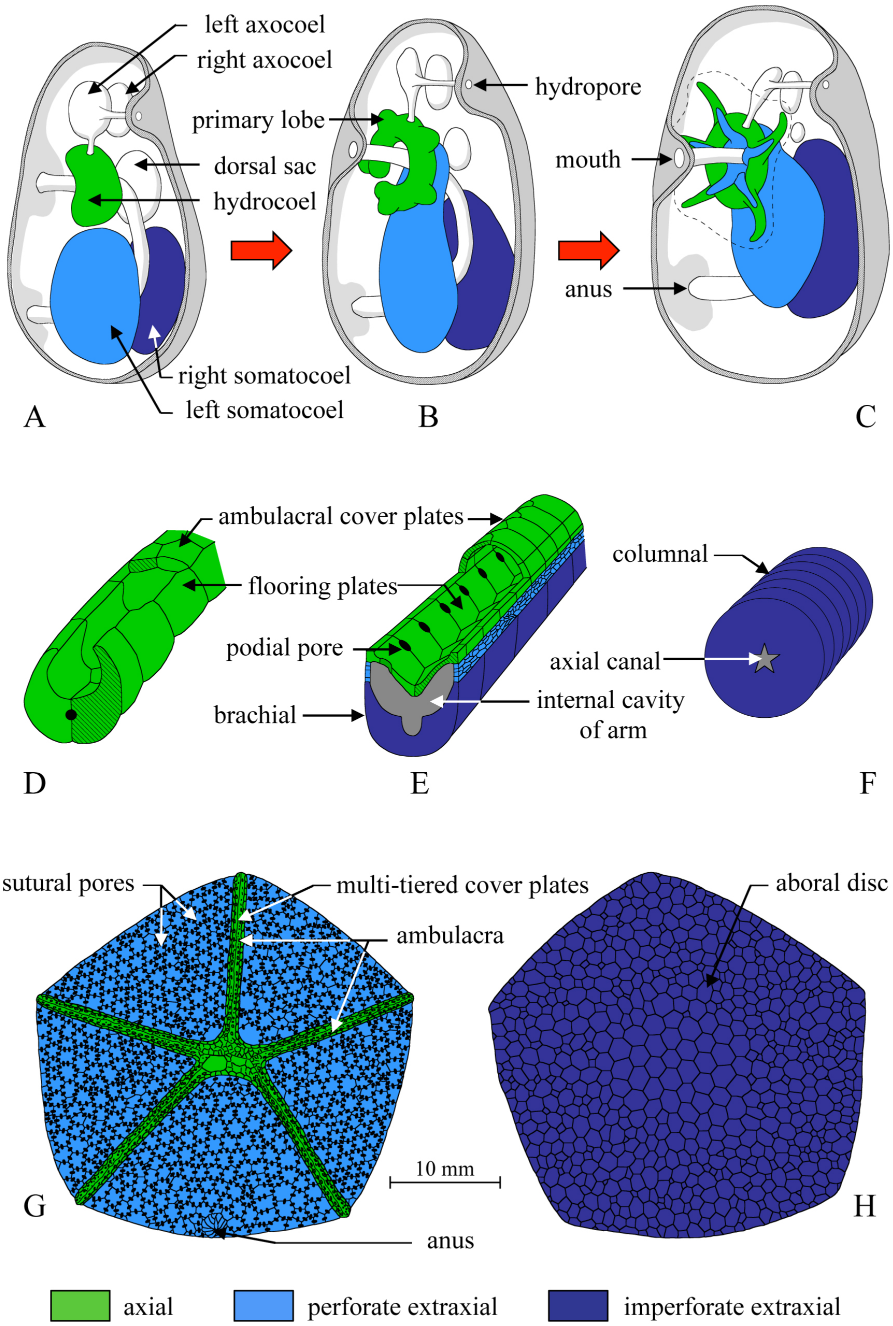

Figure 5. Interpretation of echinoderm body wall homologies based on the EAT (Mooi et al., 1994 & 2005; David & Mooi, 1999; Mooi & David, 1998 & 2008; Guensburg et al., 2020). **A-C.** Diagrammatic views of three successive stages illustrating the early development of the rudiment in echinoderm larvae (redrawn from Mooi et al., 2005; Mooi & David, 2008). **A.** Bilateral larval stage with three paired coeloms. **B.** Development of the hydrocoel as an open circumesophageal torus with five primary lobes. **C.** Later stage with hydrocoel forming closed circumesophageal ring and interacting with the left somatocoel to form the rudiment (outlined by a dashed line), with five primary lobes. **D-F.** Diagrammatic cross-sections through the three main types of echinoderm appendages. **D.** Brachiole of an early blastozoan (e.g. *Gogia*), with all skeletal elements (floor plates and cover plates) belonging to axial region of the body wall (redrawn from Mooi et al., 2005). **E.** Arm of an earliest, mid-Tremadocian *Titanocrinus*-like crinoid illustrating the plesiomorphic condition in crinoids (redrawn from Guensburg et al., 2020). These appendages are outgrowths of the entire body wall, thus containing skeletal elements of axial (cover plates, floor plates), perforate (unorganized lateral plates), and imperforate extraxial origins (brachials). In later forms, lateral extraxial plates are lost (e.g., *Aethocrinus*, *Athenacrinus*). Floor plates are not calcified in any Floian or younger crinoids. **F.** Schematic view of a crinoid-like stem. All skeletal elements belong to the imperforate extraxial part of the body wall. **G-H.** Interpretation of *Stromatocystites pentangularis* (edrioasteroid-like form), Cambrian Series 3, Czech Republic. **G.** Oral surface. **H.** Aboral surface.

1999; David et al., 2000; Guensburg & Sprinkle, 2007; Nardin et al., 2009 & 2017; Guensburg et al., 2010 & 2020; Lefebvre et al., 2015). (2) 'True arms' (including branches, such as pinnules), are composite feeding structures made of extensions of the entire body, therefore containing components of three coelomic extensions that constitute the body cavity of adult echinoderms (hydrocoel, left, and right somatocoels). True arms (Fig. 5E) are made of both axial (cover plates and floor plates) and extraxial elements (e.g., brachials), and typify asterozoans and crinoids (e.g., David & Mooi, 1999; David et al., 2000; Guensburg & Sprinkle, 2001 & 2007; Mooi et al., 2005; Guensburg et al., 2010 & 2019).

Contrasting with axial-bearing appendages in that they are not directly involved in food-gathering, extensions of the aboral, imperforate extraxial part of the body are variably expressed among several forms. Pedunculate constructs (Fig. 5F) were acquired independently in several groups of Paleozoic echinoderms, including blastozoans, crinoids, and edrioblastoids (Mooi & David, 1997; Guensburg & Sprinkle, 2001; Nardin et al., 2009; Lefebvre et al., 2015).

The disparate morphologies of carpoids and their various types of appendages and stem-like structures were interpreted using body wall homologies signified by the EAT (Fig. 4F). Mooi & David (1998) were among the first to suggest that the distal part of the stylophoran aulacophore was constructed similarly to a crinoid feeding arm. David et al. (2000) explored this idea with additional data, showing that in the aulacophore, the axial component was reduced to two sets of cover plates and an ambulacral canal borne on the internal surface of extraxial uniserial 'brachials' (Lefebvre, 2003; Lefebvre & Fatka, 2003; Guensburg et al., 2020). This implied that floor plates were not calcified in stylophorans, an interpretation compatible with the description of exceptionally preserved remains of a single ambulacral canal and associated tube feet in Ordovician cornutes (Lefebvre et al., 2019; Saleh et al., 2023), and the fact that crownward crinoids also lacked calcified floor plates (Guensburg et al., 2010 & 2020). The short appendage of solutans, made of ambulacral (axial) skeletal elements (biserial floor plates and cover plates), was interpreted as a brachiole, whereas the homoiostele was considered a stem-like appendage (David et al., 2000; Peterson et al., 2000; Sprinkle & Guensburg, 2001; Nardin et al., 2009; Noailles et al., 2014; Lefebvre & Lerosey-Aubril, 2018). The two anterior grooves radiating from the mouth and protected by axial cover plates suggested that cinctans possessed two brachioles at least partly recumbent on their anterior marginals. It followed that, as in stylophorans and derived crinoids, floor plates were not calcified in cinctans so that the WVS lies directly on modified thecal plates (marginals), accompanied by cover plates (David et al., 2000; Lefebvre & Fatka, 2003; Nardin et al., 2009). The short cinctan homostele was interpreted as an extraxial extension. David et al. (2000) suggested that the ctenidium of ctenocystoids consisted of highly modified ambulacral (axial) cover plates associated with two short brachioles, also recumbent on anterior marginals, one on each side of the mouth (Lefebvre & Fatka, 2003). Consequently, carpoids were considered a polyphyletic assemblage, with some assigned to blastozoans (cinctans, ctenocystoids and solutans) and others (stylophorans) more closely related to crinoids (Fig. 4F; David & Mooi, 1999; David et al., 2000; Lefebvre & Fatka, 2003; Sprinkle & Guensburg, 2004; Nardin et al., 2009; Lefebvre et al., 2019; Guensburg et al., 2020). This will be revisited below (see also Mooi et al., 2024).

Conclusions

The history of the two main approaches in interpreting the paleobiology and phylogenetic position of carpoids demonstrates that regardless of authorship, methodologies (e.g., comparative anatomy, phylogeny) or even sources of information (e.g., embryological, molecular, paleontological), the developed models have consistently produced the same two distinct clusters of results over a century of investigation. All studies based on conceptual concepts proceeding from theory considered the bilaterally symmetric or asymmetric morphologies of carpoids as original. That is, fossils with these morphologies were de facto plesiomorphic for the phylum (Figs 2 & 3). The explicit purpose of these approaches was not to find a place for these forms within an existing phylogenetic framework for the phylum by seeking commonalities with other echinoderms, but to emphasize differences that forced them outside of the crownward clades of the phylum. As noted as early as David & Mooi (1999), such concepts allowed carpoids to 'fall out of the tree' to positions as either pre-radial, stem-group echinoderms (e.g., Haeckel, 1896a & b; Bather, 1930; Gee, 2001a; Smith, 2005) or even completely outside of the echinoderm stem group (e.g., Jefferies, 1967).

All empirical studies of early echinoderm morphologies identified carpoids as relatively derived echinoderms that secondarily lost pentaradial symmetry characteristic of the first echinoderms, most likely as an adaptation to a vagile, epibenthic mode of life (Fig. 4). Consequently, carpoids were sometimes interpreted as closely related to edrioasteroid-like taxa (Cabibel et al., 1959), but they were more often affiliated with blastozoans and/or crinoids (Jaekel, 1918; Spencer, 1938; Haugh & Bell, 1980a & b; Sumrall, 1997; Dzik, 1999; David et al., 2000).

Both approaches have pushed outward the boundaries of knowledge about the earliest echinoderm fossils, with remarkable new material inspiring valuable opportunities to re-examine the concomitant ideas more closely, and with better data. We will turn to these ideas, and especially the nature of these data, in a companion paper (Mooi et al., 2024). The questions that arise from this re-examination go straight to the heart of studies in the origins of the Echinodermata. There are many reasons for this, particularly in the relationship between pentaradiality and divergences therefrom. However, perhaps the most basic question is also the most interesting: what is the necessary and sufficient feature to be a member of the phylum?

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