

Deuterostome phylogeny and the interpretation of problematic fossil echinoderms

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ABSTRACT: Carpoids have proved a controversial fossil group largely because it is unclear which modern taxon provides the best model for interpreting their anatomy. Recent molecular phylogenies provide a framework against which proposed morphological character assemblages attributed to carpoids can be assessed. This makes it clear that whereas it is quite plausible that deuterostomes with pharyngeal gill slits and a stereom skeleton existed, it is much less likely that stereom and a notochord co-occurred. Carpoids, when interpreted in this light, provide important insight into the pre-radiate history of echinoderms.

1 INTRODUCTION

There can be few fossils as controversial as the carpoids, an extinct group of asymmetrical organisms with a multiplated, calcitic skeleton. These forms were initially interpreted as primitive echinoderms that had evolved before pentamerous symmetry was acquired, but more recently have been championed as stem group chordates or as highly derived echinoderms that have secondarily lost their pentamery. Such uncertainty over their phylogenetic placement has arisen for one very simple reason: there is no consensus as to the basic anatomical organization in carpoids, with fundamental disagreements about what is anterior and posterior, left and right, the position of the mouth and anus, the presence or absence of ambulacra and gill slits, etc.

This lamentable situation is not the result of poor knowledge: a vast amount of research has been done on the skeletal anatomy of carpoids over the past 30 years. Yet workers remain as polarized as ever as to how to interpret the structures they see. We now understand as much about carpoid skeletal anatomy as we are ever likely to, and, in the absence of exceptional preservation of soft-tissue, the problem then is how to judge the likelihood of rival homology statements that have been proposed.

From Cuvier's day onwards, three fundamental principals have been invoked to assess whether structures in different taxa merit being interpreted as homologous (i.e. represent the same organ): similarity of structure, similarity of function and similarity of position. For extant taxa functional comparisons can be made directly and gene expression patterns can now be used

to establish homology. For example the question of whether the stomochord of hemichordates is homologous to the notochord of vertebrates has been addressed by comparing gene expression patterns in the two structures (Tagawa et al. 2001). Fossils must be interpreted through comparative anatomy with appropriate living relatives and therein lies the problem: it is not obvious with what modern organisms we should be comparing carpoids in order to interpret their structure. Jefferies et al. (1996) choose a cephalochordate or tunicate model, and nerves, pharyngeal gill slits and notochord are all plausibly reconstructed. For David et al. (2000) a modern echinoderm model is selected and ambulacra with a 'modern' (i.e. crown-group) organization, and respiratory organs are assigned to carpoid structures. Yet the character combinations that existed in basal deuterostomes or even basal echinoderms are not necessarily what we see in today's crown-group representatives. To understand what sorts of character combinations are likely to have existed a phylogenetic framework of deuterostomes is required.

2 PHYLOGENY OF DEUTEROSTOMES

The relationships of major deuterostome groups was highly contentious until recently, largely because morphological data gives a conflicting signal: larval characters mostly support the pairing of echinoderms with hemichordates while adult characters point to a hemichordate–chordate pairing. However, the rapid accumulation of gene sequence data over the past few years has provided a robust and independent guide to deuterostome relationships. All recent analyses of 18s

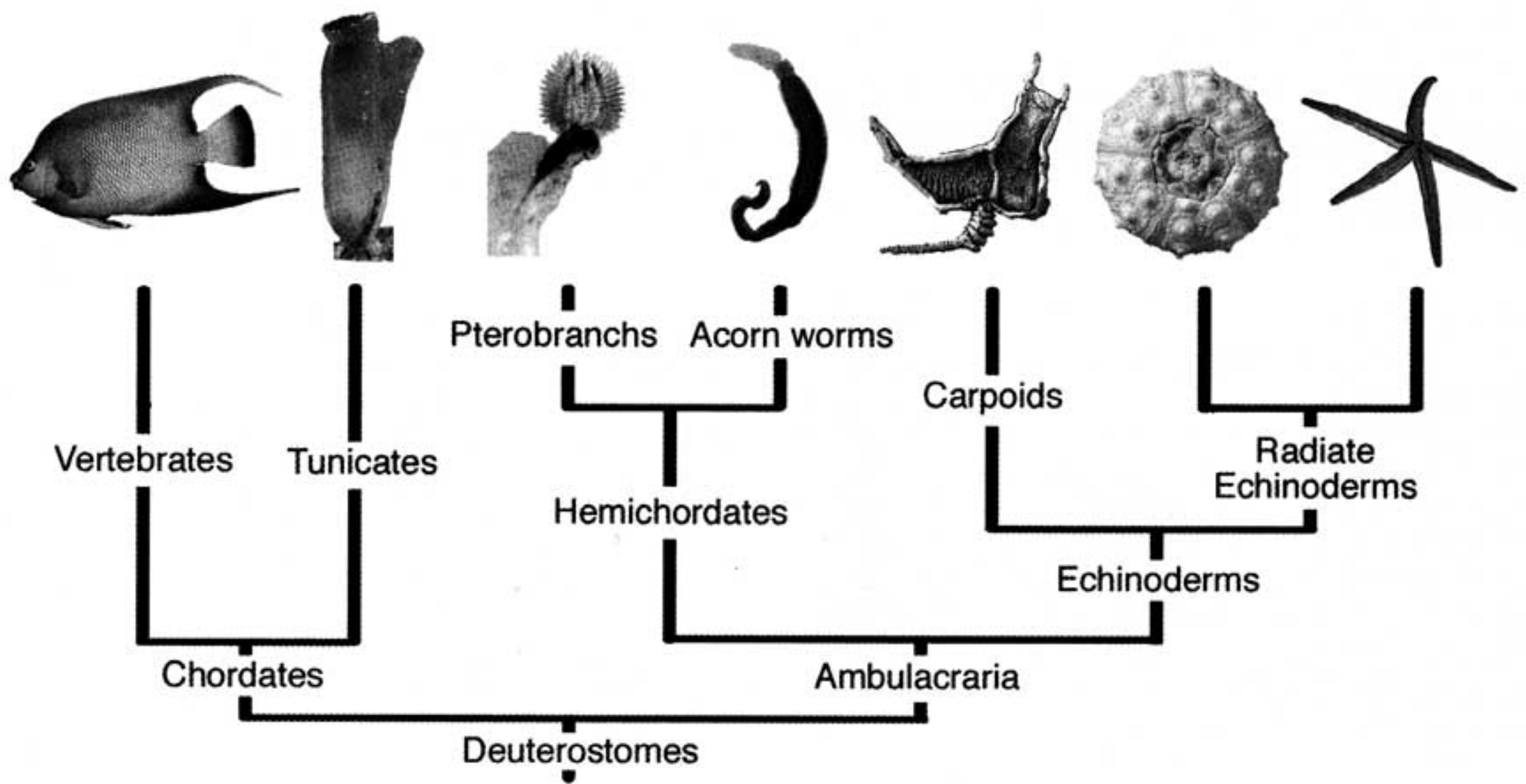


Figure 1. The phylogenetic relationships of deuterostomes. The framework of relationships for extant taxa is based on phylogenetic analysis of gene sequence data (see Bromham & Degnan 1999, Cameron et al. 2000, Winchell et al. 2002, Furlong & Holland 2002); the extinct carpoids have been added to indicate their probable position (see text).

and 28s ribosomal DNA unambiguously point to echinoderms and hemichordates as sister taxa (Bromham & Degnan 1999, Cameron et al. 2000, Peterson & Eernisse 2001, Winchell et al. 2002, Furlong & Holland 2002 – Figure 1). This has important implications for the morphology of the earliest echinoderms since character combinations that co-occur along each branch can be reconstructed, providing guidelines for the interpretation of carpoid anatomy.

3 CARPOIDS AS STEM GROUP ECHINODERMS

Two unambiguous characters place carpoids firmly within the echinoderm stem group: a mesoskeleton composed of stereom and their primary lack of radially.

The construction of the echinoderm skeleton as a three-dimensional meshwork of high magnesium calcite termed stereom is unique amongst extant Bilateria. Furthermore, no fossil that can be unambiguously assigned to the hemichordates tunicates, or chordates shows any trace of a stereom skeleton. Even the Cambrian ventulicolids, which possibly represent stem group deuterostomes (Shu et al. 2001), lack stereom. Consequently it seems reasonable to conclude that a stereom endoskeleton evolved after echinoderms had split from hemichordates but before crown group diversification. If stereom were a basal deuterostome character it would require four independent losses

(in hemichordates, urochordates, cephalochordates and craniates), which seems much less plausible than a single gain.

Another unique feature of crown group echinoderms is that all display radially (usually pentamer) symmetry that is secondarily superimposed onto an ontogenetically earlier asymmetric phase. In their ontogeny echinoderms start with paired body coeloms, but then pass through an asymmetric phase when the anterior coeloms of right-hand side are suppressed and the posterior somatocoels become vertically stacked. Secondary radially is expressed initially in hydrocoel organization and nervous system but in primitive members does not affect somatic organs such as the gonads, which remain single (edrioasteroids and primitive Palaeozoic echinoids for example have only a single gonopore). Although there are some left-right asymmetries in cephalochordate and urochordate organization, these animals retain a basically bilateral body plan with paired left and right organs. As hemichordates show little if any asymmetry in their ontogeny the massive and pronounced asymmetry seen in echinoderms must have developed after echinoderms had separated from hemichordates.

Since carpoids possess a skeleton of stereom and are fundamentally asymmetric without radially replicated appendages, they fall within the stem lineage of echinoderms. Interestingly although carpoids such as solutes and cornutes have strongly asymmetrical bodies, their posterior appendage is clearly bilaterally symmetrical.

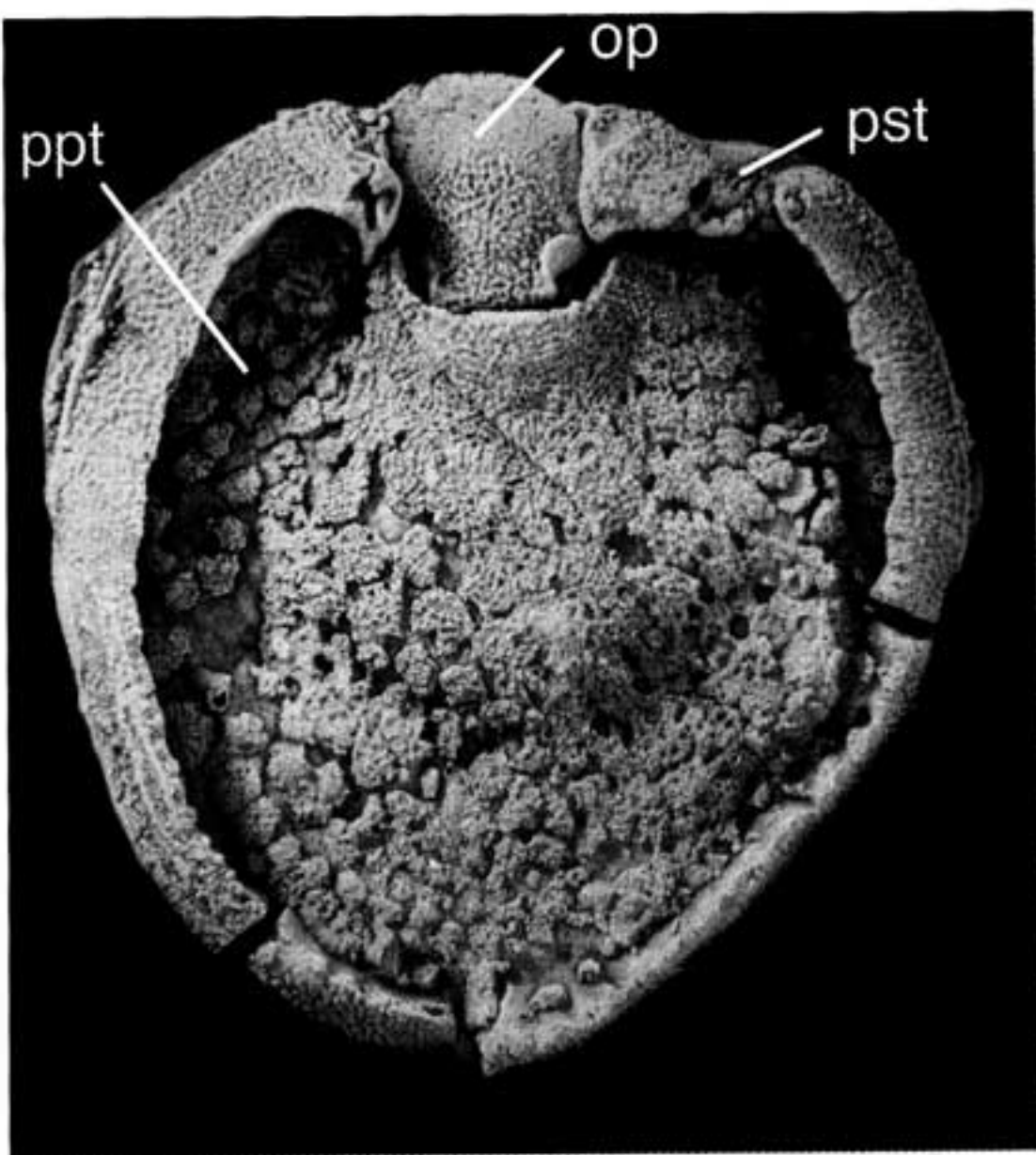


Figure 2. *The cinctan Trochocystites bohemicus* Barrande, from the Middle Cambrian of Bohemia (from Ubaghs 1967, Figure 367). This dorsal view of the theca shows the positions of the peristome (pst), periproct (ppt) and the third large opening covered by a protective flap-like plate, the operculum (op).

This is in marked contrast to the stems of true echinoderms, where pentamery is expressed to the end of the stalk.

4 CARPOID ANATOMY

After their divergence from the latest common ancestor of echinoderms and hemichordates but prior to crown group diversification, echinoderms must have lost a number of basal deuterostome features. These include pharyngeal gill slits, a muscular stalk/tail for locomotion and bilateral body plan.

Gill slits. The possession of pharyngeal gills was one of the principal characters thought to link hemichordates and chordates as sister taxa. However, having pharyngeal gill slits is most parsimoniously explained as a plesiomorphic character for deuterostomes. It is therefore conceivable that the more basal stem group echinoderms would have possessed pharyngeal gill slits.

Body openings that are potential candidates as gills occur in both stylophorans and cinctans, but not in solutes. Cinctans have three major body openings (Figure 2): a marginal hole associated with the 'ambulacral' grooves and universally identified as the peristome, a small conical structure on the aboral plated membrane that conforms closely in structure to the

periproct in echinoderms, and a massive anterior opening covered by a flap-like plate that is articulated in such a way that it can only swing outwards. In functional terms this third opening acts as an outlet valve and has no obvious counterpart in any crown-group echinoderm. It has been interpreted as an atrial opening to a pharyngeal chamber (Friedrich 1993), which certainly fits with its role as a one-way valve structure.

The putative gill slits in stylophorans are a series of large openings along one side of the theca, but here the interpretation is less clear-cut. For David et al. (2000) and Lefebvre (2003) these openings are simply respiratory structures analogous to those developed in other primitive echinoderms, whereas Jefferies et al. (1996) believe they represent serial gill slits. There are significant differences between deuterostome gill openings and the respiratory structures of primitive echinoderms that support these being gill openings.

First, gill openings pass from the pharynx to the exterior, piercing all three somatic layers, whereas the various respiratory rhomb structures in cystoids are all thin-walled regions of the outer body wall developed into deep internal corrugations separated from the main body cavity in which the gut resides. Unlike gill openings, these respiratory structures are mesodermal and do not perforate the somatocoel. Even in blastoids, where there is a complex system of internal canals, these are still separated from the main body cavity that includes the digestive system by a thin and corrugated calcified wall and are thus mesodermal.

Second, gill slits are entirely designed for venting fluid from the body whereas cystoid respiratory structures are designed to allow a one-way in-and-out flow of fluid across the thin-walled gaseous exchange surface.

In stylophorans the putative gill openings completely pierce the body wall and show no thin-walled interior partition. Furthermore, in the best preserved material (*Phyllocystis*), recently redescribed by Lefebvre (2003), it is clear that the openings were covered in life by cones of small imbricate plates. The structure of these cones is again that of an outlet valve, with the overlapping plates forming a nozzle that could be pushed open by pressure from the interior; none conform to inlet structures. Consequently, I concur with Jefferies et al. (1996) that these openings are indeed best interpreted as gill openings.

Since no convincing evidence exists for gill slits in solutes, stylophorans are interpreted as being more crownward than stylophorans.

Right mesocoel suppression. Crown group echinoderms, like pterobranch hemichordates have their hydrocoel developed as a tentacular system. In pterobranchs left and right coeloms each give rise to an independent tentacular system but the entire water vascular system in echinoderms develops by branching from just the left hydrocoel. This clearly must also have been the

case in solutes where there is a single ambulacrum and single hydropore. However, cinctans may have retained the primitive condition of left and right tentacular mesocoels. Cinctans have a left and right groove emanating from the mouth and these are generally interpreted as having housed a pair of tentacles (e.g. David et al. 2000). Amongst cinctan genera there is a pervasive tendency for the right oral groove to be greatly reduced or even lost – recalling the asymmetrical development of left and right mesocoels in crown echinoderms.

Notochord. A notochord has been postulated to be present in carpoids, but the topology of the molecular phylogeny indicates that this is unlikely. The notochord is an apomorphy of chordates and no homologue exists in extant hemichordates and echinoderms. The stomochord of hemichordates, although somewhat similar in appearance to a notochord, does not have the gene expression expected if it were homologous (Tagawa et al. 2001).

Muscular locomotory appendage. The single appendage of stylophoran carpoids has been variously interpreted as a muscular stalk, tail or ambulacrum. Hemichordates have a muscular stalk carrying both left and right metacoels for attachment and creeping locomotion. By contrast echinoderms such as crinoids have a non-muscular stalk, which carries only extensions of a single somatocoel (although it is very likely that some extinct groups such as pleurocystitid cystoids had a muscular stem, at least proximally).

Functional analysis demonstrates that the proximal part of the carpoid appendage was indeed highly muscular and its strongly expressed bilateral symmetry is consistent with there being internal paired coeloms in this part of the body.

5 CONCLUSIONS

Because echinoderms are highly derived compared to other deuterostomes, we should expect early stem group members to be radically different from their morphologically derived modern relatives. Carpoids, as asymmetric, stereom-bearing deuterostomes, are best interpreted as stem group echinoderms, and therefore give critical insight into the preradial history of this clade. Solute lie closest to crown group echinoderms since they show no evidence of pharyngeal gill slits and because they are unique amongst carpoids in having an appendage that is clearly homologous to an ambulacrum of crown-group echinoderms. Both

stylophorans and cinctans are more basal, since they primitively retain the plesiomorphic deuterostome trait of pharyngeal gill openings.

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