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Making sense of carpoids

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Reconstructing the early evolution of animals has long been a major challenge and motivation for scientists. Deuterostomes (a group of animals that includes the vertebrates, worm-shaped hemichordates and echinoderms such as sea urchins and starfish) are of special interest, as humans belong to this group; establishing the morphology of our ancient ancestors may offer fresh perspectives on our deep evolutionary roots. Carpoids are a puzzling group of fossils that could potentially inform on the early evolution of the deuterostomes. They possess a distinctive combination of traits not seen in any living animal, so determining where carpoids fit into the deuterostome evolutionary tree (phylogeny) will help us to understand the order in which important characters of modern groups were acquired. Unfortunately, the value of carpoids for this undertaking has been hampered by arguments over numerous palaeobiological details. Although many of these disagreements persist today, there are signs that by employing an holistic approach it may be possible to resolve some of the issues surrounding this bizarre fossil group.

What are carpoids?

Discovered over 150 years ago, carpoids are a contentious group of bottom-dwelling marine deuterostomes. They are also known as homalozoans or calcichordates; the abundance of names reflects the confusion they have engendered. They lived during the Palaeozoic Era, from the Cambrian to the Carboniferous, and their fossils are found today in rocks throughout the world.

Living deuterostomes are divided into four subgroups or phyla: the chordates, echinoderms, hemichordates and xenoturbellids (Fig. 1). Allying carpoids with any one of these groups has proven highly controversial, principally because of their unique combination of characters. Carpoids possess a skeleton of monocrystalline calcite plates identical to that of echinoderms; however, unlike living echinoderms, they lack fivefold radial symmetry, and the existence of an echinoderm-type water vascular system is contested. Furthermore, some carpoids may have possessed gill slits, which are present in chordates and hemichordates, but not in extant echinoderms.

There are four major groups of carpoids: ctenocystoids, cinctans, solutes and stylophorans (Fig. 2). Each of these groups has a suite of distinctive features, but they are grouped together as they possess an echinoderm-like calcite skeleton, but do not exhibit radial symmetry. In many cases, the nature and position of fundamental characters such as the mouth and anus is debated; the same is true for the systematic position and phylogenetic relationships of carpoid taxa.

Ctenocystoids (Middle Cambrian) comprise a flattened elongate body and an anterior grill-like feeding apparatus, displaying strong bilateral symmetry in outline. The body is usually framed by a double layer of upper and lower marginal plates, which surround numerous small polygonal plates. The anterior apparatus encloses a bilaterally symmetrical pair of narrow grooves; a cone-shaped exhalant opening (gill slit or anus) is located at the posterior of the body. The anterior grooves may have housed extensions of a water vascular system involved in feeding, but the organization of this system is unclear.

Cinctans (Middle Cambrian) possess a flattened body and a single posterior appendage, used to improve their stability on the sea floor. The body is composed of a rigid marginal frame enclosing small central plates (like ctenocystoids). A single left feeding groove or an asymmetrical pair of left and right grooves run along the outside of the marginal plates into an anterior

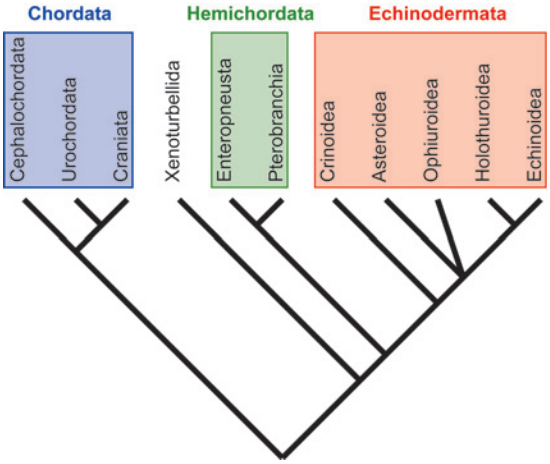


Fig. 1. Evolutionary tree of living deuterostomes.

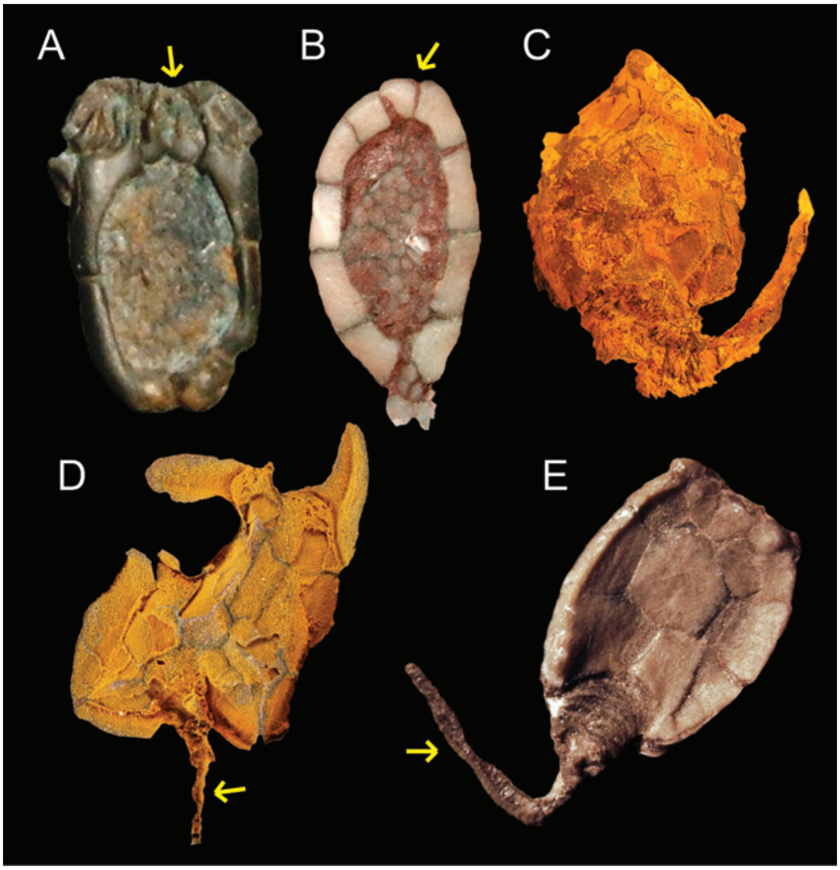


Fig. 2. Representatives of the main carpoid groups. **A.** The ctenocystoid *Ctenocystis colodon* (Cambrian, USA). The arrow indicates the anterior feeding apparatus. **B.** The cinctan *Protocinctus mansillaensis* (Cambrian, Spain). The arrow indicates the anterior body opening. **C.** The solute *Plasiacystis* sp. (Ordovician, Morocco). **D.** The stylophoran *Ceratocystis* sp. (Cambrian, Spain). The arrow indicates the major appendage. **E.** The stylophoran *Anomalocystites cornutus* (Devonian, USA). The arrow indicates the major appendage.

right mouth; the nature of the soft parts associated with these grooves is contentious. A large circular opening at the anterior midline, covered by a movable plate, is interpreted as either an anus, or an exhalant vent for internal gill slits.

Solutes (Middle Cambrian–Lower Devonian) typically have an asymmetrical body with two appendages (one at each end of the body). The longer posterior appendage is bilaterally symmetrical and centralized; in some species it served to attach the animal to the substrate. The shorter anterior appendage is offset laterally and almost certainly housed elements of a water vascular system, as it is very similar to the feeding appendages (ambulacra) of various echinoderms.

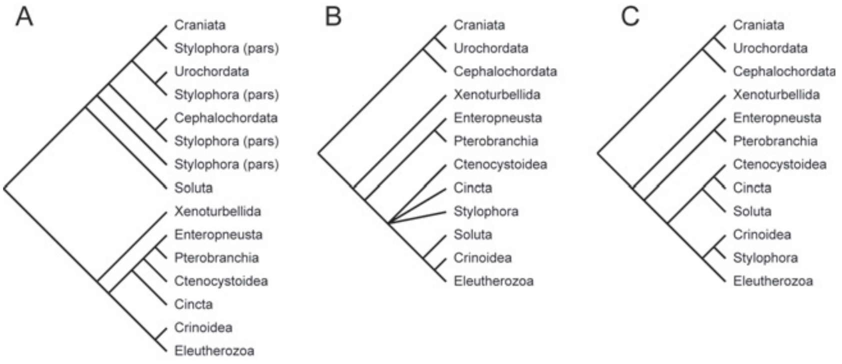
Stylophorans (Middle Cambrian–Upper Carboniferous) range from asymmetrical to bilaterally symmetrical in outline, with the plates comprising their body very variable in size and shape. A long, slender appendage is found at one margin of the body (the anterior-posterior orientation is uncertain), housing a longitudinal canal and many fine lateral channels and depressions. This appendage is variously interpreted as an ambulacrum with tube feet, a muscular tail with a notochord or a simple locomotory appendage. A series of specialized slit-like body openings occur in some species; these may represent chordate-like gill slits or echinoderm-like respiratory organs.

Biological affinities of carpoids

The first carpoids were described in the late 1850s by the Canadian palaeontologist Elkanah Billings and the French geologist and palaeontologist Joachim Barrande. Initially, carpoids were thought to be members of the extinct echinoderm class Cystoidea, but following the discovery of further species their distinctiveness became clear. Most workers in the early twentieth century regarded carpoids as a group of 'primitive' (basal) echinoderms that emerged prior to the acquisition of radial symmetry, a view that was echoed in the 1968 *Treatise on Invertebrate Paleontology*. At approximately the same time, Richard Jefferies produced a series of papers interpreting stylophorans and solutes as early chordates. Jefferies based his theory on the work of the Swedish zoologist Torsten Gislén, who remarked on a number of similarities between the carpoid and chordate body plans. In the late 1990s, a third model emerged, in which carpoids were taken as more 'advanced' (derived) echinoderms that had secondarily lost their fivefold symmetry. This hypothesis was founded on a new theory of echinoderm homologies that identified shared characters that had not previously been recognized, characters that united carpoids and echinoderms. These three dramatically different interpretations are outlined below, and in Fig. 3.

Calcichordate model—in this, carpoids are treated as early deuterostomes variously assigned to chordate, cephalochordate, craniate, urochordate or

Fig. 3. Alternative hypotheses of carpoid evolutionary position. **A.** Calcichordate model (based on Domínguez & Jefferies 2005). **B.** Echinoderm I model (based on Smith 2005). **C.** Echinoderm II model (based on David *et al.* 2000). The Eleutherozoa comprises starfish, sea urchins, sea cucumbers and brittle stars.



hemichordate stem-groups (Figs 3A, 4). They share several diagnostic characters with hemichordates or chordates (including gill slits and a complex nervous system), allowing their phylogenetic position to be deduced. The presence of a calcite skeleton is not informative, as deuterostomes possessed such a skeleton primitively.

Echinoderm I model—this suggests that carpoids are early echinoderms, originating before the evolution of radial symmetry and, hence, lying within the echinoderm stem-group (i.e. on the stem of the echinoderm evolutionary tree) (Fig. 3B). As such, they are equally distantly related to all living echinoderm taxa, lacking a number of characters found in modern forms, but possessing ancestral traits such as gill slits. Their echinoderm affinities are clearly demonstrated by the calcite skeleton, which is a defining characteristic of the echinoderms.

Echinoderm II model—here, carpoids are seen as an assemblage of echinoderms with multiple evolutionary origins, all possessing functional ambulacra, and, as such, assigned to the Crinozoa or Blastozoa (Fig. 3C). The presence of calcite, and the division into axial (ambulacra) and extraxial (rest of the body) regions, establishes carpoids as echinoderms; the apparent absence of other key echinoderm features is due to the secondary loss of characters.

Testing the models

Choosing between theories for the evolutionary position of the carpoids is problematic, largely because it is difficult to assess the strength of the arguments, based as they are on morphology. This is because many inferred characters are interpretations of subtle morphological features, and the value of these features is strongly dependant on whether carpoids are interpreted by reference to extant chordate, hemichordate or echinoderm body plans. Such assumptions permit only a measure of internal consistency; models will be flawed if the original hypotheses they are based on are incorrect.

A potentially robust means of discriminating between the alternative interpretations is to evaluate the phylogenetic predictions of each model—in other words, what kind of evolutionary tree would result? For example, a cladistic analysis (a predictive tool in evolutionary studies, relying on the concept of primitive versus derived characters) with carpoids coded according to the calcichordate hypothesis failed to reproduce the relationships of living deuterostomes predicted by this model; however, a second study with a slightly different character matrix yielded a tree consistent with the calcichordate theory. This suggests that the coding of carpoid characters may be too subjective to allow for a rigorous phylogenetic test. Another possible method of evaluation is to examine how closely rival phylogenies match the stratigraphic record; here, the calcichordate hypothesis shows a significantly poorer fit to the stratigraphic ordering of fossils than other models. While it has been argued that the carpoid fossil record is too incomplete to provide a reliable guide to phylogeny, even a weak signal in the record may offer some discrimination. Nevertheless, a rigorous, truly objective test of alternative interpretations for the affinities of carpoids is still lacking.

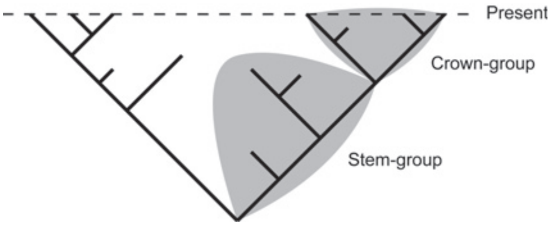


Fig. 4. Summary of the stem and crown-group concepts.

To move, or not to move?

The function of the stylophoran appendage is a long-standing issue in carpoid palaeobiology, lying at the heart of each of the competing theories discussed above. The appendage is conventionally interpreted as a feeding arm or a muscular locomotory tail, with alternative interpretations derived from differ-

Fig. 5. The stylophoran *Rhenocystis latipedunculata* (Devonian, Germany) and associated trace fossil. Scale bar = 10 mm.

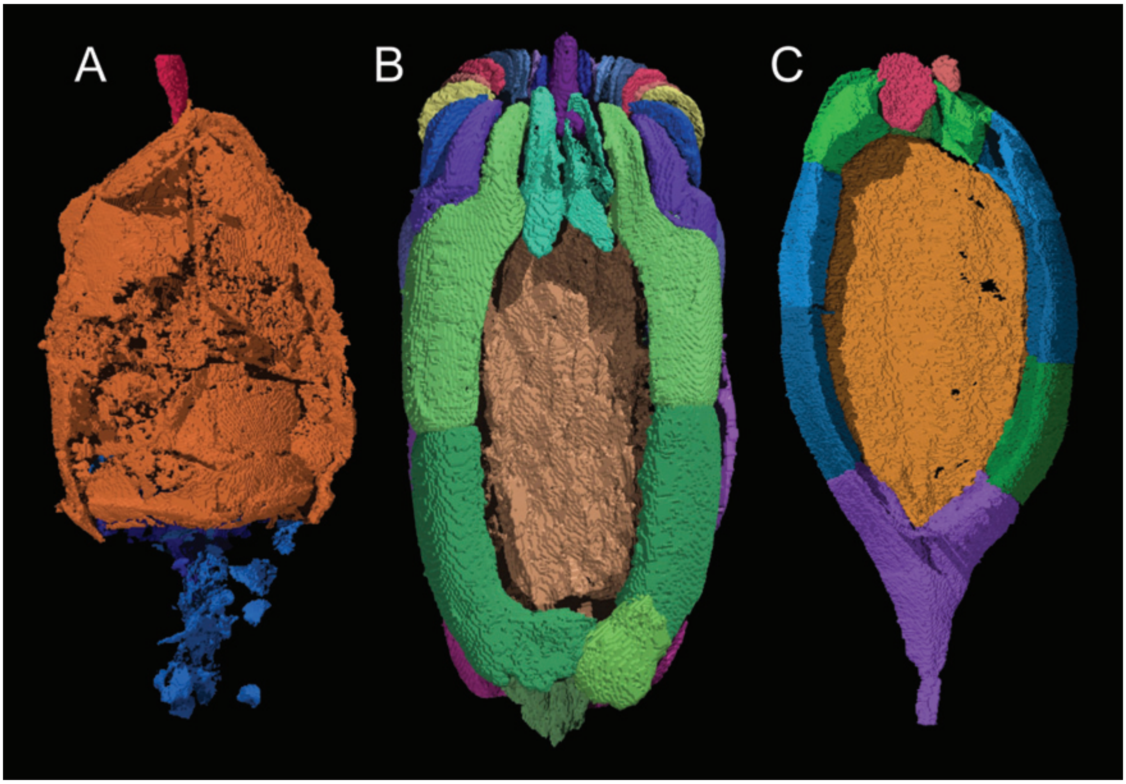


Fig. 6. Computer reconstructions of carpoids based on micro-CT data. **A.** The stylophoran *Anatifopsis barrandei* (Ordovician, Czech Republic). **B.** The ctenocystoid *Ctenocystis utahensis* (Cambrian, USA). **C.** The cinctan *Protocinctus mansillaensis* (Cambrian, Spain).

ent inferences for the soft parts inside the appendage. However, because soft tissues are never preserved in carpoids, it is difficult to distinguish between these interpretations.

The skeleton of carpoids (and all echinoderms) consists of multiple plates constructed from a three-dimensional calcitic mesh (stereom). Stereom is rarely well preserved in the fossil record, but where it is, it may provide a reliable guide to the nature of the investing soft parts. An investigation of stereom microstructure in the Middle Cambrian stylophoran ?*Ceratocystis* sp. found that the base of the appendage housed extensive musculature, and that at its other end elements were tightly bound together by ligamentary tissues (during life). These results suggest that the appendage may have been capable of significant movement. Furthermore, there is no evidence that appendage plates could open outwards, as required by the echinoderm-type feeding arm hypothesis.

More indirect insights into the functional morphology of the appendage were obtained through studies of stylophoran behaviour predicted from fossil evidence. Several individuals of the Lower Devonian stylophoran *Rhenocystis latipedunculata* were described on slabs of slate associated with ribbon-like trace fossils (Fig. 5). Doubts have been raised over the relationship between some of the trace and body fossils, but in the majority of these specimens the connection appears genuine. The most plausible explanation for the traces is the movement of *R. latipedunculata* through the sediment, with the appendage the likely source of motive power. Therefore, two robust, independent sources of data support the interpretation of the stylophoran appendage as a locomotory organ rather than a feeding appendage, even if a combination of both functions cannot be definitively ruled out.

Virtual palaeontology

Accurate, detailed descriptions of fossils form the foundations upon which all rigorous interpretations of carpoids are based; as a result, carpoid workers have often sought ways of acquiring novel morphological data. X-ray microtomography (micro-CT) is a powerful approach that has the potential to provide such information. Here, a fossil is digitally imaged and reconstructed on computer, allowing visualization of its internal and three-dimensional form. High-resolution micro-CT was used to study several carpoid species in this manner, visualizing a complex internal skeleton in the stylophoran *Anatifopsis barrandei*, a previously unknown chamber in the ctenocystoid *Ctenocystis utahensis* and a large inner depression in the cinctan *Protocinctus mansillaensis* (Fig. 6). Moreover, reconstructions of the stylophorans *Jaekelocarpus oklahomensis* and *Lagynocystis pyramidalis* allowed intricate comb-like structures to be described in far greater detail than previously possible. While the interpretation of these characters is still subject to debate, it seems evident that the detailed description of fossils afforded by micro-CT is the optimal means of obtaining new insights into carpoid morphology, and can be hoped to drive further investigations into these unusual fossils.

Significance of stereom

Perhaps the most familiar trait of carpoids is their stereomic calcite skeleton, which is indistinguishable from that found in echinoderms. Stereom is either seen as a derived character of echinoderms (echinoderm I and echinoderm II models), or as a character primitively present in all deuterostomes that was secondarily lost in all extant groups apart from echinoderms (calcichordate model).

One way to differentiate between these possibilities is to examine evidence from living species, specifically the genes deployed during the development of the echinoderm skeleton. If such a skeleton was present in the latest common ancestor of the deuterostomes (as predicted by the calcichordate theory), we might expect to find homologues for the genes involved in the formation of stereom in chordates, hemichordates and xenoturbellids. Comparisons of genetic sequences from the echinoderm *Strongylocentrotus purpuratus*, the hemichordate *Saccoglossus kowalevskii* and various chordates showed that the family of genes responsible for stereom deposition in *S. purpuratus* is dissimilar to any sequences in current data sets for non-echinoderm deuterostomes. This strongly suggests that stereom is unique to echinoderms, in conflict with the calcichordate hypothesis.

The future of carpoid research

The integration of data from multiple independent sources is an approach that has shown considerable promise in addressing issues of contention surrounding carpoids. Molecular biology is perhaps the most exciting source of novel data, with recent results demonstrating that a calcite skeleton of stereom is in all likelihood a derived character shared by carpoids and echinoderms. Obtaining sequence data for a wider range of deuterostome taxa (particularly echinoderms and hemichordates) should serve to test this hypothesis.

As stated above, the interpretation of the carpoid fossil record is contentious; however, it may be possible to overcome many of these difficulties by employing new, sophisticated analytical techniques. The high-resolution images generated by modern micro-CT scanners allow very fine three-dimensional morphological features to be described in a previously unattainable manner. Moreover, reconstructions of fossils may be studied quantitatively, using computer-modelling techniques such as finite element analysis or computational fluid dynamics to obtain novel functional morphological insights. Molecular and computational methods will form important parts of the twenty-first century palaeontologist's toolkit, particularly for those brave (or foolhardy) enough to study the enigmatic carpoids.

Suggestions for further reading

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