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Fossil Focus: Diploporitans

by [Sarah L. Sheffield](#)^{*1}

Introduction:

[Echinoderms](#), a group of marine animals that includes familiar organisms such as sea stars and sea urchins, were much more [diverse](#) in the past than they are today. There are five living classes of echinoderms (sea stars, sea urchins, brittle stars, sea cucumbers and crinoids), but more than 20 extinct classes are known only from the fossil record. During the [Palaeozoic](#) Era (542 million to 251 million years ago), especially, echinoderms were incredibly diverse and thrived all over the globe (Fig. 1). This was a time of significant environmental change, with the climate ranging from very warm oceans with high sea levels and high atmospheric carbon dioxide concentrations to much colder oceans, with extensive glacial ice. By studying how fossil echinoderms evolved in response to these dramatic climate shifts, we can better understand how climate change today might affect modern echinoderms and other animals.

Blastozoans are a major group of now-extinct echinoderms, and include a number of highly diverse forms (such as [blastoids](#) and [paracrinoids](#)) that each have very distinct body features. They have traditionally been classified on the basis of the types of respiratory structure present on their body; these structures were used for breathing. Each large group of blastozoans was defined by a specific type of respiratory structure with a distinctive [morphology](#) (for example, eocrinoids have epispires, which are single pores found across the body, and parablattoids have cataspides, which are internal folds). Diploporita, the group of blastozoan echinoderms highlighted in this article, is defined by the presence of a diplopore-type (double pore) respiratory structure (Fig. 2). However, as further research has been carried out on these fossils, it has become apparent that respiratory structures are not a good way to separate them into groups. New fossil finds indicate that many of the respiratory structures thought to be unique to particular groups might in fact have evolved more than once across the evolutionary tree of the echinoderms.

Diversity:

Diploporitans first appear in the fossil record in Lower [Ordovician](#) rocks (485 million to 478 million years old) of the Prague Basin (now in the Czech Republic). These organisms quickly spread to ocean basins all over the world, becoming one of the most species-rich groups of blastozoan echinoderms (with an estimated nearly 200 species throughout the Ordovician Period). The majority of these taxa are found in fossil deposits in the United Kingdom, Scandinavia, Asia (especially China), northern Africa and southern Europe, with only a few examples found in North America. Although diploporitans show high species diversity, many of these Ordovician species are represented by a limited number of specimens. This means that every new diploporitan fossil greatly improves our understanding of their evolution, [palaeoecology](#) and [biogeography](#).

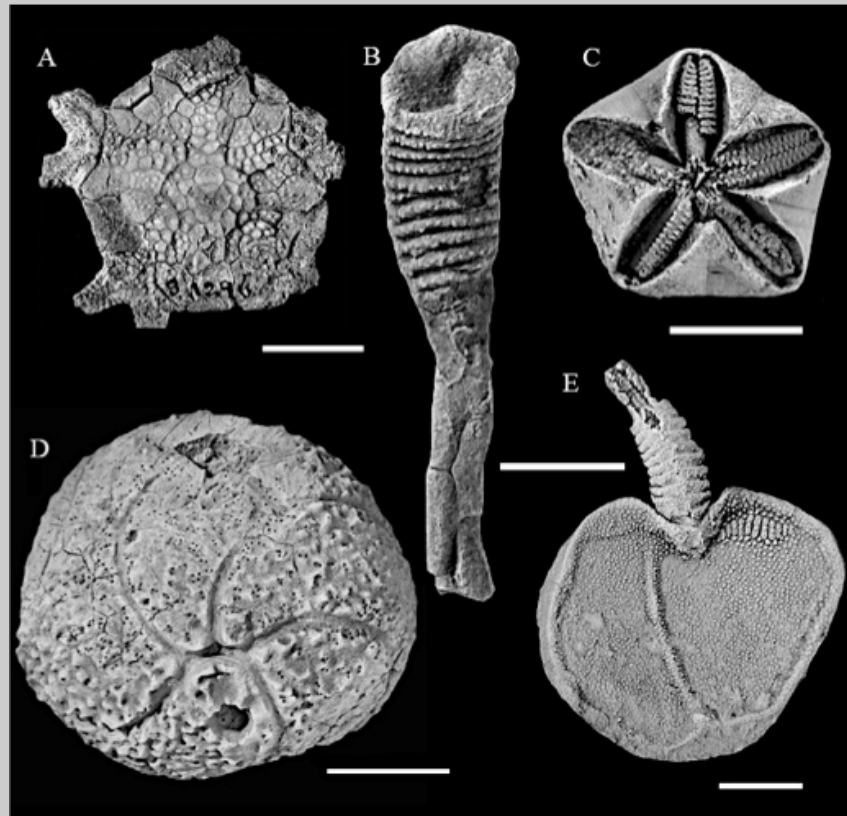


Figure 1 — Palaeozoic echinoderms show highly diverse body morphologies. A. *Marsupiocrinus stellatus* (Crinoidea; USNM S1296); modified from Kammer *et al.* (2013). B. *Minervacystis* sp. (Eocrinoidea, USNM 143); modified from Sumrall *et al.* (1997). C. *Troosticrinus reinwardti* (Blastoidea, CMCIP 67717); modified from Sumrall and Waters (2012). D. *Gomphocystites indianensis* (Diploporita, FMNH, 19708); modified from Sheffield and Sumrall (2017). E. *Cardiocystella prolixora* (Stylophora, 1791TX13); modified from Zamora *et al.* (2013). All specimens from localities in the United States. USNM, United States National Museum; CMCIP, Cincinnati Museum Center Invertebrate Paleontology; FMNH, Field Museum of Natural History; TX, University of Texas. Scale bars, 1 centimetre.

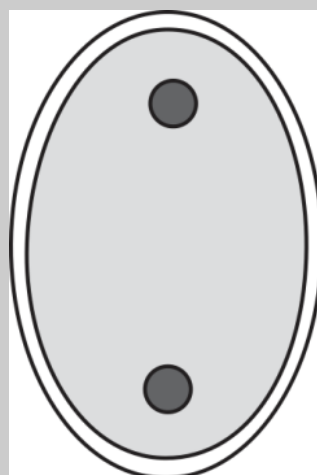


Figure 2 — A diagram of a diploporite respiratory structure. The two pores are connected by a non-mineralized tube, which is not generally preserved in the fossil record. These pores sit in a shallow depression (a peripore); multiple sets of peripores can exist on a single skeletal plate of a diploporite-bearing echinoderm (figure modified from Sheffield *et al.* 2017).

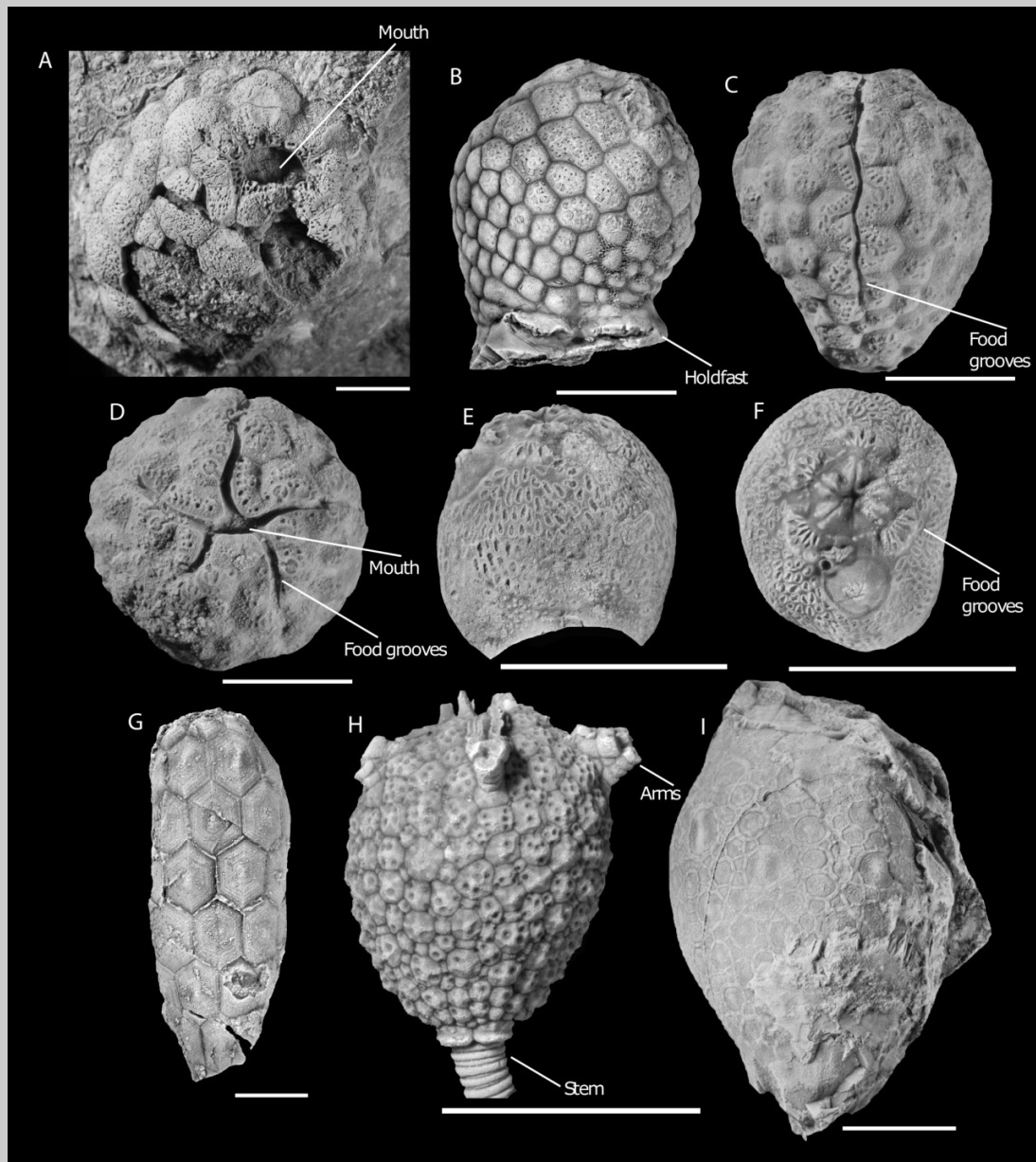


Figure 3 — A representative sample of diplopore-bearing echinoderm fossils. A. *Holocystites salmoensis* (Ordovician Anticosti Island, Quebec, Canada) with large mouth and short food grooves (GSC126899; modified from Sheffield *et al.* 2017). B. *Paulicystis sparsus* (Silurian, Indiana, USA) with buried diplopores that are exposed only if the fossil has been weathered (SUI 48164; modified from Sheffield and Sumrall 2017). C. Side view of *Estonocystis antropoffi* (Ordovician, Estonia), with long, relatively wide food grooves (GIT 540-80; modified from Sheffield and Sumrall 2019b). D. Top view of *Estonocystis antropoffi* (GIT 540-80; modified from Sheffield and Sumrall 2019b). E. Side view of *Haplosphaeronis* sp. (Ordovician, Estonia) with wide holdfast that would attach to a hard surface during life (GIT 540-3; modified from Sheffield and Sumrall 2019b). F. Top view of *Haplosphaeronis* sp. with short, branched food grooves (GIT 540-3; modified from Sheffield and Sumrall 2019b). G. *Holocystites cylindricus* (Silurian, Indiana) with an elongated and narrow shape (YPM 19175; modified from Sheffield and Sumrall 2017). H. *Eumorphocystis multiporata* (Ordovician, Oklahoma) with arm structures that come off the surface of the body and a stem, as opposed to a holdfast (SUI 97599; modified from Sheffield and Sumrall 2019a). I. *Amphoracystis irregularis*, a diploporitan without diplopores or other known respiratory structures (NM-L 13063; modified from Sheffield and Sumrall 2019b). GSC, Geological Survey of Canada; SUI, the University of Iowa; GIT, Geological Institute of Tallinn; YPM, Yale Peabody Museum; NM-L, Prague National Museum. Scale bars, 1 centimetre.

Most groups of diploporitans went [extinct](#) during the global ice age that marks the end of the Ordovician and the start of the [Silurian](#) Period (approximately 444 million years ago). Only a few survived, in isolated places. The most prominent of the diploporitan groups to survive this extinction are the holocystitids (informally known as the *Holocystites* Fauna; Fig. 3A,B), which are found in unusually high numbers across the midcontinent of North America (primarily Indiana, Ohio, Tennessee and Wisconsin) in middle Silurian rocks (approximately 430 million to 426 million years old). Apart from the holocystitids, there are only isolated occurrences of diploporitans in China, southern Europe, the United Kingdom, Australia and North America in the Silurian and [Devonian](#) Period (419 million to 359 million years ago), when the last few diploporitan species became extinct.

Morphology:

Diploporitans show extreme morphological variation. This includes differences in the structures of their food grooves, their body shapes, their respiratory structures and the structures they used to attach themselves to rocks. Some diploporitans have food grooves that are short, thin and completely contained in the mouth region of the body (Fig. 3A), whereas in others they are relatively wide, long and spiralled across the majority of the body (Fig. 3C,D) or branched into multiple grooves (Fig. 3E). Some species are globular (Fig. 3A,B,E,F), whereas others are narrow and thin (Fig. 3G). Most have holdfast attachment structures (Fig. 3A,B,E,F), which are thought to have secreted a substance that allowed the organism to attach and remain stuck to a particular surface in life, but others have stems that anchored them to the sediment (Fig. 3H). Finally, some groups, like *Holocystites*, have diplopores that have been modified and buried beneath a layer of calcium carbonate mineral, or [stereom](#), on skeletal plates (Fig. 3A,B), whereas others have lost the diplopores entirely (for example, *Amphoracystis*; Fig. 3I).

The recognition of these diverse features is the main reason that scientists traditionally placed diplopore-bearing taxa into three subgroups of Diploporita: Sphaeronitida, Glyptosphaeritida and Asteroblastida. However, these subgroups all contain creatures of many different forms, which is a strong indication that they are not closely related to one another. Moreover, the presence of diplopore respiratory structures in other groups of extinct echinoderms (such as *Thresherodiscus*, an edrioasteroid) suggests they should not be used to classify fossil forms into particular groups.

Phylogenetic relationships:

A recent study (Fig. 4) suggested that some groups of blastozoan echinoderms include both diploporitans and other, non-diplopore-bearing species. This indicates that Diploporita is not a [clade](#): not all forms traditionally assigned to this group evolved from a common ancestor. This evolutionary tree was constructed using carefully selected characteristics that reflect [homologous](#) skeletal elements (those that are inherited from a common ancestor) to avoid grouping different features into the same category (as an example, birds and pterosaurs both have wings; however, these wings are constructed differently and should not be considered the same character in a [phylogenetic](#) analysis). The tree also used well-preserved specimens that represent all the known morphological diversity in these echinoderms.

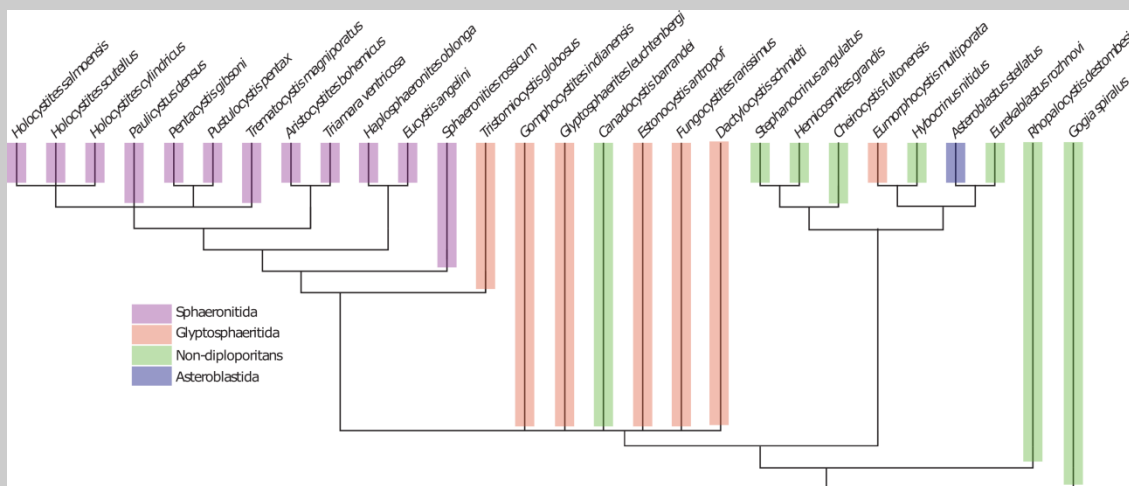


Figure 4 — An evolutionary tree of diplopore-bearing and non-diplopore-bearing echinoderms. It indicates that Diploporita is not a valid grouping of echinoderms, because its three groups (Sphaeronitida, Asteroblastida, Glyptosphaeritida) are not closely related and are polyphyletic. Overall, this analysis suggests that diplopore-type respiratory structures have re-evolved multiple times across Echinodermata. Sphaeronitida, purple; Glyptosphaeritida, tan; Asteroblastida, blue; non-diploporans, green (modified from Sheffield and Sumrall 2019).

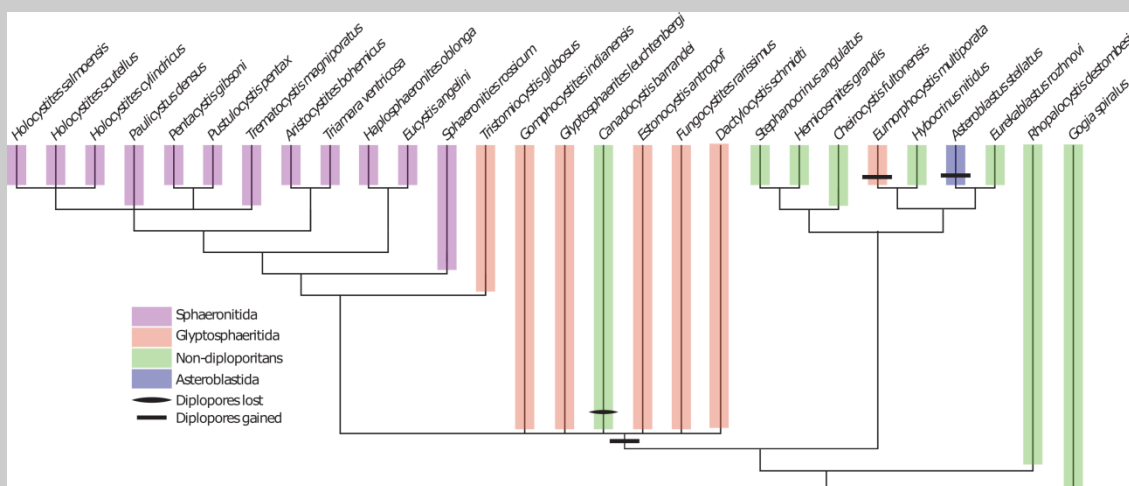


Figure 5 — A hypothesis of how many times diplopores may have evolved across diplopore-bearing echinoderms. This is based on the fewest number of changes (that is, the fewest number of times diplopores have been lost or gained); we hypothesize that there were three independent gains of diplopores and one loss across this tree. Further study will shed light on why diplopores re-evolved multiple times throughout echinoderm evolution (modified from Sheffield and Sumrall 2019).

The results indicate that diplopore-bearing echinoderms are [polyphyletic](#), meaning that they did not share a recent common ancestor, with diplopore respiratory structures evolving [convergently](#) in multiple separate lineages (Fig. 5). One of the original diploporitan groups does represent a clade: the Sphaeronitida (which includes the holocystitid group discussed previously). By contrast, the Glyptosphaeritida are scattered throughout the evolutionary tree of echinoderms, with one diplopore-bearing species (*Eumorphocystis*; Fig. 3H) most closely related to *Hyocrinus*, a crinoid. This suggests that *Eumorphocystis* is a transitional form between blastozoans and crinoids. Asteroblastida

(represented in this analysis by *Asteroblastus*) is found to be most closely related to another group of blastozoans, the parablestoids; however, because only one species of Asteroblastida was included in this analysis, it remains uncertain whether this is a valid group.

Evolutionary significance:

The polyphyletic grouping of diplopore-bearing echinoderms has important implications for understanding evolutionary pressures throughout the early Palaeozoic. The phylogenetic tree indicates that diplopore respiratory structures evolved multiple times across the echinoderm tree (Fig. 5), which begs the question: why? Why are these respiratory structures evolutionarily advantageous enough to appear multiple times in different groups? This question is difficult to answer, but a better understanding of how blastozoan echinoderms responded to changes in climate and the types of sediments present during the early Palaeozoic will probably help.

During the Ordovician, there were two climatic regimes: a warmer regime, which promoted the formation of carbonate-based rocks, near the equatorial regions of large portions of the supercontinent Laurentia; and a cooler regime, in which silicate-based rocks were more commonly formed, in the more polar regions of the supercontinent Gondwana. Further confounding these differences, there was an extreme rise in global sea surface temperature for a short time (termed the Boda Warming Event) just before the ice age at the end of the Ordovician. It is possible that diplopores evolved in response to changing pressures during this period in Earth's history. To fully characterize these changes, however, a comprehensive phylogenetic analysis of blastozoan echinoderms must be carried out. This work will have direct implications for understanding how modern echinoderms might respond to rapid climate change today, because they are similarly sensitive to changes in temperature, sedimentation and ocean acidity.

Suggestions for further reading:

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