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# The geological history of deep-sea colonization by echinoids: roles of surface productivity and deep-water ventilation

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The origins and geological history of the modern fauna of deep-sea echinoids is explored using a combination of palaeontological and molecular data. We demonstrate that, whereas generalist omnivores have migrated into the deep sea in low numbers over the past 200 Myr, there was a short time-interval between approximately 75 and 55 Myr when the majority of specialist detritivore clades independently migrated off-shelf. This coincides with a marked increase in seasonality, continental run-off and surface water productivity, and suggests that increasing organic carbon delivery into ocean basins was an important controlling factor. Oceanic anoxic events, by contrast, appear to have played a subsidiary role in controlling deep-sea diversity.

**Keywords:** biodiversity; deep-sea; echinoids; palaeo-productivity; ocean anoxia

## 1. INTRODUCTION

When scientific investigation of the deep-sea fauna began in the nineteenth century, the peculiar echinoderms discovered (e.g. stalked crinoids, flexible-tested echinoids) were seen as archaic hangovers from a much earlier age, and the deep sea became thought of as a refuge for lineages pushed off the continental shelf by superior competitors or predators. Although this view has persisted until quite recently (e.g. Tunnicliffe 1992), and is implicit in explanations advanced for the apparent onshore to offshore migration of marine benthos over time (e.g. Vermeij 1995), arguments have usually focused upon whether the deep-sea fauna is predominantly Mesozoic or Cenozoic in origin (Zenkevitch & Birstein 1960; Madsen 1961; Mirnov 1980; Wilson 1999) and whether global oceanic anoxic events (OAEs) prevented the establishment of the modern deep-sea fauna until the late Cretaceous (Jacobs & Lindberg 1998; Horne 1999).

Species richness in today's deep sea is comparable with, or even exceeds, that of shelf environments (Gray *et al.* 1997), but establishing when and how this diversity arose is not simple. Although oceanic cores provide a direct record of palaeo-biodiversity patterns for deep-sea meiofauna (e.g. Mognilevsky & Whatley 1996), much less is known about the origins and geological history of macrofaunal and megafaunal biodiversity in the deep sea. The diversity of deep-sea benthic groups such as echinoderms in the geological past cannot be measured directly because identifiable fossils are almost never retrieved from cores, and there are few unmetamorphosed, fossiliferous deep-sea deposits at outcrop (one notable exception being the early Miocene Morozaki Group of Japan in which a bathyal fauna of echinoderms and other taxa is preserved; Oji 2001). Deep-sea vent and cold-seep faunas have occasionally been preserved from the early Ordovician onwards, and show a marked increase

in taxic diversity during the Cretaceous (Little 2002; Little & Vrijenhoek 2003) but represent a highly specialized community.

The most direct evidence for the geological history of benthic diversity in the deep sea comes from trace fossils (e.g. Bottjer & Droser 1994; Wetzel & Uchman 1998), and burrow traces can record the presence of echinoids in the absence of body fossils (Smith & Crimes 1983). Although trace fossils indicate the presence of macrofauna in deep-sea environments from the Ordovician onwards, trace-fossil diversity increased markedly in the Upper Cretaceous (Crimes 1974; Seilacher 1974). This suggests that in geological terms, high deep-sea biodiversity may be a relatively new phenomenon.

Here, we combine evidence from calibrated phylogenetic trees and molecular clock estimates, to examine when the modern fauna of echinoids migrated into the deep-sea.

## 2. MATERIAL AND METHODS

For the purposes of this paper, an echinoid species is defined as part of the deep-sea fauna if its minimum depth range is greater than 500 m or its maximum depth range greater than 2000 m. There are 156 species (19% of all species whose depth is recorded) distributed among 66 genera that fit our criteria of 'deep-sea' taxa. These are widely distributed taxonomically (figure 1) and comprise 41 independent deep-sea clades (i.e. clades whose immediate sister taxon is not a deep-sea inhabitant). In terms of diet, these fall into two groups: generalist omnivores comprising echinoids with a lantern that feed on benthic organisms such as sponges and bryozoans, on seasonal macrophytal falls, or on meiofauna in or on the sediment (Young *et al.* 1993; Jacob *et al.* 2003), and surface phytodetritivores—echinoids lacking a lantern that harvest flocculated organic fluff from the sediment–water interface (Lauerman & Kaufmann 1998) or graze on surface sediment for its particulate organic content (De Ridder & Lawrence 1982).

We have used phylogenies calibrated against the known fossil record (see supplementary data) to bracket the time

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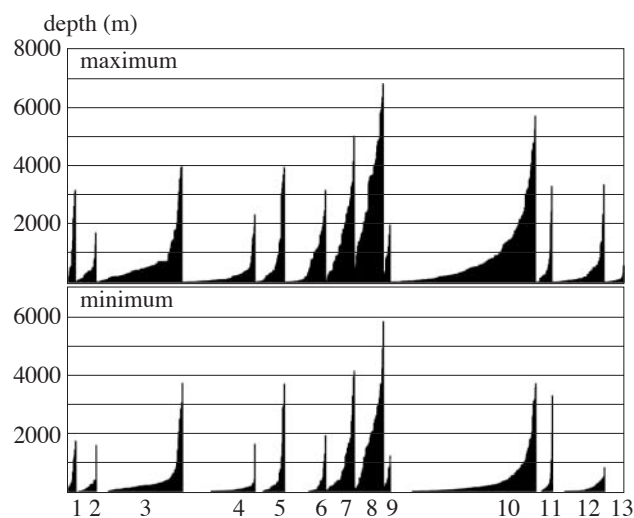


Figure 1. Maximum and minimum depths for 840 extant species of echinoids belonging to 13 major clades and plotted as cumulative curves. 1, Calycina; 2, Cassiduloida; 3, Cidaroida; 4, Clypeasteroida; 5, Diadematoidea; 6, Echinoida; 7, Echinothurioida; 8, Holasteroida; 9, Pedinoida; 10, Spatangoida; 11, Stirodonta; 12, Temnopleuroidea; 13, Toxopneustina. 8 and 10 are phytodetrivores, the others are generalist omnivores.

when 38 of these deep-sea clades moved off-shelf into the deep-sea environment as follows (the phylogenetic relationships of the other 3 remain poorly constrained):

- (i) the latest time by which a deep-sea lineage was established is set by the last occurrence of its sister group in sediments of shelf or upper bathyal environments. For example, the deep-sea *Aeropsis* has no fossil record, but its (plesiomorphic) sister group is *Sphenaster* (Stockley *et al.* 2005), which last occurs in an upper bathyal setting of the Danian age. As there are no subsequent records of *Sphenaster* in shelf or upper bathyal deposits, a deep-sea lineage is unlikely to have been established later than the Danian.
- (ii) A deep-sea lineage can be no earlier than the first occurrence of its shallow-water sister group. For example, there is one extant deep-sea species of *Echinus* today, although many species are present in shelf or upper bathyal habitats. In the absence of a reliable species-level phylogeny, the earliest fossil record of any species of *Echinus* in shallow water environments sets the lower bound on when the deep-sea lineage could have been initiated.

We have also used a penalized maximum likelihood approach to estimate divergence times for three taxa with bathyal distribution and little or no fossil record. This is based on a molecular phylogeny for 24 taxa of spatangoid (all detritivore), constructed from partial 28S rRNA 16S rRNA and COI gene sequences (see Stockley *et al.* (2005) for full details). To calculate divergence times of the bathyal taxa, we ran a relaxed variable rate likelihood model with non-parametric rate smoothing (Sanderson 2002) using five calibration points established from the fossil record of exclusively shallow water clades.

### 3. RESULTS

Figure 2 shows minimum and maximum estimates of time of origin for the 38 living deep-sea echinoid clades plotted

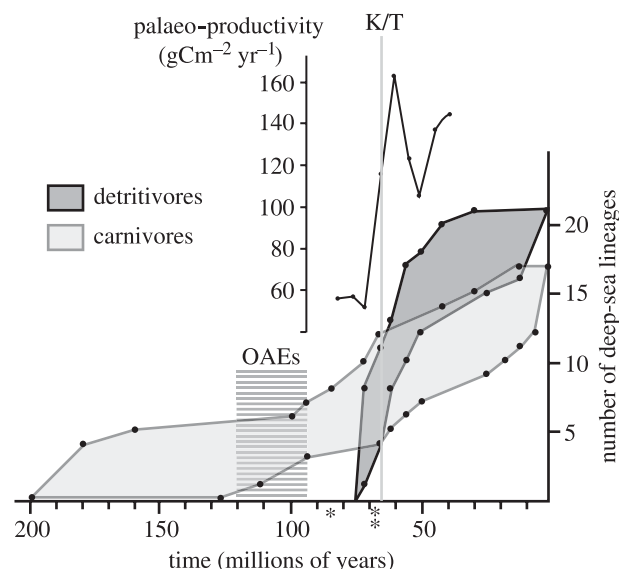


Figure 2. Cumulative frequency curves for maximum and minimum times of origin for 38 clades of extant deep-sea echinoid. Echinoids have been divided according to diet (17 clades of omnivorous and 21 clades of detritivorous echinoids). OAEs, Ocean Anoxic Events; periods when there was widespread development of anoxic bottom water conditions. Palaeo-productivity estimates for tropical Atlantic DSDP sites from 40 to 80 Myr taken from Handoh *et al.* (2003). \*, molecular estimates for time of origin of three lineages of bathyal detritivores. K/T=Cretaceous–Tertiary boundary.

as cumulative curves, and with detritivores distinguished from generalist omnivores. Whereas the modern fauna of deep sea omnivore lineages has appeared gradually over the last 150–200 Myr, detritivore lineages, by contrast, are no older than 75 Myr, even though they existed in shallow water environments since about 145 Myr. The majority of the modern deep-sea detritivore lineages were established by 50 Myr.

The divergence dates of the three bathyal spatangoid clades are estimated at between 65 and 85 Myr from the molecular data (figure 3).

### 4. DISCUSSION

#### (a) *Passive expansion into the deep or ecological trigger?*

Figure 2 can be considered as an age-frequency distribution for living deep-sea echinoids as estimated from the fossil record of shallow-water sister taxa. This of course tells us nothing about extinct clades of echinoids that might have previously colonized the deep sea. The trace fossil record clearly shows that deep-sea deposit feeders have existed since at least the Ordovician (Bottjer & Droser 1994). Indeed, the presence of disasteroids in deep-water alpine flysch deposits of latest Jurassic early Cretaceous age shows that at least one extinct echinoid clade of detritivores had exploited this environment in the geological past.

However, our data show that the two trophic groups making up today's deep-sea fauna have had different evolutionary histories. Before considering what biological significance this may have, we need to establish that this is a genuine pattern worth explaining.

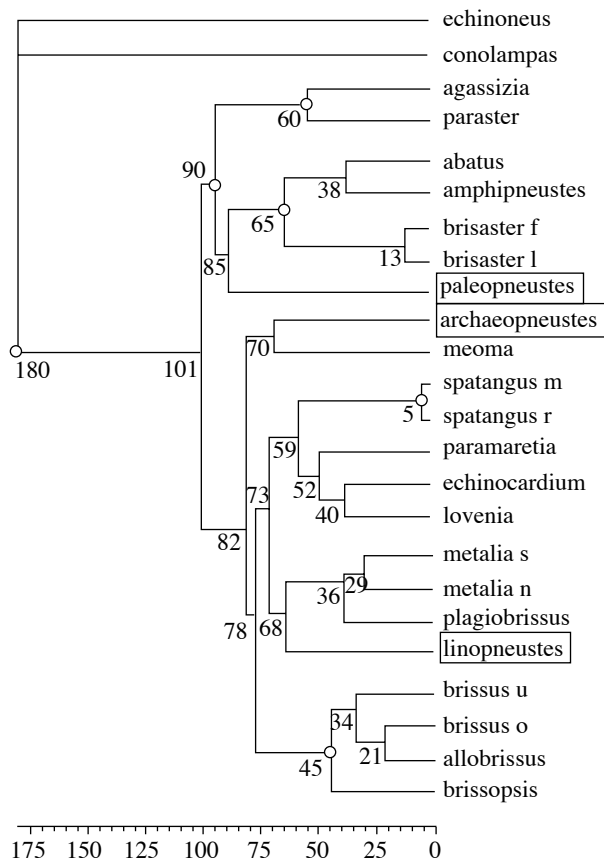


Figure 3. Calibrated phylogeny for 24 irregular echinoids with estimated divergence times based on a relaxed variable rate likelihood model<sup>(14)</sup> applied to a Bayesian tree constructed from combined 28S rRNA, 16S rRNA and COI partial gene sequences (data from Stockley *et al.* 2005). Open circles, nodes whose dates were treated as fixed, based on the fossil record of shallow-water taxa. The three taxa indicated by rectangles are the bathyal taxa with poor fossil record. Note that the immediate shallow-water sister taxon of the bathyal species has not necessarily been sampled and so the dates are likely to overestimate the time of origin of the deep sea lineage.

One complicating factor is that living deep-sea detritivore clades are, on average, younger than many of the living deep-sea omnivore clades. Just two of the 13 echinoid clades are detritivores (the Holasteroidea and Spatangoida; sister groups originating close to the base of the Cretaceous, approximately 145 Myr ago), whereas the oldest of the omnivore clades with deep-sea representatives dates from 260 Myr. So, does the pattern then reflect no more than a general trend for older clades to have had a longer time and thus more opportunity to give rise to multiple independent lineages in the deep sea? The answer to this seems to be very definitely no. There is no correlation between number of deep-sea lineages within a clade and its time of origin (figure 4), within the two detritivore clades, origins are not randomly distributed but peak concurrently, well after the initiation of either clade.

This, combined with the marked increase in deposit feeder trace fossils in the Upper Cretaceous, argues strongly against the observed pattern representing a passive expansion of one clade (Holasteroidea and Spatangoida) and suggests that some sort of ecological trigger was involved.

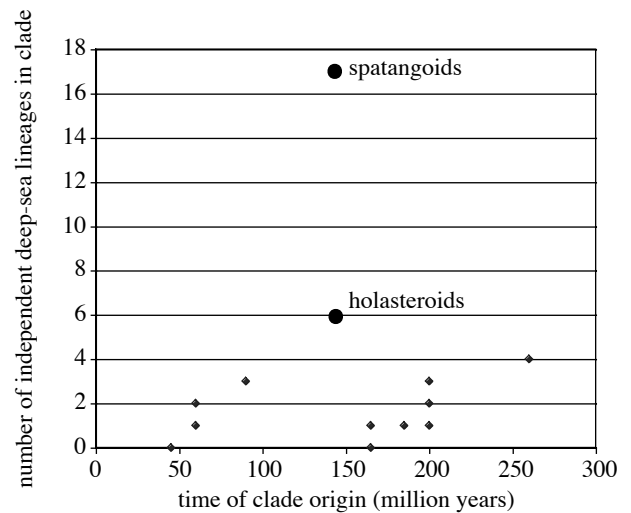


Figure 4. Time of origin plotted against number of independent deep-sea lineages for 13 major clades of echinoid (listed in Figure 1; see supplementary data). Large circles indicate the two detritivore groups; diamonds indicate omnivore groups.

### (b) What controlled faunal migration into the deep sea?

Two principal factors control whether megafauna can survive in deep bathyal to abyssal settings: nutrient levels and oxygen levels. Each needs to be considered.

It is clear that conditions in the early mid-Cretaceous deep sea were very different from those prevailing now. Bottom water temperatures were much higher and ocean venting much weaker (Bralower & Thierstein 1984; Norris *et al.* 2001). As a consequence, bottom dysoxic conditions arose relatively frequently in isolated oceanic basins during the Aptian to end Cenomanian period, and much of the deep ocean floor was presumably inhospitable to life (Jacobs & Lindberg 1998).

Some support for this comes from the sparse Mesozoic deep-sea echinoid data that we have. Latest Jurassic–early Cretaceous flysch sediments of the high Alps represent probable bathyal deposits and yield a sparse and low diversity echinoid fauna dominated by disasteroids, especially *Cardiolampas* (e.g. Ooster 1865). *Cardiolampas* is a detritivore that closely resembles modern deep-sea pourtalesiids and presumably followed a similar lifestyle. Disasteroids did not survive beyond the Albian, with only one taxon surviving beyond the Berriasian (*ca* 125 Myr). It is probably no coincidence that the decline and eventual extinction of this group coincided with a period of increasing ocean basin stagnation.

However, our data also indicate that a small number of deep-water clades survived OAEs. These are exclusively generalist omnivores, notably the Aspidodiadematidae and Echinothurioida. These are known from Jurassic continental shelf environments, but then disappear from the fossil record and are known today only from deep-water settings. This suggests that deep-water refugia existed through time.

Following the last global OAE at the end of the Cenomanian, approximately 93 Myr, interbasinal deep-water connections rapidly became established and mid- and deep-water ventilation intensified, leading to predominantly oxygenated oceans (Norris *et al.* 2001; Poulsen *et al.* 2001) in which abyssal benthic agglutinated

foraminifera diversified (Horne 1999). Yet there is no evidence that echinoid clades started moving into the deep-sea in marked numbers at this time. Other major oceanographic changes in deep-water circulation also fail to be reflected in our data. The end Palaeocene Thermal Maximum, which represents the last ocean basin stagnation event and which eradicated about 50% of deep sea benthic foraminiferans (Kennett & Stott 1991; Kelly 2002), was followed by a marked increase in deep sea venting possibly related to a first pulse of high-latitude glaciation (Norris *et al.* 2001), but this largely postdates the burst of origination among detritivorous echinoids. Similarly, the establishment of vigorous deep-water circulation with the development of the circum-Antarctic current in the early Oligocene generates no clear signal in the echinoid data. A significant change in deep-water ventilation patterns in the latest Cretaceous has been proposed (MacLeod 1994; MacLeod & Huber 1996), based on extinction of inoceramids and a marked increase in bioturbation fabrics. However, other workers (Corfield & Norris 1996; Frank & Arthur 1999; D'Hondt & Arthur 2002) dispute this. This lack of obvious correlation suggests that factors other than ocean bottom water ventilation triggered the pulse of echinoid migration into the deep-sea.

The second controlling factor is nutrient availability: the deep sea is a strongly food-limited environment (Graf 1992; Nees & Struck 1999). Nutrifaction of the oceans has been recognized as a driving factor in the evolution of life (Vermeij 1995; Martin 1996, 2003), and organisms will exploit food sources wherever they can. So, the elevated rate at which detritivore lineages moved into the deep-sea could be a response to increasing nutrification of the oceans.

The Maastrichtian-early Paleocene was a time of falling sea level and substantial mountain building (Gale 2000), and rising  $\delta^{13}\text{C}$  levels in the Paleocene indicate rapidly increasing burial of carbon (Faul *et al.* 2003). Major climatic changes were taking place with rapidly falling surface sea temperatures and a shift from arid to humid climates, while more vigorous upwelling and greatly increased run-off boosted inorganic nutrient input to the ocean basins (Gale 2000; D'Hondt & Arthur 2002; Handoh *et al.* 2003; MacLeod 1994). Palaeoproductivity doubled in parts of the Atlantic Ocean from 52 to 116  $\text{gC m}^{-2} \text{yr}^{-1}$  during the last 5 Myr of the Maastrichtian and rose further still between 65 and 55 Myr (Handoh *et al.* 2003). Faul *et al.* (2003) also found a relative rise in carbon export to the sea floor in the Maastrichtian and a peak at about 61 Myr in the western North Atlantic. They calculated that export productivity at that time was as high as is found today in modern equatorial upwelling zones. The late Cretaceous was also a time of rising levels of eukaryotic phytoplankton diversity (Falkowski *et al.* 2004) and a marked increase in burrowing activity in the deep sea (MacLeod 1994). Diatoms, which today are responsible for about half of the net carbon export to ocean interiors, show a small peak in diversity near the end of the Cretaceous, although their major rise to dominance did not take place until the end Eocene (Falkowski *et al.* 2004). Species diversity of benthic foraminifera doubled during the latest Cretaceous and remained high during the Paleocene (MacLeod *et al.* 2000). All of this indicates that a significant increase in palaeo-productivity was taking place in the latest Cretaceous-early Palaeogene oceans.

However, it may not just be the amount of organic material reaching the sea floor that is important, but also the delivery of that organic material that determines whether it is exploitable by megafauna. Nees & Struck (1999) identify four sources of organic material that benthic fauna can exploit. The most nutritional of these, and the one primarily exploited by detritivorous echinoderms (Lauerman & Kaufmann 1998; Beaulieu 2002), is generated by seasonal pulsed phytoplankton blooms and creates aggregates of fresh phytodetrital 'fluff' on the deep ocean floor. Pulsed fluff accounts for the majority of organic Carbon exported to the marine deep-sea benthos with diatoms primarily responsible for their creation (Beaulieu 2002). Evidence for increasing seasonality of climate in the latest Cretaceous comes from isotope data (Steuber 1996).

Macrofauna have probably always migrated into the deep-sea environment, but the coeval origin of many independent deep-sea lineages of detritivore echinoids between 75 and 55 Myr ago is unexpected and requires explanation. The striking difference in the history of deep-sea colonization by omnivore and phytodetritivore echinoids is compelling evidence that nutrification of the oceans over geological time has played a key role in driving deep-sea diversity through benthic-pelagic coupling (Graf 1992; Beaulieu 2002). It seems likely that increasing organic delivery into deep-sea environments in the late Cretaceous, driven by higher surface water productivity, made life more feasible for deposit feeders at depth and led to habitat expansion as macrobenthos tapped into this resource. This, together with the lack of evidence for older lineages preferentially moving into deep sea habitats, suggests that echinoids migrated into the deep sea to exploit newly available food sources, not to escape from 'superior' competitors or ever-more effective predators evolving in shallow water environments.

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