RAPID COMMUNICATION

Geological history of bathyal echinoid faunas, with a new genus from the late Cretaceous of Italy

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Abstract

The Scaglia Rossa of central and northern Italy yields a late Cretaceous bathyal echinoid fauna. Comparison with Jurassic and Cenozoic bathyal faunas highlights that (i) there have been at least three phases of colonization of bathyal settings from the continental shelves, with successive faunas replacing the earlier; and (ii) bathyal echinoid faunas encompass an increasing range of feeding strategies and greater diversity of taxa through time, paralleling increasing nutrification of the oceans. A new Santonian deep-sea spatangoid, *Bathyovulaster disjunctus* gen. et sp. nov., is described from sediments deposited at > 1500 m water depth at Gubbio, Umbria–Marche region, Italy.

Keywords: evolution, Atelostomata, spatangoids, deep sea, phylogeny

1. Introduction

Today the echinoid fauna found living at water depths greater than 1500 m is dominated by specialist deep-sea genera that are rarely encountered in shelf or even upper bathyal settings. The great majority of these echinoids belong to just a small number of clades: two irregular clades (spatangoids and holasteroids) and four regular clades (echinothurioids, aspidodiadematids, micropygids and cidaroids), as reviewed in Smith & Stockley (2005). The geological history of this deep-sea fauna is very poorly known, as the fossil record of echinoids is overwhelmingly that of the continental shelves with only the occasional upper bathyal fauna reported (e.g. Smith & Gale, 2009). Articulated macrofauna are unknown from deep-sea sediment cores and so current knowledge of the geological history of the truly deep-sea echinoid fauna has had to be pieced together from a combination of our knowledge of the shelf faunas and molecular clock studies (e.g. Smith, 2004; Smith & Stockley, 2005). This approach demonstrates that all the current deep-sea taxa belong to clades that have evolved in the last 250 Ma. While some of the regular echinoids now living in the deep sea clearly have a long history extending back to early Jurassic time, the irregular clades are undoubtedly more recent immigrants, as they only evolved during the Cretaceous period (Kroh & Smith, 2010).

The chalk facies that is so widely distributed in the late Cretaceous comprises hemipelagic deposits formed as open ocean settings flooded over the continental shelves, and provides a window onto faunas living at upper bathyal depths of a few hundred metres. However, truly deep-water settings over 1000 m water depth are particularly rare, and are preserved on land only in tectonic regions where back-arc basins have been uplifted or plate-to-plate collision has occurred. One of the best know of these is the Scaglia Rossa Formation of Italy.

2. The Scaglia Rossa Formation and its macrofauna

The Scaglia Rossa Formation is a deep-water deposit widely distributed across central and northern Italy. It is a pink to red pelagic limestone succession largely composed of calcareous plankton that ranges in age from Turonian to early Eocene. The succession in the Umbria–Marche region has been the focus of a great deal of attention, largely because of the important Bottaccione Section that encompasses the Cretaceous–Palaeogene boundary (see Alvarez, 2009). The beds here are considered to have been deposited at depths of well over 1000 m in a continental slope environment (Galeotti *et al.* 2002), in part under turbidity currents (Stow *et al.* 1984). While the magnetostratigraphy and micropalaeontology of the formation has been extensively studied (Lowrie & Alvarez, 1977; Monechi & Thierstein, 1985; Premoli Silva & Sliter, 1995; Alvarez, 2009), preservation of the microfauna is often poor and macrofauna are rarely encountered.

However, macrofossils have been reported from the Scaglia Rossa Formation, primarily from outcrops in the northeast of Italy (Trentino and Veneto provinces) (see Giusberti, Fantin & Buckeridge, 2005). Here a sparse deep-sea fauna of echinoids has been known since the early part of the nineteenth century when Catullo (1827) described a small number of irregular echinoids. The fauna was later reviewed and updated by Airaghi (1903, 1907, 1931), who recognized 16 species in total, all but two of them irregular echinoids. The two regular echinoids are cidaroids (*Cidaris pseudopistillum* Cotteau and *Tylocidaris clavigera* (Koenig)), both represented only by isolated spines and thus potentially allochthonous, transported from shallower water settings. Of the irregular echinoids, few have detailed stratigraphical data. *Lampadocorys airaghii* Lambert and *L. dallagoi* (Airaghi) are both recorded from the Maastrichtian of Padova province (Astolfi & Colombara, 2003; Giusberti, Fantin & Buckeridge, 2005, under the names *Stegaster sulcatus* and *S. dallagoi*). *Ovulaster protodecimae* Giusberti *et al.*, from the same province, is firmly dated as Danian (Giusberti, Fantin & Buckeridge, 2005). Of the remaining species, two (*Micraster massalongianus* Zigno and *Isopneustes lamberti* Airaghi)

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are based on internal chert moulds and are thus strictly speaking indeterminate. Three more (*Echinocorys vulgaris, Coraster* sp. and *Offaster pilula* (Lamarck)) have never been figured: the first is possibly a *Stenonaster* and the last may be synonymous with the genus described here. *Stenonaster tuberculata* (Desor), *Rispolia subtrigonatus* (Catullo), '*Cardiaster*' *dallagoi* Airaghi, *Micraster fastigatus* Gauthier, *Ovulaster zignoanus* Cotteau and *Scagliaster concava* Catullo are reasonably well known but all currently lack precise stratigraphic placement within the sequence.

These rather unusual taxa probably represent a truly deepwater community specialized for life in pelagic sediments at upper bathyal depth. However, all of these finds come from the northeastern region of Italy and are considered to have been deposited in water depths of maybe up to 1000 m (Giusberti, Fantin & Buckeridge, 2005). Here we describe a new genus of sea urchin from the Scaglia of the Umbria–Marche region, central Italy, where water depth is considered to have been considerably greater, at around 1500–2000 m (Galeotti *et al.* 2002).

3. The geological history of deep-sea echinoid faunas

Although palaeontologists only have very occasional glimpses of deep-water echinoid faunas through geological time, these provide a unique insight into how the deep sea came to be occupied. The oldest deep-water echinoid faunas are those from upper Jurassic and lower Cretaceous flysch deposits of the French and Swiss Alps (Ooster, 1865), and from a deep-water carbonate cold seep deposit in France (Gaillard, Neraudeau & Thierry, 2011). These yield rare tithoniid disasteroids belonging to two genera, *Tithonia* and *Corytha*. Tithoniids are an extinct group that has no extant descendants and whose latest record is from the Albian of Antarctica (Smith & Crame, 2012). While the subglobular shape and downward-facing mouth of *Corytha* suggests it was epifaunal and used its perioral tubefeet to select particles in feeding, *Tithonia* has an oral furrow leading to an anterior facing peristome, like many of the extant deepwater holasteroids, suggesting that, like them, it harvested flocculated detritus from the sediment layer.

By late Cretaceous time, disasteroids had become extinct and we find a different and slightly more diverse fauna of spatangoids and holasteroids living at bathyal depths in the Scaglia Rossa and in the upper Cretaceous and lower Palaeocene deep-water flysch deposits of northwestern Spain and the western Pyrenees (Smith *et al.* 1999). These faunas contain representatives of three guilds: generalist flat-based epifaunal deposit feeders (*Stenonaster* and *Scagliaster*), epifaunal detritus harvesters (*Stegaster*, *Lampadocorys* and *Rispolia*), and, for the first time, more or less infaunal deposit feeders (*Ovulaster*, *Sphenaster* and *Bathyovulaster*) that presumably harvested organic material from within the sediment.

The Recent deep-sea echinoid fauna contains yet another suite of novel taxa largely unrelated to the Jurassic or Cretaceous forms but occupying very similar niches. It is dominated by meridosternate holasteroids and several groups of spatangoids. Pourtalesiids, like disasteroids and stegasterids before them, have a well-developed funnel-like oral groove leading into the peristome and harvest flocculated organics from the surface of the sediment (Gage, 1987). Urechinids and Eurypatagidae lack such a funnel and are flat-based epifaunal tube-feet pickers of organic material, and hemiasterids are infaunal deposit feeders. This fauna was already present by Miocene time as shown by the Tatsukuroiso Formation in northwestern Honshu, Japan

(Kikuchi & Nikaido, 1985), where pourtalesiids have been recorded.

These rare glimpses of deep-sea echinoid faunas through time highlight two important evolutionary patterns. Firstly, there is little or no direct phylogenetic link between the irregular bathyal echinoids of the late Jurassic, late Cretaceous–earliest Paleocene and Neogene to Recent (Fig. 1). This implies at least three phases of colonization from the continental shelves. As the latest disasteroids are Albian in age (Smith & Crame, 2012), and latest stegasterids are Maastrichtian (Smith & Kroh, 2012), it is likely that the Cenomanian–Turonian microplankton crash (Leckie, Bralower & Cashman, 2002) and end Maastrichtian crash (Gallagher, 2002; Smith & Jeffery, 1998) are the two major shapers of the deep sea. Life in bathyal settings is much more precarious than on the shelf, as it is dependent primarily on the rain of flocculated organic material that is generated by surface water productivity (Rex *et al.* 2005). The amount of organic material reaching the sea floor decreases as depth and distance from land increase and is seen as a key limiting factor of abyssal biodiversity (Rex *et al.* 2005). Any serious curtailment or interruption of this supply, as for example created by crashes in surface water productivity, would have had a devastating effect on bathyal echinoid faunas.

Secondly, although based on only a small sample, an increasing range of feeding strategies and greater diversity of taxa inhabiting bathyal environments is apparent through time. This correlates with increasing nutrification of the deep sea (Martin, 1996, 2003; Falkowski *et al.* 2004; Smith & Stockley, 2005; Martin, Quigg & Podkovyrov, 2008; Cardenas & Harries, 2010). The implication from echinoids is that nutrient supply to bathyal depths in late Jurassic time had reached sufficient levels to sustain epifaunal harvesters. By late Cretaceous time, nutrient levels in the sediment had risen further to support infaunal deposit feeders. Finally, coincidental with a massive diversification of diatoms in Neogene time (Falkowski *et al.* 2004; Martin, Quigg & Podkovyrov, 2008), which resulted in better delivery of organics into the deep-sea environment (Beaulieu, 2002), the deep sea was colonized by irregular echinoids in ever-greater numbers.

4. Systematic palaeontology

Order SPATANGOIDA Agassiz, 1840
Family OVULASTERIDAE Lambert, 1896
Genus *Bathyovulaster* nov.

Type species. *Bathyovulaster disjunctus* sp. nov.

Diagnosis. Ovulasterid spatangoid lacking an anterior sulcus; apical disc ethmophract and ambulacra apetaloid. Labral plate separated from sternal plates by ambulacral plates I.b.2 and V.a.2; sternal plates asymmetric.

Description. As for species, see below.

Remarks. The presence of an ethmophract apical disc in *Bathyovulaster* shows it to be a spatangoid, and readily distinguishes it from the somewhat similarly shaped holasteroid *Offaster*. Spatangoids with a disjunct plastron are extremely rare, with only some late-stage micrasterids (*Gibbaster norfolkensis* Smith & Wright) and rare maretiids (*Homolampas* Agassiz) showing this pattern. Both are easily differentiated from *Bathyovulaster*. Maretiids have a completely different test shape, being flat-based, and bear large primary tubercles and spines over their upper surface, while micrasterids have well-developed petals and a more compact apical disc plating. The new genus is very like
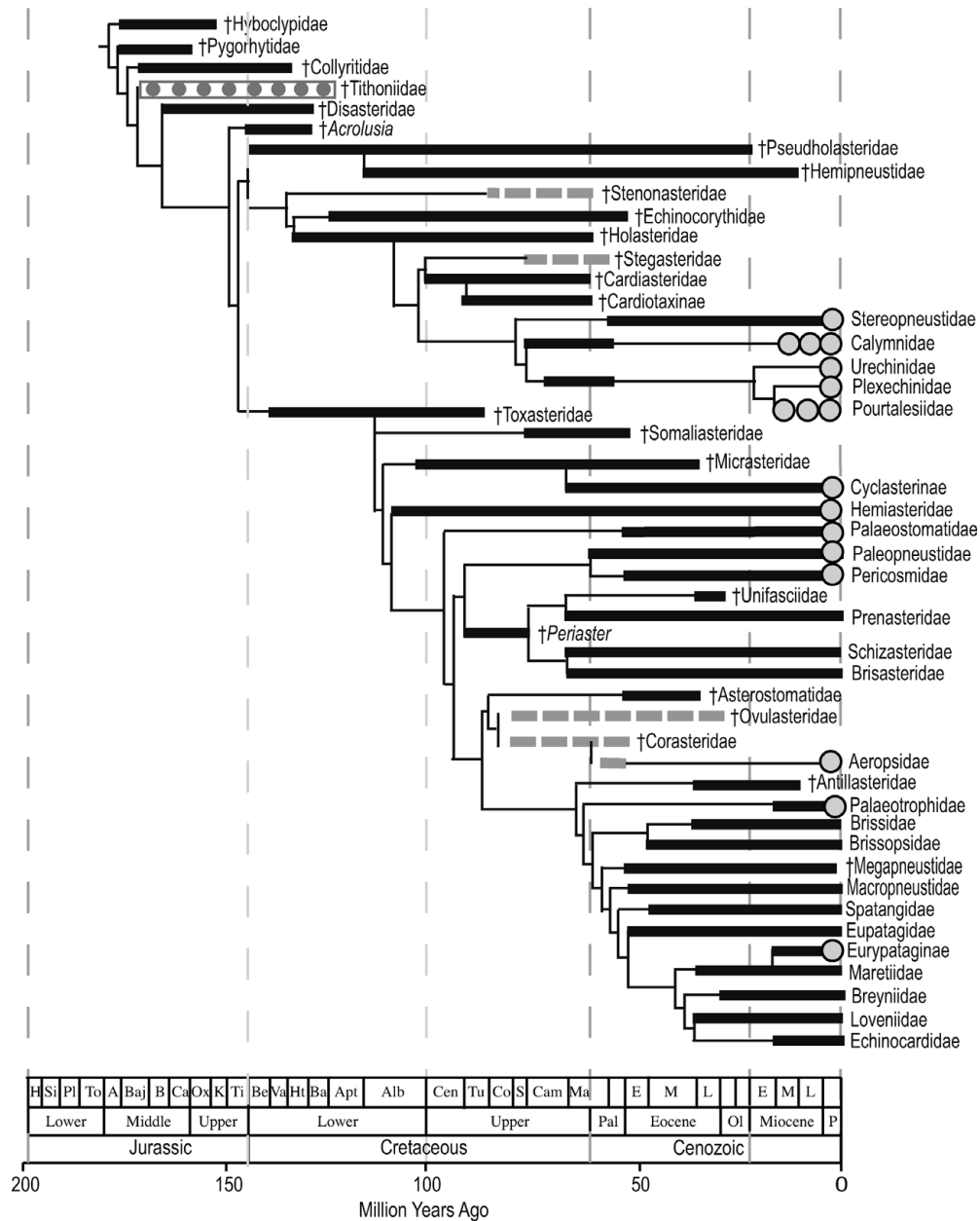
Figure 1. Phylogeny of post-Palaeozoic atelostomate echinoids calibrated against the fossil record (modified from Kroh & Smith, 2010) highlighting the lack of phylogenetic continuity of the three deep-water echinoid assemblages recognized here. Families that include exclusively deep-water taxa are indicated by dashed lines and filled circles. Abbreviations as follows: A – Aalenian; Alb – Albian; Apt – Aptian; B – Bathonian; Ba – Barremian; Baj – Bajocian; Be – Berriasian; Ca – Calovian; Cam – Campanian; Cen – Cenomanian; Co – Coniacian; E – Early; H – Hettangian; Ht – Hauterivian; K – Kimmeridgian; L – Late; M – Middle; Ma – Maastrichtian; P – Pliocene/Pleistocene; Pal – Paleocene; Pl – Pliensbachian; Ol – Oligocene; Ox – Oxfordian; S – Santonian; Si – Sinemurian; Ti – Tithonian; To – Toarcian; Tu – Turonian; Va – Valanginian.

Ovulaster Cotteau, both having a similar subglobular shape and a lack of petals, but is immediately distinguished from that taxon by its disjunct plastron.

Bathyovulaster disjunctus sp. nov.
Figures 2, 3

Types. Holotype and only known specimen. NHM EE112345.

Occurrence. Scaglia Formation, Santonian–lower Campanian, upper Cretaceous, river cliff beside the restaurant in Botticcione Gorge, Gubbio, Umbrian Apennines, Italy (43° 21′ N, 12° 24′ E).

Diagnosis. Test tumid with a faint anterior sulcus. Apetaloid, with aboral ambulacral plates large and polygonal; two to

each interambulacral plate. Periproct slightly invaginated and opening on the posterior face. Plastron disjunct, with labral and sternal plates separated by a pair of ambulacral plates.

Description. Test ovate in outline with rounded anterior and widest point anterior of centre; tapering to a rounded point posteriorly. Length 23.0 mm, width 19.1 mm (83 % of length). In lateral profile with a flattened lower and upper surface; tallest point coincident with apex of ambulacrum III, anterior of centre. Anterior rounded in lateral profile and posterior subvertical. Apical disc large and anterior-posteriorly elongate, ethmophract with four large genital plates each with a small subcentral gonopore (Fig. 3a). Ocular plates II and IV small and not abutting; posterior paired
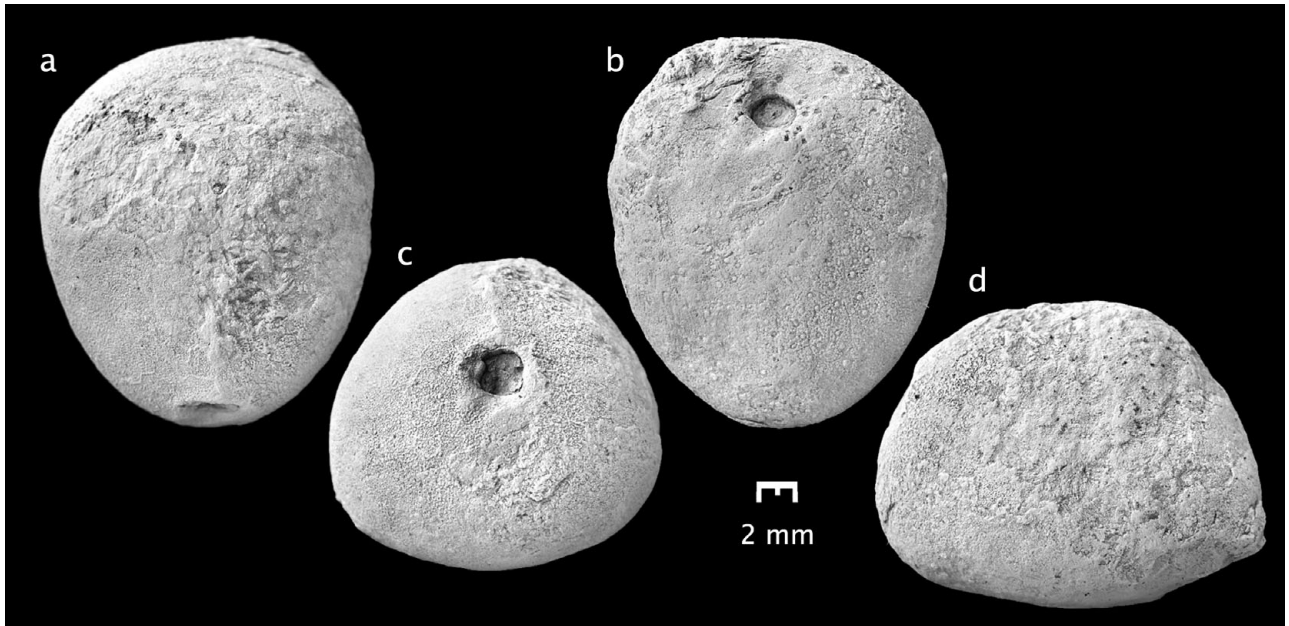
Figure 2. *Bathyovulaster disjunctus* gen. et sp. nov. NHM EE112345 (holotype); Santonian, Botticcione Gorge section, Umbrian apennines, Italy. (a) Apical; (b) oral; (c) posterior; (d) lateral views.
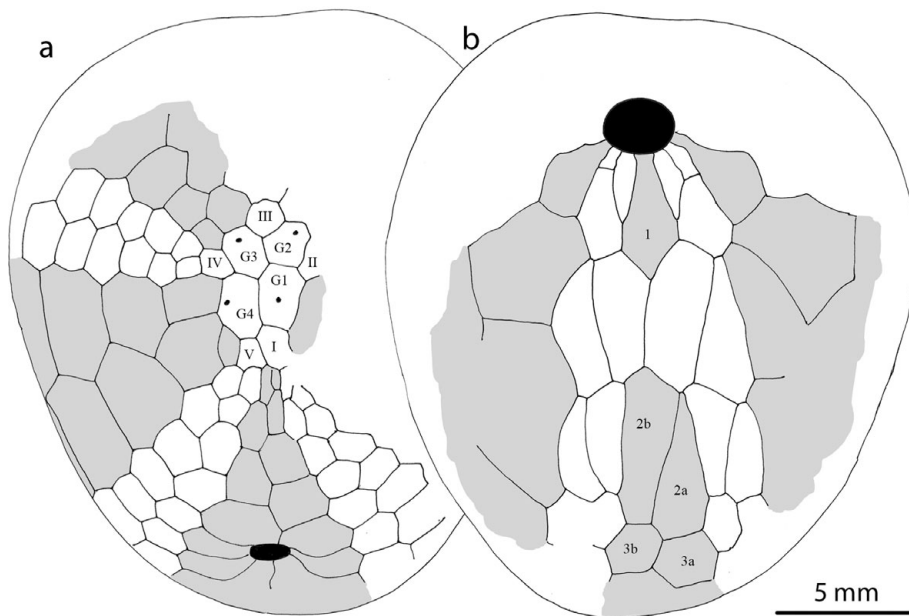

Figure 3. *Bathyovulaster disjunctus* gen. et sp. nov. NHM EE112345 (holotype); Santonian, Botticcione Gorge section, Umbrian apennines, Italy. Camera lucida drawings of (a) adapical and (b) adoral test plating.

ocular plates abutting. Genital plate 2 with relatively few hydropores.

Ambulacra apetaloid, composed of relatively large polygonal plates; pores microscopic on aboral and ambital plates. Two ambulacral plates for each interambulacral plate. At ambitus, ambulacra are approximately half the width of the interambulacral zones. On oral surface, plates large and elongate (Fig. 3b). In posterior ambulacra, second ambulacral plates meet behind the labral plate and separate labral plate from sternal plates. Interambulacral plates large and polygonal aborally. On oral surface plating is meridosternous and contiguous in interambulacra 1 and 4 and meridosternous and disjunct in interambulacrum 5. Sternal plates paired but with an oblique median suture, followed by small, biserially-offset episternal plates.

Peristome circular and 2.5 mm in diameter; positioned 3.4 mm from the anterior border; downward facing and without an anterior sulcus. Periproct 2 mm tall, subcircular and slightly invaginated around its lower half; positioned 9.3 mm above base in posterior view (opening subcentral).

Surface of plates where preserved shows a fine reticulate ornament and fine tubercles. Unfortunately, the test is too worn to tell if fascioles were present either marginally or subanally.

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