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Miocene *Clypeaster* from Valencia (E Spain): Insights into the taphonomy and ichnology of bioeroded echinoids using X-ray micro-tomography

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ABSTRACT

Taphonomic analysis and X-ray micro-tomography (μCT) were applied to *Clypeaster* specimens from the Miocene of Fuente del Jarro (Valencia, Spain). This enabled the identification of various preservational features, including encrustation, bioerosion, abrasion and post-depositional cracking. Approximately 15% of the studied specimens were affected by encrusters and/or borers. Of particular interest was a single intensely-bored specimen preserving numerous cross-cutting bioerosion structures. These structures exhibit a distinctive morphology consisting of clavate or flask-shaped chambers with a circular to oval cross-section, a narrow neck region near the figure-of-eight-shaped aperture and a chimney extending outside the *Clypeaster* test. The excellent preservation and characteristic morphology, as revealed by the μCT scan, coupled with the observation that (in some cases) articulated bivalve shells are still present within the chambers, allows for the identification of the tracemaker as the boring bivalve *Rocellaria*, reaffirming these tube-dwelling animals as borers, burrowers and crypt-builders. The trace fossils described herein are semi-endoskeletal dwellings, representing a combination of bioerosion through the plates of the echinoids, bioturbation in the form of burrowing into the sediment infill of the *Clypeaster* specimen and carbonate secretion resulting in a crypt. The morphologies of the different dwellings are influenced by the limited available space within the echinoid tests. This study confirms the importance of the relatively stable and thick *Clypeaster* shells as benthic islands in Cenozoic sandy littoral settings. The high degree of multiple colonizations, as well as the uniform orientation of the burrows, suggests a long-term stable position of this secondary substrate at or near the sediment surface.

1. Introduction

Settlement is a critical stage in the development of many benthic marine invertebrates, which can strongly influence the structure and ecology of adult populations. Taxa are adapted for the colonization of different substrates – such as soft sediments or hard surfaces like rocks, wood and the skeletons of living and dead organisms – with larvae settling in response to a range of biological, chemical and physical cues (e.g., Schäfer, 1972; McKinney and Jackson, 1989; Goldring, 1999; Savazzi, 1999; Glover et al., 2013). Finding a suitable substrate is therefore key to survival; for example, the availability of skeletal remains in environments with soft substrates can promote their use as benthic islands by epibionts (encrusters) and endobionts (borers). This type of behaviour can also be inferred in the fossil record, and there is ample trace-fossil evidence of post-mortem colonization of skeletal remains (e.g., Kauffman, 1978; Mitrović-Petrović, 1984; Martinell et al., 1986; Riba-Viñas and Martinell, 1986; Nebelsick et al., 1997; Muñiz et al., 2010; Belaústegui et al., 2012a, 2012b, 2013; Boessenecker, 2013).

The study of fossilized epibionts is typically straightforward as they are exposed on the surfaces of encrusted substrates. Describing the geometry of endobiont traces, however, as well as identifying the tracemakers and elucidating their colonization history, can be problematic because the fossils are normally only observed from the exterior, or from two-dimensional cross-sections. X-ray micro-tomography (μCT) and computer-aided visualization can potentially help address this issue; previous work has demonstrated that this approach is a powerful tool for non-destructively imaging trace fossil–body fossil associations in three dimensions (Lin et al., 2010). Here, a highly-colonized *Clypeaster* fossil from the Fuente del Jarro outcrop is digitally reconstructed in order

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to elucidate the relationship between the hard substrate (echinoid test) and the boring endobionts (bivalves). In addition, the taphonomy of additional *Clypeaster* specimens from the same outcrop is described. This enables: 1) detailed description of the traces produced by boring and burrowing; 2) identification of the colonizing animals to the genus level; 3) reconstruction of the colonization history of the echinoid by the associated bivalves; and 4) analysis of the taphonomic processes that affected both the echinoid skeleton and its endobionts.

1.1. Morphology and taphonomy of Clypeaster

Clypeaster is a relatively large, thick-shelled, irregular echinoid, which possesses a highly differentiated external surface and internal morphology (see Mortensen, 1948; Durham, 1966; Mooi, 1989; Mihaljević et al., 2011 for details of the test and its appendages). The genus is common in both carbonate- and siliciclastic-dominated Neogene sediments (e.g., Mitrović-Petrović, 1984; Rose, 1984; Rose and Poddubiuk, 1987; Kroh and Nebelsick, 2003, 2010; Santos and Mayoral, 2008; Belaústegui et al., 2012b, 2013; Mancosu and Nebelsick, 2013, 2015). The taphonomy of *Clypeaster* has been studied using actualistic approaches (e.g., Nebelsick and Kampfer, 1994; Nebelsick, 1999, 2008), as well as through the analysis of fossil material (e.g., Nebelsick, 1999; Belaústegui et al., 2012b, 2013; Mancosu and Nebelsick, 2013), and this has revealed that it is affected by a range of different taphonomic processes. The decay of soft tissue leads to the loss of all spines, as well as other isolated calcareous elements embedded within soft tissues. The internal jaw apparatus – which is attached by a series of auricles that surround the peristome – also disarticulates post-mortem, but due the relatively large size of some of its elements, the remains can still be found within fossilized tests.

The skeletons of denuded *Clypeaster* are restricted to the ambulacral and interambulacral plate rows and the apical disc. The surface of the test is characterized by: 1) ambulacral pores of the respiratory tube feet as found in the petals, as well as accessory pores associated with podia; 2) differentially sized tubercles to which the primary and smaller miliary spines were attached; 3) holes in the apical disc including gonopores and hydropores; 4) simple, straight food groves on the oral side of the test; and 5) relatively large openings of the peristome and periproct.

1.2. Clypeaster from the Neogene of Spain

A large number of nominal species of *Clypeaster* have been described from the Neogene of the Mediterranean basin and neighbouring areas. The difficulties of distinguishing species of *Clypeaster*, as summarized by Rose and Poddubiuk (1987), include: 1) widely differing species concepts; 2) substantial morphological variation within populations (ecophenotypes); 3) the limited number of structural innovations; 4) rarely discernible gradual phyletic change; and 5) the fact that adaptive strategies are commonly repeated. Nominal differences in species are thus based on somewhat equivocal features which are not always preserved in fossil specimens, including test size and profile, test outline along the ambitus and in cross-section, petal characteristics, periproct position and tuberculation.

As in other Mediterranean areas, a large number of different Neogene *Clypeaster* species have been described from parts of Spain, including several historical monographs as well as more recent publications. Several species included in the *Clypeaster* monograph of Michelin (1861) are reported to occur in Spain. Lambert (1907) describes seven different species of *Clypeaster* from the Miocene of Catalonia and Menorca. This list was expanded by Lambert (1927) to 13 species, ranging from flattened to highly-domed forms with inflated petals. *Clypeaster* occurring in Spain were also reported (among a total of some 120 species) from the Mediterranean and adjoining basin by Cottreau (1914). Montenat and Roman (1970) incorporated 20 different species from Neogene deposits of Spain into seven groups, acknowledging the difficulties of identifying morphologically divergent forms when using a strict typological species concept. In addition, Bajo Campos (2002) described seven species from the upper Miocene of the Guadalquivir Basin.

A few publications have discussed facies distributions and the taphonomy of *Clypeaster* from the Spanish Neogene. Néraudeau et al. (1999, 2001) and Rose and Wood (1999) described the distribution and palaeoecology of different species from the upper Miocene of the Sorbas Basin (SE Spain). In these publications, the highly-domed *Clypeaster altus* is reconstructed as an epibenthic feeder similar to the recent *Clypeaster rosaceus*, while the flattened *Clypeaster marginatus* is compared to the endobenthic burrowing *Clypeaster subdepressus* and *Clypeaster humilis*. Santos and Mayoral (2008) described and interpreted the intense encrustation of a single, highly-domed Miocene *Clypeaster* specimen from the Guadalquivir Basin by balanid barnacles. Finally, Belaústegui et al. (2012b) described the environment of deposition and taphonomy of clypeasteroids including *Clypeaster* from accumulations from the Miocene of NE Spain, while Belaústegui et al. (2013) described in detail the occurrence of *Clypeaster* tests as benthic islands for gastrochaenid bivalve colonization.

2. Geographical and geological setting

The study area is located within the Valencia region, Spain, in the east of the Iberian Peninsula (Fig. 1A). The Fuente del Jarro outcrop (named for a nearby industrial park) is situated on the shoulder of the A-7 highway at the north of the municipality of Manises, very close to the city of Valencia (39°30′47.65″N/0°28′54.74″W; Fig. 1B). Miocene marine sediments around the city of Valencia, Spain, were first described almost a century ago (Gignoux, 1922), but their fossil content remains poorly documented (although see Usera, 1972, 1974 and Acuña, 1978 for studies of fossil foraminifera and molluscs, respectively). Among the known outcrops, Fuente del Jarro is particularly noteworthy for the abundance of well-preserved echinoids and oysters. The unusually good preservation of the fossils from this outcrop makes it potentially ideal for detailed taphonomic and ichnological studies, which could inform on the palaeoenvironment.

This area is situated in the southern part of the Iberian Cordillera (Fig. 1A). Anadón et al. (2004) described two groups of Cenozoic Basins in this cordillera: 1) 'basins of the Paleogene cycle' (Paleocene to lower Miocene), characterized by synclines and filled with continental sediments; and 2) 'basins of the Neogene cycle' (Miocene to Pliocene), comprising mostly continental deposits, except in those parts closer to the Mediterranean coastline where marine deposits also occur. Sedimentary rocks from the Fuente del Jarro outcrop are part of the marine Miocene fill of the 'Valencian Coastal Depression' (Anadón et al., 2004), which belongs to the second of these groups. Marine deposits from this depression are in turn part of the southern onshore sector of the Valencia Trough ('Catalan–Valencian Domain'), an extensional system developed during the latest Oligocene and Miocene between the eastern part of the Iberian Peninsula and the Balearic Islands (Fontboté et al., 1990; Roca et al., 1999) (Fig. 1A).

The marine sediments close to the city of Valencia consist mainly of sandstones and calcareous mudstones with intercalations of bioclastic limestones, and are Tortonian in age (Gignoux, 1922; Alonso Pascual and García Rodrigo, 1954; Usera, 1972, 1974; Acuña, 1978; Acuña et al., 1979). The Fuente del Jarro outcrop exposes a 20 m section of shallow marine sandstones and marls (Fig. 1C). The base of the sequence is a horizontally laminated marl with a high content of mollusc fossils (mainly gastropods and bivalves). The contact with the overlying sediments is marked by an erosive surface. The 5-m-thick unit above consists of intercalations of fine-grained sandy units and cemented fine-grained sandstones, with invertebrate fossils consisting mainly of oysters, but also cirripeds, gastropods and rare occurrences of the sand dollar *Amphiope* and callianassid crustaceans, as well as vertebrate remains (osteichthian and selachian teeth and sirenian bones). The next