



Palaeoecology and taphonomy of spatangoid-dominated echinoid assemblages: A case study from the Early-Middle Miocene of Sardinia, Italy



Andrea Mancosu^{a,*}, James H. Nebelsick^b

^a Dipartimento di Scienze Chimiche e Geologiche, Università degli studi di Cagliari, Via Trentino 51, 09127 Cagliari, Italy

^b Institut für Geowissenschaften, Universität Tübingen, Sigwartstraße 10, D-72076 Tübingen, Germany

ARTICLE INFO

Article history:

Received 17 September 2016
Received in revised form 28 November 2016
Accepted 29 November 2016
Available online 3 December 2016

Keywords:

Spatangoids
Sublittoral environments
Infaunal tiering
Preservation potential
Bioturbation

ABSTRACT

The Early-Middle Miocene marine sedimentary succession of the Borutta Formation cropping out at Porto Torres (northern Sardinia) represents one of the most diverse and well-preserved spatangoid-dominated sedimentary successions in the Miocene of the Mediterranean area. The echinoid-bearing succession is studied with the two-fold purpose of firstly reconstructing the palaeoenvironmental setting in which these echinoids occurred, and secondly investigating factors influencing the preservation potential of spatangoid echinoids in the fossil record. These goals are accomplished by 1) detailed logging of sedimentary facies, 2) applying functional morphological interpretations of echinoid skeletons in order to reconstruct their behaviour and life habits, 3) quantifying the relative abundance of taxa and taphonomic features of test preservation, and 4) analyzing associated trace fossils within the beds.

The sedimentary succession is composed mainly of fine-grained sandstones which are intensely bioturbated by *Thalassinoides*-like burrows. Spatangoid abundance is high throughout the profile declining only in intercalated dm-thick rhodolith beds. A 20-cm-thick bed with a bedding surface of approximately 250 m² was investigated in detail with respect to relative abundance of spatangoid taxa and taphonomic signatures. The echinoids consist almost exclusively of deposit-feeding irregular forms with a dominance of the spatangoids *Ova* and *Brissopsis* and the minute clypeasteroid *Echinocyamus*. The spatangoids *Opissaster*, *Holanthus*, *Metalia* and *Hemipatagus* as well as the clypeasteroid *Clypeaster marginatus* are also present.

A low energy, moderately deep, outer sublittoral environment with high rates of bioturbation and episodes of sediment deposition by storms is inferred. Interspecific competition among deposit-feeding echinoids appears to be limited by their different burrowing depths, feeding strategies and resource partitioning. The gregarious behaviour of spatangoid echinoids, their habitat in quiet, deeper environments and episodes of rapid deposition seem to represent the main factors leading to this spatangoid-bearing deposit. Since both shallow- and deep-burrowing spatangoid echinoids are well represented as complete specimens, mode of life does not appear to play a major role in their preservation potentials.

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1. Introduction

Spatangoids are the most highly diversified of all extant echinoid orders (Ghiold, 1989). They evolved in the Early Cretaceous and underwent a major diversification in the Cenozoic resulting in a rich fossil record (Villier et al., 2004; David et al., 2009). Spatangoids inhabit a wide spectrum of marine environments from littoral to abyssal depths (Stockley et al., 2005). They are predominantly infaunal, burrowing to various depths in different types of sediments.

Spatangoid echinoids show a wide variety of test shapes, ranging from globular to flattened to wedge-shaped, and display numerous morphological features closely linked to their distinctive infaunal habitats and associated burrowing mechanisms (Nichols, 1959; Gibbs, 1963; Smith, 1980b; Kanazawa, 1992; Saitoh and Kanazawa, 2012; Walker and Gagnon, 2014). Depth of burrowing can vary even within a species depending on numerous factors including test size, rate of movement, nature of the sediment (grain size and permeability), water temperature and energy, spawning period and gonadal ripeness, and even time of day (Chesher, 1969). Some burrowing species, such as *Brissopsis lyrifera*, emerge for feeding when abundant particulate organic matter is present on the sea floor (Hollertz, 1999). The ability of several lineages for burrowing deeply into the sediment is a key factor for their evolutionary success as they exploited new food resources as well as

* Corresponding author at: Via Doria 33, 09025 Sanluri, Italy.
E-mail addresses: andrea.mancosu@gmail.com (A. Mancosu), nefelsick@uni-tuebingen.de (J.H. Nebelsick).

benefitting from reduced competition and predation (e.g. Saucède and Villier, 2005).

Most spatangoids possess a dense coat of highly differentiated spines. Various types of fascioles are also present which generate water circulation within their burrows to assist in both respiration and elimination of excretory wastes. In addition, fascioles produce a mucus sheet that stabilizes the burrow walls helping to prevent fine-grained sediment from falling in between the spines and blocking the respiratory tube feet. Deeply sunken ambulacra which also prevent sediment contact to respiratory tube feet. Furthermore, those forms living in fine, impermeable sediments use their adapical tube-feet in the frontal ambulacrum to construct a respiratory funnel. The general change of form within evolutionary lineages leads to widely differing plate sizes and morphologies especially with respect to the expanded oral plastron plates. The frontal, anterior and posterior paired ambulacra often show distinctly different morphologies with respect to length, indentation, and ambulacral pore morphologies. The ambulacral tube feet and spines are correspondingly highly variable according to position and function.

Spatangoids are among the most important burrowers and bioturbators in modern marine environments (Bromley and Asgaard, 1975; Lohrer et al., 2005; Dashfield et al., 2008; Gibert and Goldring, 2008). During deposit feeding, spatangoids move through the substrate (Chesher, 1969; De Ridder et al., 1985; Hollertz and Duchêne, 2001) displacing and mixing the sediment (De Ridder et al., 1987; Kanazawa, 1992, 1995; Saitoh and Kanazawa, 2012; Walker and Gagnon, 2014). Bioturbation by spatangoids can play a key role in structuring infaunal communities and maintaining high levels of diversity (Schin and Thompson, 1982; Widdicombe and Austen, 1998; Widdicombe et al., 2000; Dashfield et al., 2008). They furthermore increase oxygen penetration depths as well as facilitate nutrient flux and mixing (Osinga et al., 1995; Widdicombe and Austen, 1998; Lohrer et al., 2004; Vopel et al., 2007).

Although there have been extensive studies on the morphology of both extant and fossil spatangoids, there are few studies concerning their palaeoecology (Kanazawa, 1992, 1995), preservation potential and how these factors together influence their fossil record. Actualistic studies based on laboratory and field observations have helped to clarify the taphonomic processes affecting echinoid skeletons after death (Allison, 1990; Kidwell and Baumiller, 1990; Greenstein, 1991, 1993a, 1993b, 1995; Nebelsick, 1992b, 1999, 2008; Nebelsick and Kampfer, 1994; Sadler and Lewis, 1996; Lewis et al., 2000; Schein and Lewis, 2000; Banno, 2008; Dynowski, 2012). These studies have shown how taphonomic processes are influenced by constructional morphology, including test architecture and nature of connective tissues, life habits and the complex interplay of various environmental conditions such as temperature, oxygen content, bacterial activity and transport mechanisms.

Kier (1977) and Néraudeau (1991) stated that the infaunal mode of life seems to be the predominant factor favoring exceptional preservation of spatangoid echinoids in fossil faunas. These echinoids, being covered by sediments at the time of their death, are rarely affected by biostratinomic processes such as rapid destruction by scavengers and currents. Kier (1977) reported for the extant spatangoid *Schizaster* (previously attributed to the genus *Paraster*) that this echinoid lives deeply burrowed in mud and many dead specimens are found buried in the sediments, while only rarely are dead tests found on the sediment/water interface. Smith (1984) and Greenstein (1993b, 1995) highlighted other factors such as skeletal architecture and environmental conditions influencing the preservation potentials of spatangoids. These echinoids, which evolved and diversified as deposit feeders, are often buried within unconsolidated substrates in areas of active sedimentation in shallow to deeper water environments. This leads to a better fossil record of spatangoids compared to that of regular sea urchins (Kier, 1977; Smith, 1984) which diversified as grazers on firm or rocky substrates in shallow water environments, which represent areas of active erosion where echinoid tests have little chance of preservation.

Herein, a spatangoid-rich sedimentary succession from the Early-Middle Miocene of Porto Torres (northern Sardinia) is studied with the twofold aim of reconstructing palaeoecological and associated palaeoenvironmental conditions, and investigating factors influencing the preservation potential of spatangoid echinoids. This is accomplished by 1) detailed logging of sedimentary facies, 2) applying the functional morphological reconstructions of echinoid skeletons and interpreting their behaviour and life habits, 3) quantifying various taphonomic features of test preservation, and 4) analyzing associated trace fossils within the beds.

Echinoids are widely distributed throughout the sedimentary sequence at Porto Torres and have been described by Cotteau (1895), Airaghi (1905), Capeder (1906), Lambert (1907, 1909), Lovisato (1914), Di Giorgio (1923), Comaschi Caria (1972) and Valducci (1973). Although identification to species level in the present study was attempted whenever possible, a rigorous taxonomic revision of echinoid taxa at species level is ongoing and will be published elsewhere.

2. Geological framework

The Oligo-Miocene sedimentary succession of Sardinia, which is subdivided into three main sedimentary cycles, is mainly located in the NNW-SSE-oriented Sardinian Basin ("Fossa sarda" *Auctorum*), a tectonic trough that extends from the Gulf of Sassari in the northwest to Cagliari in the south and comprises a number of minor sub-basins (Fig. 1A). The origin of the Sardinian Basin was related to the Oligo-Miocene counter-clockwise rotation of the Corsica-Sardinian block due to the opening of the Western Mediterranean back-arc basin and subduction of Neotethyan oceanic crust to the east of Sardinia (Cherchi and Montandert, 1982; Thomas and Gennesseaux, 1986; Carmignani et al., 2001; Facenna et al., 2002; Speranza et al., 2002).

The northern part of the Sardinian Basin consists of a generally N to S striking halfgraben system, the western branch of which consists of the Porto Torres Basin in the North, which is separated from the southern Logudoro Basin by the E-W oriented transtensive Ittiri Fault (Thomas and Gennesseaux, 1986; Funedda et al., 2000; Benisek et al., 2009; Murru et al., 2015; Reuter et al., 2016). Calcalkaline magmatic activity accompanied the halfgraben formation and includes andesitic and basaltic flows and pyroclastic and ignimbritic events, which are Aquitanian to Middle Burdigalian in age (Lecca et al., 1997; Funedda et al., 2000). Continuous subsidence led to marine conditions from the Burdigalian onward with the formation of a mixed siliciclastic-carbonate succession (Funedda et al., 2000; Casula et al., 2001).

The tectono-sedimentary development and the stratigraphic framework of the Porto Torres Basin are partially comparable to that of the well-known, adjacent Logudoro Basin (Martini et al., 1992; Funedda et al., 2000; Vigorito et al., 2006; Murru et al., 2015). In both basins, the second and third Miocene sedimentary cycles were recognised by Mazzei and Oggiano (1990) and Funedda et al. (2000, 2003). The sedimentary sequence is subdivided into five main lithostratigraphic units (Mazzei and Oggiano, 1990; Funedda et al., 2000) (Fig. 2) and starts with fluvio-deltaic conglomerates and litharenitic sands of the Oppia Nuova Formation (?Middle-Upper Burdigalian) (Funedda et al., 2000). The overlying Mores Formation (Late Burdigalian) consists of calcarenites, bioclastic limestones and subordinate quartz-rich, poorly cemented, fossiliferous coarse-grained sandstones and conglomerates of shallow water origin (Mazzei and Oggiano, 1990; Funedda et al., 2000). Above the Mores Formation lies the Borutta Formation, to which the studied sedimentary succession of Porto Torres belongs. The Borutta Formation, which is assigned to the Late Burdigalian-Langhian based on calcareous nannoplankton (biozones NN4/NN5 of Martini, 1971) by Mazzei and Oggiano (1990) and Francolini (1994) and planktonic foraminifera (biozone N7 of Blow, 1969) by Bossio

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