

Comparative drilling predation on time-averaged phosphatized and nonphosphatized assemblages of the minute clypeasteroid echinoid *Echinocyamus stellatus* from Miocene offshore sediments (Globigerina Limestone Formation, Malta)

Tobias B. Grun,¹ Andreas Kroh,² and James H. Nebelsick¹

¹Department of Geosciences, University of Tübingen, Hölderlinstraße 12, 72074 Tübingen, Germany (tobias.grun@uni-tuebingen.de), (nefelsick@uni-tuebingen.de)

²Department of Geology and Palaeontology, Natural History Museum Vienna, Burgring 7, 1010 Wien, Austria (andreas.kroh@nhm-wien.ac.at)

Abstract.—Fossilized tests of 1,053 *Echinocyamus stellatus* (Capeder, 1906) from the Miocene Globigerina Limestone Formation exposed on the northern coast of Gozo (Maltese Islands) were analyzed for predation traces. Specimens mixed by time-averaging processes can be clearly separated into two distinct samples according to their preservation as phosphatized or nonphosphatized individuals. Overall, 11.1% of the tests reveal holes that are referred to the ichnospecies *Oichnus simplex* (Bromley, 1981). Because of the hole morphology and diameter, the holes are interpreted as predatory drill holes, most likely produced by cassid gastropods. Redeposited phosphatized echinoids derived from an earlier period of reduced sedimentation rates show drilling frequencies of 20.5%. Younger, autochthonous, nonphosphatized echinoids show drilling frequencies of 8.1%. In both samples, predators predominantly targeted the aboral side of the echinoid test, particularly on the petalodium.

Introduction

The geological deep-time record has revealed that drilling predation can be used as a tool to recognize ecological interactions in both fossil and extant communities (e.g., Kelley, 1989; Kowalewski et al., 1998; Harper, 2003). Drilling frequencies have increased over time (e.g., Huntley and Kowalewski, 2007) and thus represent a useful proxy for a better understanding of the development of ecological interactions through time (e.g., Bengtson and Zhao, 1992; Conway Morris and Bengtson, 1994; Kowalewski et al., 1998; Kowalewski et al., 2005). Early examples of predatory drill holes in echinoderms have been reported from Late Ordovician stylophorans and other Paleozoic echinoderms (Deline, 2008 and references therein). There is a rich record of predation on echinoids that has generally been attributed to a number of different organisms (e.g., Nebelsick, 1999; Kowalewski and Nebelsick, 2003). Maximum rates of drilling predation on echinoids increase in intensity from the Early Cretaceous to the Recent (Kowalewski and Nebelsick, 2003).

The comparison of drilling predation patterns on the fossil and Recent clypeasteroid echinoid *Echinocyamus*, which can be studied in large numbers from different habitats, serves to increase the knowledge of predator–prey relationships among echinoids through time. Data on drilling predation exist for several Recent fibulariids including *Echinocyamus* (Nebelsick and Kowalewski, 1999; Grun et al., 2014; Grun and Nebelsick, 2015) and *Fibularia* (Nebelsick and Kowalewski, 1999). In addition, drillings have been examined for fossil counterparts of

Echinocyamus (Ceranka and Złotnik, 2003; Złotnik and Ceranka, 2005) and *Fibularia* (Meadows et al., 2015). *Echinocyamus* can be abundant in near-to-offshore habitats varying from tropical to cold-water environments (e.g., Mortensen, 1927, 1948; Ghiold, 1982; Schultz, 2006). The test of these echinoids can be well preserved due to internal supports linking the oral and aboral side and thus strengthening the test (e.g., Seilacher, 1979; Mooi, 1989; Nebelsick, 1999, 2008; Grun et al., 2014).

This study aims to investigate differences in drilling intensity and site selectivity for predation in two time-averaged Miocene *Echinocyamus stellatus* (Capeder, 1906) (Fig. 1) samples from different paleoenvironmental settings of the Globigerina Limestone Formation in Malta. The tests were analyzed with respect to: (1) test length; (2) drilling frequencies; (3) drill hole length; (4) size selectivity; and (5) site selectivity. The results are compared to previous work on drilling predation on both Recent (Nebelsick and Kowalewski, 1999; Grun et al., 2014) and fossil (Ceranka and Złotnik, 2003; Złotnik and Ceranka, 2005) *Echinocyamus*.

Drill holes, predators, and echinoids

Drilling predation in marine shells can be used as an ecological signal for the interpretation of predator–prey relationships in both modern and fossil environments and has thus been investigated for a number of Recent and fossil organisms such as foraminifera and ostracods (e.g., Reyment, 1966), polychaetes (e.g., Young, 1969), mollusks (e.g., Kelley, 1988, 2001;

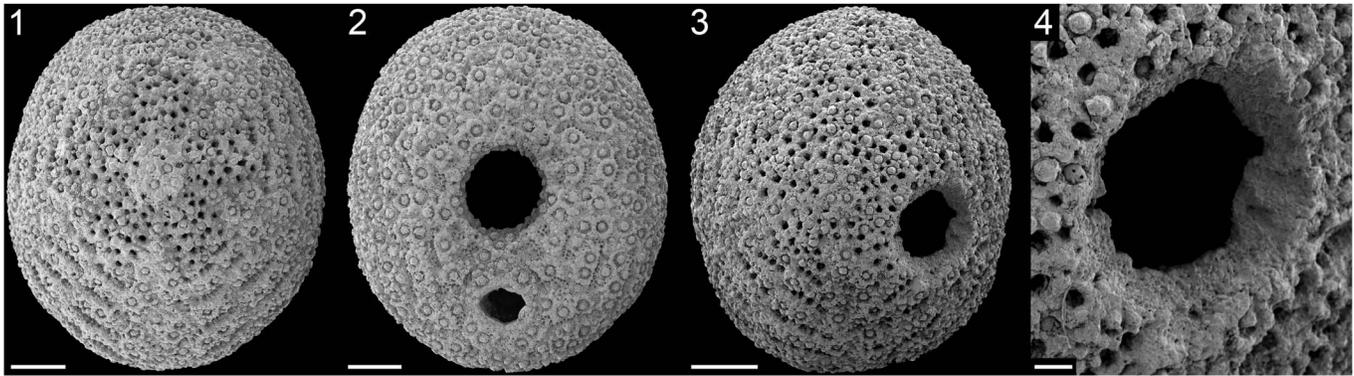


Figure 1. SEM microphotographs of nonphosphatized *Echinocyamus stellatus* from middle Miocene of Malta: (1) aboral view NHMW 2014/0401/0715; (2) oral view (NHMW 2014/0401/0715); (3) test with drill hole (NHMW 2014/0401/0033); (4) the drill hole of (3) in detail. (1–3) Scale bars = 500 μ m; (4) scale bar = 100 μ m.

Hoffmeister et al., 2004), brachiopods (e.g., Carriker and Yochelson, 1968; Baumiller et al., 1999, 2006; Hoffmeister et al., 2004), crustaceans (e.g., Palmer, 1982), and echinoderms (e.g., Hughes and Hughes, 1971, 1981; Warén and Crossland, 1991; Warén et al., 1994; Baumiller, 2003). Common drillers have been identified as predatory gastropods including capulids, eulimids, naticids, nudibranchs, muricids, and tonnacids (e.g., Bromley, 1981; Carriker, 1981; Kelley, 1988; Hoffmeister et al., 2004).

Well-known predators of echinoids are cassid gastropods (e.g., Hughes and Hughes, 1971, 1981; Nebelsick and Kowalewski, 1999; Złotnik and Ceranka, 2005; Grun et al., 2014). The morphology and size range of holes make it possible to identify potential predators (e.g., Nebelsick and Kowalewski, 1999; Kowalewski and Nebelsick, 2003; Kroh and Nebelsick, 2006; Złotnik and Ceranka, 2005; Grun et al., 2014). The drill hole diameters produced by cassid gastropods in fibulariids show an extensive range of sizes, for example 0.04 to 1.8 mm in samples from the Miocene of Poland (Złotnik and Ceranka, 2005) and 0.10 to 4.00 mm from Recent samples (Nebelsick and Kowalewski, 1999; Grun et al., 2014). The identification of holes in fossil echinoids can, however, be difficult since the traces may be altered by taphonomic processes and may lack distinctive characteristic features. The drilling of echinoids by cassid gastropods has been studied in detail by Hughes and Hughes (1971, 1981), who identified that cassid gastropods use sulfuric acid during drilling to dissolve the calcareous stereom and then remove the etched material by radula movement to expose the underlying stereom to the acid. A circular groove is then cut into the test, and the central disc is pushed into the test cavity. The drill holes produced by cassids are generally circular or elliptical in shape and increase in diameter with the size of the predator (Hughes and Hughes, 1971). Drill hole outline can vary from smooth to highly ragged if test surface characters such as ambulacral pores, spine tubercles, and glassy tubercles are intersected (Nebelsick and Kowalewski, 1999; Grun et al., 2014). Drill holes in echinoids show concave walls in cross section, caused by differences in stereom density between the plate center and the inner and outer surfaces (Grun et al., 2014).

Other known drilling gastropods of echinoids are ectoparasitic eulimids (e.g., Lützen and Nielsen, 1975; Warén and Crossland, 1991; Warén et al., 1994). Numerous eulimid

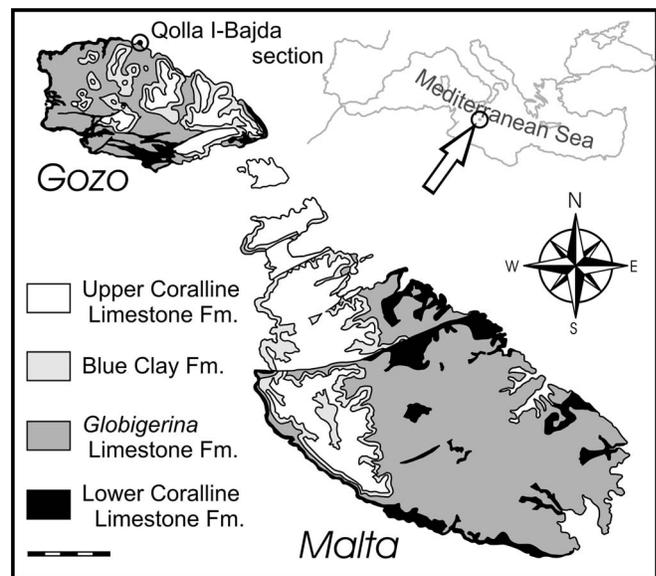


Figure 2. Map of Malta and Gozo including geological formations. Sample site (Qolla I-Bajda) is highlighted. Scale bar = 5 km. From Kroh (2004: fig. 1).

gastropods can parasitize a single individual, and each of these can potentially produce several drill holes with a distinct morphology. Such parasitic drill holes show a deeply convex imprint of the eulimid's snout and a nearly centric complete penetration of the host's test (Lützen and Nielsen, 1975) and range from 0.1 to 2.3 mm (Warén and Crossland, 1991).

Geological setting

The Maltese Islands are situated on the Malta-Ragusa Platform and are composed of Cenozoic rocks ranging from late Oligocene (Chattian) to late Miocene (late Tortonian) in age. The succession consists of five major lithostratigraphic units that are well exposed in vertical cliffs around the islands. The strata are generally horizontal, but the stratigraphic succession is locally complicated by synsedimentary tectonics and subsidence (Pedley et al., 2002). Within the succession, two major hiatuses exist that are associated with the deposition of phosphorites.

The studied outcrop is located in northwestern Gozo (Figs. 2, 3), where the strata of the Middle and Upper Globigerina

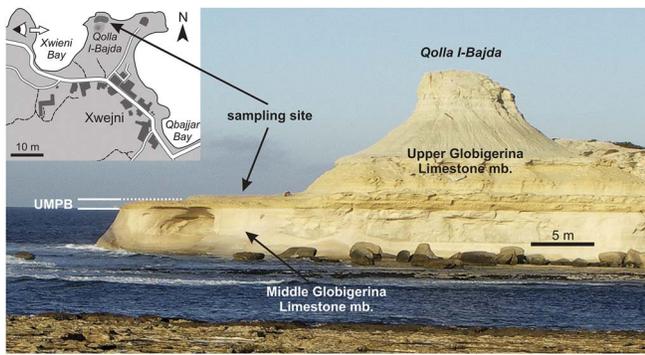


Figure 3. Field photograph of the Qolla I-Bajda hill near Xwejni, seen from the west. Boundaries of lithostratigraphic units are indicated by white bars, as is the sampling area (hatched in inset). Inset shows the exact position of the site in relation to the surrounding area.

Limestone members (MGLM and UGLM, respectively) are exposed in the Qolla I-Bajda section ($36^{\circ}4'47''\text{N}$, $14^{\circ}14'59''\text{E}$) at Xwejni Bay. This section is directly exposed to the open sea and thus subject to intense weathering. The uppermost few millimeters of the otherwise very durable *Globigerina* Limestone are relatively soft, presumably due to the constant cycle of seawater soaking and drying. The more resistant parts of the succession of Qolla I-Bajda, namely the terminal hardground of the Middle *Globigerina* Limestone and associated phosphate conglomerate (Upper Main Phosphate Bed – UMPB), form ledges on which the weathered material accumulates.

Lithostratigraphy and sedimentary environment.—Deposition in the western margin of the Malta-Ragusa Rise represents a major province of Miocene phosphogenesis with a complex origin, transport, and sedimentation of the phosphatized clasts (Pedley and Bennett, 1985). The occurrence of large amounts of phosphatized components is generally attributed to marine settings with high organic productivity, low oxygen levels, low sedimentation rates, and low terrigenous input (e.g., Föllmi et al., 2008; Tapanila et al., 2008). Following Pedley and Bennett (1985), the phosphatized clasts were deposited during periods of turbulence, interrupted by nondeposition resulting in the formation of hardgrounds as well as the deposition of normal pelagic marine sediments. Rehfeld and Janssen (1995) proposed a multiphased development of beds rich in phosphate controlled by sea-level oscillations.

The studied beds follow a prominent horizon in the upper part of the *Globigerina* Limestone Formation (GLF), which ranges from Aquitanian to Langhian in age. The GLF is predominantly composed of pelagic carbonate limestones deposited offshore. It is subdivided into three members—Lower (LGLM), Middle (MGLM), and Upper *Globigerina* Limestone (UGLM) members—on the basis of two prominent horizons that can be followed throughout the Maltese Archipelago. The second horizon separates the pale-gray marly limestones of the MGLM from yellowish marly limestones of the UGLM (Pedley, 1992; Föllmi et al., 2008).

The basal sediments of the UGLM consist of an ~1 m thick bed containing phosphatic nodules and clasts, phosphatized fossils, and nonphosphatized components within a marly limestone matrix (Pedley and Bennett, 1985; Föllmi et al., 2008). The sediments overlie an intensely borrowed hardground

or omission surface. Various terms have been used to designate these beds (see Bennett, 1980; Pedley et al., 1978, 1985; Föllmi et al., 2008) as well as the preceding hardground surface (Gruszczynski et al., 2008).

The top of the MGLM shows distinct relief, with a topographic seafloor high in NW and W Gozo (Pedley et al., 2002), where it ends with a distinct terminal hardground with a thalassinoid burrow system extending up to 1.5 m into the MGLM. In that area, bed thickness of the UMPB is greatest and clast size is largest (Bianucci et al., 2011). The phosphorite intraclasts and a matrix of planktonic foraminiferal packstones of the overlying UGLM infill this hardground. According to Bianucci et al. (2011), the areas where the UMPB is associated with an underlying hardground represent autochthonous phosphatization associated with topographic seafloor highs.

Toward the south and east, clast size and bed thickness decrease. The UMPB Bed is composed of two horizons of phosphorite intraclasts floating in the matrix at Malta and up to five similar horizons at Gozo (Pedley and Bennett, 1985; Carbone et al., 1987; Rose et al., 1992). For these occurrences, an allochthonous origin and clast transportation over short distances, presumably from a topographic high in NW Gozo, are assumed.

Different interpretations for the depositional depth estimates assigned to the UMPB can be found in the literature; Carbone et al. (1987) estimated depositional depths at 25–65 m, while Bennett (1980) considered the environment to range from deep shelf margin to open shelf sea (see Boggild and Rose, 1984). According to Challis (1980), the UMPB was deposited at shallower conditions than the MGLM, which is currently thought to have been deposited at depths in excess of 400 m on the basis of the absence of planktonic foraminifera and presence of chert nodules (see Bianucci et al., 2011). More agreement exists for the paleoenvironment of the UGLM, which is consistently attributed to an upper bathyal setting at 500–600 m (Bellanca et al., 2002; Abels et al., 2005) or 500–800 m depth (Bianucci et al., 2011).

The fauna of the UMPB has been intensively studied and includes both phosphatized and nonphosphatized components. The former comprises vertebrate bones, mollusks including pteropods and cephalopods, corals, serpulids, barnacles, terebratulid brachiopods, bored pebbles, and echinoderms. Nonphosphatized biogenic components include bivalves, barnacles, and echinoids (Pedley and Bennett, 1985). Phosphatized skeletons can be well preserved including thin-shelled pteropods, which are preserved as phosphatic internal molds (Rehfeld and Janssen, 1995; Janssen, 2012).

Biostratigraphy.—The terminal hardground of the MGLM is associated with a hiatus of unknown duration, and hence dates given for the UMPB in the literature vary from late Burdigalian to Langhian. The history of chronostratigraphic position of the UGLM is discussed in detail in Bianucci et al. (2011) and Foresi et al. (2011). The base of the UGLM has been traditionally assigned to the Langhian on the basis of calcareous nannoplankton and planktonic foraminiferans (nannozone CN4, NN5; Giannelli and Salvatorini, 1972; Mazzei, 1985). Föllmi et al. (2008, fig. 11) place the UMPB at the Burdigalian/Langhian

boundary. Foresi et al. (2011) assigned the base of the UGLM (and thus the UMPB) to the Burdigalian. Difficulties in giving a chronostratigraphic age to the UMPB bed are exacerbated by the fact that: (1) the base of the Langhian has not been formally defined; (2) there is a significant time gap represented by the hardground at the base of the UMPB (Föllmi et al., 2008); (3) the base of the UMPG across the Maltese Archipelago has a diachronous nature (Foresi et al., 2001); and (4) these marker beds can be followed by one or more omission surfaces (up to five in all) making exact correlation difficult. In Gozo, five individual horizons constitute the UMPB bed, while only one or two are present in the rest of the Maltese Archipelago (see also Föllmi et al., 2008).

Studied fauna

Malta is known for its rich echinoid fauna, which has been studied by numerous authors (e.g., Wright, 1855, 1864; Gregory, 1891; Stefanini, 1908; Lambert, 1909; Cottreau, 1914; Zammit-Maempel, 1969). Challis (1979, 1980), in a study of the paleoecology and taxonomy of Maltese echinoids, recognized 13 echinoid biofacies with *Echinocyamus* showing a wide distribution ranging from lagoonal to offshore facies. The UMPB at the base of the UGLM contains a macrofauna including the echinoid genera *Echinocyamus*, *Pericosmus*, *Lovenia*, *Spatangus*, *Schizaster*, *Echinolampas*, *Brissopsis*, *Psammechinus*, and *Sardocidaris*. *Echinocyamus* is particularly common in the basal part of the member, directly on top of the underlying hardground.

The minute clypeasteroids from the GLF were first assigned to the species *Fibularia melitensis* by Lambert (1909). Cottreau (1914), in his revision of Mediterranean Neogene echinoids, synonymized *Fibularia melitensis* with *Echinocyamus stellatus* (Capeder, 1906), a species first reported from coeval strata of the northern coast of Sardinia. Subsequent authors including Rose (1974, 1975) and Challis (1980), working on the Maltese echinoid fauna, followed Cottreau (1914). Since more than 30 fibulariid species names appear in the literature of the Mediterranean Miocene, and since 18 of these species names were established by Capeder (1906) alone, it is likely that the diversity of European Neogene fibulariids is overestimated. According to the descriptions of Capeder (1906), *Echinocyamus stellatus* seems to be the best match for the Maltese specimens.

Sedimentary environment

The investigated echinoids are preserved in two distinct modes, as phosphatized and as nonphosphatized specimens. Phosphatized tests originate from a period of low sedimentation rate and accumulated at the top of the terminal hardground of the MGLM at a topographic high in NW Gozo. The nonphosphatized specimens, by contrast, derive from a slightly later period when sedimentation rate was higher and phosphatization was absent. Bioturbation is most likely responsible for sediment mixing and time-averaging of the two samples. Age difference between the two samples is poorly constrained because the exact duration of the hiatus linked with phosphatization is unknown. The phosphatized bioclastic sediments are closely associated with the underlying hardground on top of a topographic high on the paleoseafloor, which is interpreted as the site where

phosphatization occurred (Bianucci et al., 2011). By contrast, there is no evidence of transport for the nonphosphatized material that can be considered of autochthonous origin.

Materials and methods

Materials.—Fossil tests of the clypeasteroid echinoid *Echinocyamus stellatus* (Fig. 1) were picked from two bulk sediment samples of the UMPB at the base of the UGLM exposed in the Qolla I-Bajda section at Xwejni Bay, northern coast of Gozo, Malta. The material was collected from the lowermost part of this member, 0.5 to 1.5 m above the weathered terminal hardground of the MGLM (hatched area in Fig. 3).

Material preparation.—Bulk sediment samples were dry sieved in the field with an effective mesh size of 1.5 mm. Sieved residuals were processed in the lab by wet sieving through standard sieve sets. Specimens with complete ambitus were cleaned in hydrogen peroxide and an ultrasonic bath. For SEM analysis, tests were additionally cleaned in Rewoqat (Lierl, 1992) to remove fine particles and photographed with a Jeol JSM 6610-LV scanning electron microscope.

Specimens were separated into phosphatized and nonphosphatized specimens. Phosphatized specimens are easily recognizable by their typically brown color and waxy, worn appearance, while the nonphosphatized echinoids are light gray to white and often retain a well-preserved test surface.

Measurements.—Tests are measured using an ocular scale. All deviations of the mean or median are listed as standard deviations. The test length is the longitudinal axis, which represents the maximum distance between the anterior and posterior ambitus; test width is the maximum distance between the lateral test margins, perpendicular to the longitudinal axis. Test length and width were compared using Pearson's correlation coefficient to detect possible allometry. Differences of test length between phosphatized and nonphosphatized specimens were analyzed using a Mann-Whitney U test.

Drill holes.—Drill holes are examined for the: (1) outline; (2) length and width; (3) position of drill hole center; and (4) section profile. The drill hole length is the longest distance between drill hole margins, and drill hole width is the widest distance between margins perpendicular to the drill hole length. Spearman's rho was used in order to test for correlation of drill hole length and width. Potential differences of the drill hole length between specimen types were examined using a Mann-Whitney-U test.

The drilling frequency is defined as the number of drilled tests, either single or multiple drilled, divided by the total specimen number. Pearson's chi-square was used to test for differences in drilling frequencies between sample types.

Size and site selectivity.—Spearman's rho was used to test for size selectivity between test length and drill hole length. Site-dependent drilling preference was explored using four binomial tests comparing drilling frequencies between the (1) oral and aboral side; (2) petal area and ambital disc aboral side;

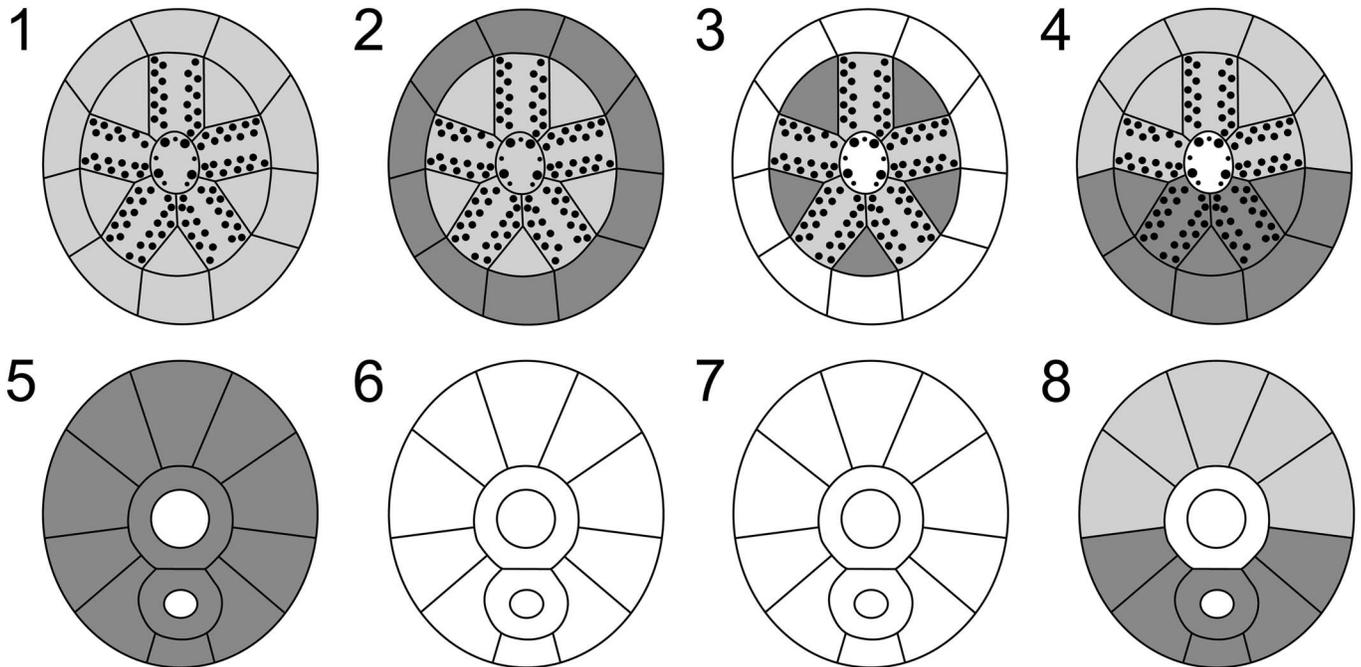


Figure 4. Model of *Echinocyamus stellatus* from the Miocene of Malta: (1–4) aboral test side; (5–8) oral test side. Compared areas are (1, 5) oral vs. aboral site; (2, 6) petal area vs. ambital area; (3, 7) ambulacral fields vs. interambulacral fields; (4, 8) anterior vs. posterior. Compared areas are highlighted in dark and light gray. White areas are not included in the comparison.

(3) ambulacral and interambulacral fields; and (4) anterior and posterior (Fig. 4).

The oral side is that part of the test that is visible in perpendicular view from above the peristome. In the same way, the aboral side is that part that is visible in perpendicular view from above the apical disc. Since the test is almost planar, all parts of the tests are covered. The petal area is the expansive petalodium (Zachos, 2015), which is the sum of ambulacral and interambulacral fields enclosed by the ends of the petals. The ambital area is the area between the petal area and the ambitus (outline of the test). Ambulacral fields correspond to the ambulacra; interambulacral fields correspond to the interambulacra. The anterior of the test is the oral and aboral area of the test that is located anterior of the sutures between interambulacrum 1 and ambulacrum II and ambulacrum VI and interambulacrum 4. The posterior of the test is the oral and aboral area of the test that is located posterior of this line. The apical disc and the peristomal area are excluded in this comparison.

The application of a binomial test on unequally dimensioned areas requires an adjustment of the compared area proportions. Thus, the ratios of the compared areas were calculated by dividing the area of each zone by the total area of all of the examined zones (Eq. 1):

$$A_r = \frac{A_i}{A_{i+j}} \quad (1)$$

where A_r = area ratio; A_i = surface area I; A_j = surface area j; A_{i+j} = total area of all involved zones.

Repositories and institutional abbreviations.—Specimens were exported under the Malta National Museum of Natural History's permit no. T/00/1 and are stored at the Department of Geology and Palaeontology at the Natural History Museum Vienna

(NHMW) under the repository numbers NHMW 2014/0400/0001 to NHMW 2014/0401/0724.

Results

A total of 1,053 tests were collected, 259 were phosphatized (24.6%) and 794 (75.4%) were nonphosphatized specimens. In total, 136 drill holes are distributed on 117 individuals (overall drilling frequency = 11.1%): 101 tests feature single drill holes; 14 feature two; 1 features three; and 1 features four drill holes. Only a single drill hole could not be measured or have its position assigned due to taphonomic alteration. Another drill hole could not be measured due to abrasion, although its position was determined. From the 101 tests with single drill holes, 44 are phosphatized and 57 are nonphosphatized. Both the phosphatized and nonphosphatized samples feature seven double-drilled tests each, while specimens with three and four drill holes are phosphatized.

Drill hole morphology.—The drill holes are circular to subcircular (Fig. 1.3, 1.4) with outlines ranging from smooth to ragged depending on the position of the hole on the test. Drill holes crossing ambulacral pores tend to be more ragged in outline than those located on pore-free areas. Drill hole margins crossing tubercles or glassy tubercles are also more ragged due to the higher local stereom densities of these structures. In cross section, drill hole walls are slightly concave as the diameter of inner and outer surfaces is narrower than that of the intermediate area of stereom. This concave section can, however, be affected by abrasion of the margins. Healed or incomplete drill holes as well as radula scratching traces or attachment scars around or within the drill holes are absent.

Test size.—Tests vary from 1.90 to 5.75 mm (mean = 3.44 ± 0.65 mm) in length and from 1.50 to 4.90 mm (mean = 2.88 ± 0.57 mm) in width for the phosphatized specimens. Non-phosphatized individuals range from 1.55 to 5.15 mm (mean = 2.81 ± 0.62 mm) in length and 1.20 to 4.50 mm (mean = 2.41 ± 0.56 mm) in width (Fig. 5). The Pearson’s correlation coefficient indicates that test lengths and test widths are strongly correlated ($r = 0.98$, $p < 0.001$, $N = 1,053$; Fig. 6). Phosphatized individuals are significantly larger than nonphosphatized individuals (t -test = -14.13, $p < 0.001$, $N = 1,053$; Fig. 5).

Drill hole size.—Drill holes in phosphatized individuals vary from 0.25 to 4.00 mm (median = 1.05 ± 0.73 mm; Fig. 7) in length and from 0.25 to 2.90 mm (median = 0.93 ± 0.64 mm) in width. Drill holes in nonphosphatized individuals vary in length from 0.35 to 2.10 mm (median = 0.90 ± 0.44 mm) and in width from 0.25 to 1.70 mm (median = 0.75 ± 0.39 mm). Spearman’s correlation coefficient indicates that drill hole length and width are strongly correlated ($\rho = 0.93$, $p < 0.001$, $N = 134$, Fig. 8). Drill holes in tests from phosphatized and nonphosphatized specimens are similar in length (Mann-Whitney $U = 1,899.50$, $p = 0.129$, $N = 134$, Fig. 7).

Drilling frequencies.—The phosphatized specimens show a drilling frequency of 20.5% (53 individuals), while non-phosphatized specimens show a frequency of 8.1% (64 individuals; Fig. 9). This difference is statistically significant ($\chi^2 = 29.03$, $p < 0.001$, $N = 1,052$, $p < 0.001$, $N = 1,052$).

Size and site selectivity.—The analyses indicate that a significant correlation between test length and drill hole length is present for phosphatized specimens ($\rho = 0.48$, $p < 0.001$, $N = 64$, Fig. 10), while no significant correlation has been detected in the nonphosphatized sample ($\rho = 0.19$, $p = 0.180$, $N = 70$, Fig. 10).

The binomial tests indicate that drillers of both phosphatized and nonphosphatized samples drill predominantly into the aboral test side (Table 1, Fig. 4). Predators drill equally into the anterior and posterior areas in both of the two samples (Table 1, Fig. 4). The petal area of the phosphatized samples is more frequently drilled than the ambital area, as the ambulacral fields are also more frequently drilled than the interambulacral fields (Table 1, Fig. 4). By contrast, nonphosphatized individuals show no evidence for selectivity of petal area or the ambulacral fields (Table 1).

Discussion

Drill hole origin and morphology.—The trace fossils documented here can be assigned to the ichnotaxon *Oichnus simplex*

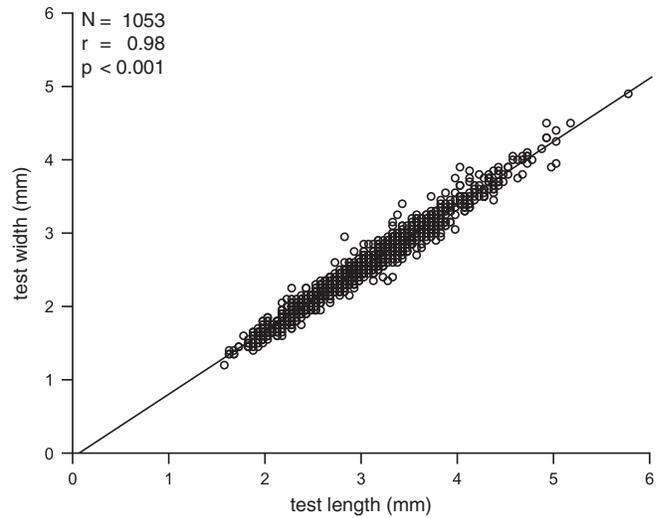


Figure 6. *Echinocyamus stellatus* from the Miocene of Malta. Pearson’s correlation between test length and test width. N = number of involved individuals; r = Pearson’s correlation coefficient; p = p -value of the statistical test.

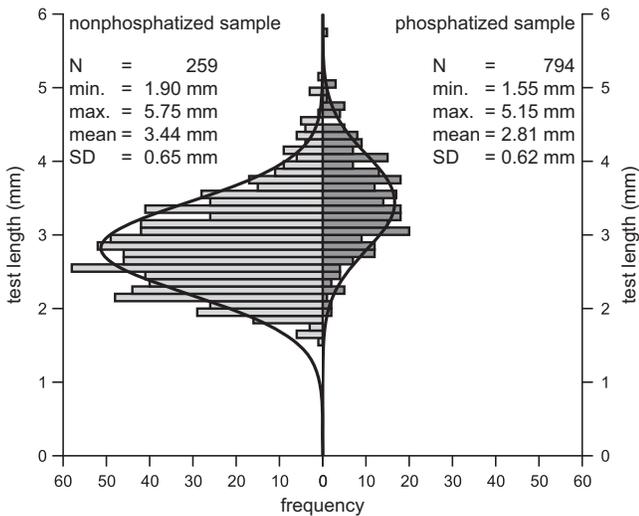


Figure 5. *Echinocyamus stellatus* from the Miocene of Malta. Test lengths compared among phosphatized and nonphosphatized individuals. N = number of involved individuals; min. = minimum test length; max. = maximum test length; mean = mean test length; SD = standard deviation; frequency = absolute numbers.

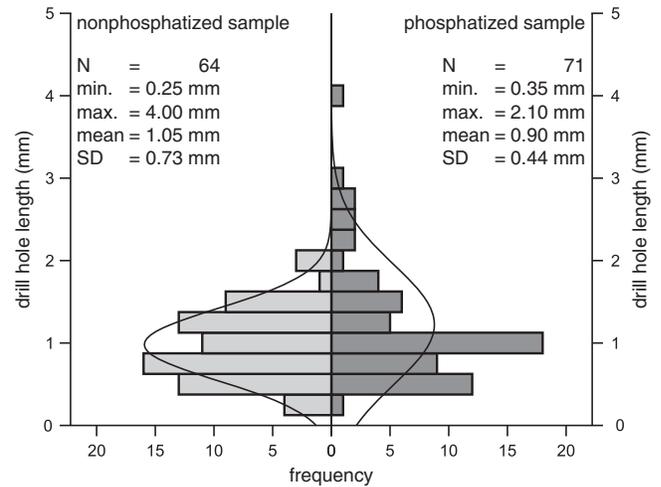


Figure 7. *Echinocyamus stellatus* from the Miocene of Malta. Drill hole lengths compared among phosphatized and nonphosphatized individuals. N = number of involved individuals; min. = minimum drill hole length; max. = maximum drill hole length; mean = mean drill hole length; SD = standard deviation; frequency = absolute numbers.

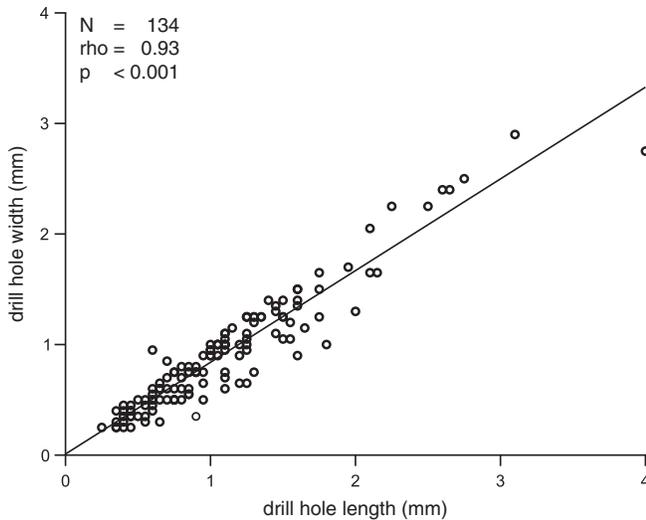


Figure 8. *Echinocyamus stellatus* from the Miocene of Malta. Spearman's correlation between drill hole length and drill hole width. N = number of involved individuals; rho = Spearman's correlation coefficient; p = p-value of the statistical test.

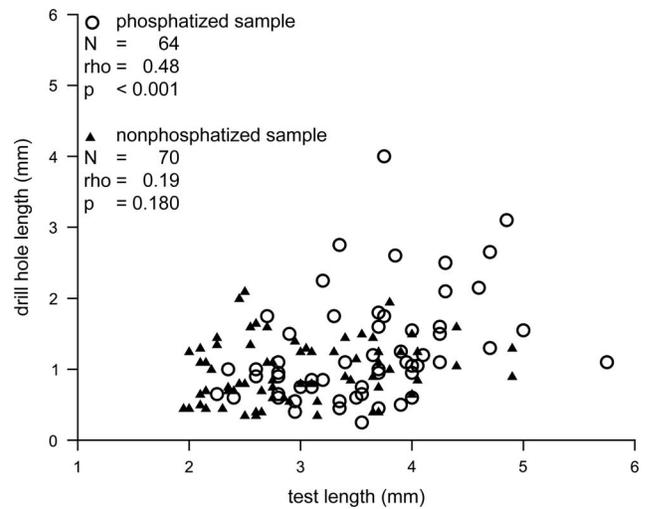


Figure 10. *Echinocyamus stellatus* from the Miocene of Malta. Spearman's correlation between test length and drill hole length among phosphatized and nonphosphatized individuals. N = number of involved individuals; rho = Spearman's correlation coefficient; p = p-value of the statistical test.

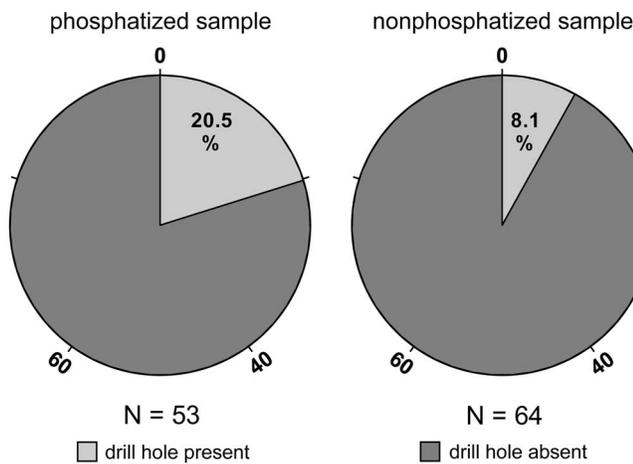


Figure 9. *Echinocyamus stellatus* from the Miocene of Malta. Drilling frequencies compared between phosphatized and nonphosphatized individuals. N = number of involved individuals.

(Bromley, 1981) (see Wisshak et al., 2015 for a discussion of purported synonymy between *Oichnus* and *Sedilichnus*). Cassids are known drilling predators of echinoids (e.g., Hughes and Hughes, 1971, 1981) and are interpreted as the cause of drill holes in both Recent (Nebelsick and Kowalewski, 1999; Grun et al., 2014) and fossil (Złotnik and Ceranka, 2005) fibulariids. According to previous morphological descriptions of the drill holes (Hughes and Hughes, 1971, 1981; Nebelsick and Kowalewski, 1999; Grun et al., 2014; Meadows et al., 2015), with respect to shape and size, cassid gastropods (Tonnacea) are the most likely drillers of the Maltese *Echinocyamus*. It is highly unlikely that eulimids are the producers of drill holes in the studied Maltese samples as Lützen and Nielsen (1975) reported much smaller drill hole diameters for eulimid drillings. SEM micrographs of eulimid drill holes published by Warén and Crossland (1991) are obliquely cylindrical or conical as opposed

to the drill holes in the Maltese echinoids, which are perpendicular to the test surface. In addition, attachment scars on the test surface attributed to parasitic eulimids are missing.

Echinocyamus stellatus from middle Miocene sediments of Malta do not show allometric growth during ontogeny. These results are similar to those found in Recent *Echinocyamus* samples from the Red Sea (Nebelsick and Kowalewski, 1999) and the Mediterranean Sea (Grun et al., 2014), as well as in fossil examples from Poland (Złotnik and Ceranka, 2005). The studied echinoids from the two preservation modes show clear differences in average test length, suggesting that they indeed belong to separate samples (Fig. 5). There may be several reasons for such separation, including primary differences in the test size or taphonomic bias due to transport mechanisms during winnowing.

By contrast, drill hole length does not vary significantly between the samples. The drill hole diameter can be correlated to the size of the radula and thus to the size of the gastropod predators (Hughes and Hughes, 1971, 1981). The similar drill hole lengths in both echinoid samples suggest similar predators of similar size range. The drill holes in *Echinocyamus stellatus* are between 0.25 to 4.00 mm in length, reflecting the lower end of drill hole diameters reported for Recent cassid gastropods by Hughes and Hughes (1981) on regular adult sea urchins. This is similar to the size range observed for drill holes in modern fibulariids (Nebelsick and Kowalewski, 1999). The variation from small to larger drill holes in *Echinocyamus stellatus* and the comparison to drill hole lengths produced by adult cassids species suggest that *Echinocyamus stellatus* served as a food source for both juvenile and adult cassid gastropods.

There is a trend of increasing drill hole length with increasing test length in the phosphatized sample. It cannot be rejected that predators selected the prey by test size, but it is likely that relatively large drill holes weaken the test integrity more than smaller drill holes. Bioturbation, transport, and extended exposure on the seafloor during phosphogenesis may

Table 1. Drilling site comparison on tests of *Echinocyamus stellatus*. An 'X' in 'site selectivity' indicates the exact binomial test (exact p°) is significant, based on a significance level of 0.05.

Sample	Site	Total drill holes	Number of drill holes in each area	Relative area (%)	Observed probability	Test probability	Exact p°	Site selectivity evaluation	
								Selective	Nonselective
Phosphatized	Oral	64	53	50.4	0.828	0.504	<0.001	X	
	Aboral		11	49.6	0.172	0.496			
	Petal area	45	34	47.9	0.756	0.479	<0.001	X	
	Ambital area		11	52.1	0.244	0.521			
	Ambulacral fields	34	29	65.6	0.853	0.656	0.009	X	
	Interambulacral fields		5	34.4	0.147	0.344			
Nonphosphatized	Anterior	56	34	54.9	0.607	0.549	0.230		X
	Posterior		22	45.1	0.393	0.451			
Nonphosphatized	Oral	71	55	50.4	0.775	0.504	<0.001	X	
	Aboral		16	49.6	0.225	0.496			
	Petal area	46	28	47.9	0.609	0.479	0.053		X
	Ambital area		18	52.1	0.391	0.521			
	Ambulacral fields	28	21	65.6	0.750	0.656	0.200		X
	Interambulacral fields		7	34.4	0.250	0.344			
	Anterior	63	38	54.9	0.603	0.549	0.231		X
	Posterior		25	45.1	0.397	0.451			

have resulted in a taphonomic filter against the preservation of larger drill holes on smaller tests. By contrast, the more autochthonous, rapidly buried, nonphosphatized material does not show such a trend even though they feature drill holes of the same length range as the phosphatized material. The absence of size selectivity was also reported for drilled fibulariid samples from the Miocene of Poland (Złotnik and Ceranka, 2005), Oligocene of New Zealand (Meadows et al., 2015), Recent Red Sea (Nebelsick and Kowalewski, 1999), and Recent Mediterranean Sea (Grun et al., 2014).

Drilling frequencies.—The drilling frequencies of phosphatized and nonphosphatized samples are clearly different. This mirrors the results from Recent studies in the Red Sea where frequencies differed highly among facies from around 60.6% to 80.2% for *Echinocyamus crispus* (Mazzetti, 1893) and 22.0% to 83.3% for *Fibularia ovulum* (Lamarck, 1816) (Nebelsick and Kowalewski, 1999). Grun et al. (2014) also reported highly variable drill hole frequencies in samples taken around a single island in the Mediterranean Sea ranging from absent to 21.7%. It is difficult to ascertain the reason for the different rates of drillings in the Recent material (Grun et al., 2014), and even more complicated for the fossil material examined in the present study. The higher frequencies shown by phosphatized (20.5%) over the nonphosphatized (8.1%) samples may be due to a number of ecological parameters both biotic (population densities of both predators and prey) and abiotic (such as sedimentation rates) in their contemporary environment.

The frequencies of drilling predation (8.1% and 20.5%) in *Echinocyamus stellatus* from the Maltese Globigerina Limestone are similar to those reported from the Miocene of Poland. Złotnik and Ceranka (2005) show drilling frequencies of 3.8%, 10.9%, and 15.2% for *Echinocyamus linearis* (Capeder, 1906), *Echinocyamus pusillus* (Müller 1776), and *Echinocyamus pseudopusillus* (Cotteau, 1895), respectively. These results are similar to the Oligocene of New Zealand, where Meadows et al. (2015) reported a drilling frequency for *Fibularia* sp. of 7.0%. Nebelsick and Kowalewski (1999), however, revealed clearly higher frequencies from the Recent Red Sea (60.6% to 80.2% for *Echinocyamus crispus* and 22.0% to 83.3% for *Fibularia ovulum*).

A possible taphonomic filter against large drill holes in small tests may result in an underrepresentation of drilling frequencies. Such a filter should, however, have a rather small effect on the overall drilling frequency since the test length distribution of drilled specimens roughly follows the normal distribution of nondrilled specimens (Fig. 4).

Site selectivity.—The selectivity for the aboral test side in the Maltese *Echinocyamus stellatus* has also been reported for several *Echinocyamus* species from both fossil and Recent environments (Nebelsick and Kowalewski, 1999; Złotnik and Ceranka, 2005; Grun et al., 2014) as well as for *Fibularia* (Nebelsick and Kowalewski, 1999; Meadows et al., 2015). The drilling preference to the aboral side, especially to the petalodium, may reflect an optimization strategy of the predator reducing the amount of energy (e.g., for producing less acid or by removing less stereom due to pore occurrences) and thus may reduce the time for drilling, leading to potentially less disturbance and more drillings over time. The reduction in drilling time for optimization is reasonable since: (1) the predator attacks the buried prey from the aboral side and thus reduces handling time; (2) the aboral side of the test is thinner than the oral side and thus less energy is needed to drill into the test (Złotnik and Ceranka, 2005); (3) the presence of ambulacral pores on the aboral side of the test means that less material needs to be removed; (4) targeted internal organs are located underneath the petalodium; and (5) in *Echinocyamus*, internal supports are present beyond the petal area.

The preference for the petal area seems to be characteristic in *Echinocyamus* prey (Nebelsick and Kowalewski, 1999; Złotnik and Ceranka, 2005; Grun et al., 2014). The fact that there is no significant preference for drilling into the petal and the ambital areas of the nonphosphatized individuals may be due to the generally smaller size of these echinoids. Smaller prey size with constant drill hole diameters results in less specific site selectivity as opposed to the phosphatized examples. There is also evidence for selectivity by predators of the larger phosphatized individuals for the ambulacral areas, which contain relatively large ambulacral pores, rather than the interambulacral areas. Again, the smaller, nonphosphatized individuals show no such selectivity.

Conclusions

The two distinct samples of phosphatized and nonphosphatized *Echinocyamus stellatus* from the Miocene Maltese Island Gozo can be statistically distinguished with respect to test length and drill hole frequency, but they cannot be distinguished on the basis of drill hole length alone. Drilling patterns are quite similar, while minor differences in site selectivity may be size specific.

The holes in the Miocene Maltese echinoid tests are interpreted as *Oichnus simplex* (Bromley, 1981) trace fossils. The drill holes are circular to subcircular in outline. Drill hole margins are smooth or ragged depending on the microstructures of the drilling area. The drill hole wall is concave in section and perpendicular to the test surface.

Comparisons of the morphological characteristic and sizes of the drill holes from Malta with descriptions of other drill holes in *Echinocyamus* species indicate that the drillers of the Miocene *Echinocyamus stellatus* are most likely cassid gastropods.

Drilling frequencies vary from 8.1% in nonphosphatized echinoids to 20.5% in phosphatized echinoids. Variations in drilling frequencies may be due to variations of predator densities or a number of environmental differences and mirror the high variation of reported drilling frequencies within various Recent depositional environments.

The fact that predators drill more frequently into the aboral test side may be due to handling effects and the time and energy saved by drilling the thinner, highly porous areas of the test. The position of internal organs and internal supports may also be important factors.

Drilling predation traces can be used for analyzing direct predation patterns on well-preserved fossil echinoid tests. The drill holes can also provide indirect evidence for the existence of predators and allow for the analyses of specific drill hole morphologies, sizes, and drill site preferences.

Acknowledgments

We thank G. Zammit-Maempel (formerly Malta National Museum of Natural History) for the collection and export permit. Thanks to the Natural History Museum Vienna, Austria, for providing lodging during a research stay. Thanks also to T. Baumiller (Department of Earth and Environmental Sciences, University of Michigan, USA), G. Dietl (Department of Earth and Atmospheric Sciences, Cornell University, USA) and S. Zamora (Instituto Geológico y Minero de España, Zaragoza, Spain) for reviewing, editing, and constructive suggestions.

References

Abels, H.A., Hilgen, F.J., Krijgsman, W., Kruk, R.W., Raffi, I., Turco, E., and Zachariasse, W.J., 2005, Long-period orbital control on middle Miocene global cooling: Integrated stratigraphy and astronomical tuning of the Blue Clay Formation on Malta: *Paleoceanography*, v. 20, p. 1–17.

Baumiller, T.K., 2003, Evaluating the interaction between platyceratid gastropods and crinoids: A cost-benefit approach: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 201, p. 199–209.

Baumiller, T.K., Leighton, L.R., and Thompson, D.L., 1999, Boreholes in Mississippian spiriferide brachiopods and their implications for Paleozoic

gastropod drilling: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 147, p. 283–289.

Baumiller, T.K., Bitner, M.A., and Emig, C.C., 2006, High frequency of drill holes in brachiopods from Pliocene of Algeria and its ecological implications: *Lethaia*, v. 39, p. 313–320.

Bellanca, A., Sgarrella, F., Neri, R., Russo, B., Sprovieri, M., Bonaduce, G., and Rocca, D., 2002, Evolution of the Mediterranean Basin during the late Langhian–early Serravallian: An integrated paleoceanographic approach: *Rivista Italiana di Paleontologia e Stratigrafia*, v. 108, p. 223–239.

Bengtson, S., and Zhao, Y., 1992, Predatorial borings in late Precambrian mineralized exoskeletons: *Science*, v. 257, p. 367.

Bennett, S.M., 1980, *Palaeoenvironmental studies in Maltese mid-Tertiary carbonates* [Ph.D. dissertation]: London, University of London, 347 p.

Bianucci, G., Gatt, M., Catanzariti, R., Sorbi, S., Bonavia, C.G., Curmi, R., and Varola, A., 2011, Systematics, biostratigraphy and evolutionary pattern of the Oligo-Miocene marine mammals from the Maltese Islands: *Gebios*, v. 44, p. 549–585.

Boggild (née Challis), G.R., and Rose, E.P.F., 1984, Mid-Tertiary echinoid biofacies as palaeoenvironmental indices: *Annales Géologiques des pays Helléniques*, v. 32, p. 57–67.

Bromley, R.G., 1981, Concepts in ichnology illustrated by small round holes in shells: *Acta Geológica Hispánica*, v. 16, p. 55–64.

Capeder, G., 1906, *Fibularidi del Miocene medio di S. Gavino a mare* (Portotorres) Sardegna: *Bollettino della Società Geologica Italiana*, v. 25, p. 195–534.

Carbone, S., Grasso, M., Lentini, F., and Pedley, H.H., 1987, The distribution and palaeoenvironment of early Miocene phosphorites of southeast Sicily and their relationships with the Maltese phosphorites: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 58, p. 35–53.

Carriker, M.R., 1981, Shell penetration and feeding by naticacean and muricacean predatory gastropods: A synthesis: *Malacologia*, v. 20, p. 403–422.

Carriker, M.R., and Yochelson, E.L., 1968, Recent gastropod boreholes and Ordovician cylindrical borings: U.S. Geological Survey Professional Paper, v. 953, p. 1–26.

Ceranka, T., and Zlotnik, M., 2003, Traces of cassid snails predation upon the echinoids from the middle Miocene of Poland: *Acta Palaeontologica Polonica*, v. 48, p. 491–496.

Challis, G.R., 1979, Miocene echinoid biofacies of the Maltese Islands: *Annales Géologiques des Pays Helléniques*, tome hors série, v. 1, p. 253–262.

Challis, G.R., 1980, *Palaeoecology and Taxonomy of mid-Tertiary Maltese echinoids* [Ph.D. dissertation]: London, University of London, 401 p.

Conway Morris, S., and Bengtson, S., 1994, Cambrian predators: Possible evidence from boreholes: *Journal of Paleontology*, v. 68, p. 1–23.

Cotteau, G.H., 1895, *Echinides recueillis par M. Lovisato dans le Miocène de Sardaigne*. Mémoires de la Société Géologique de France: *Palaeontologie, Mémoire*, v. 13, p. 1–56.

Cottreau, J., 1914, *Les Échinides néogènes du Bassin Méditerranéen*: *Annales de l'Institut Océanographique Monaco*, v. 6, p. 1–192.

Deline, B., 2008, The first evidence of predatory or parasitic drilling in stylophoran echinoderms: *Acta Palaeontologica Polonica*, v. 53, p. 739–743.

Föllmi, K.B., Gertsch, B., Renevey, J.-P., de Kaenel, E., and Stille, P., 2008, Stratigraphy and sedimentology of phosphate-rich sediments in Malta and south-eastern Sicily (latest Oligocene to early late Miocene): *Sedimentology*, v. 55, p. 1029–1051.

Foresi, L.M., Verducci, M., Baldassini, N., Lirer, F., Mazzei, R., Salvatorini, G., Ferraro, L., and Da Prato, S., 2011, Integrated stratigraphy of St. Peter's Pool section (Malta): New age for the Upper Globigerina Limestone Member and progress towards the Langhian GSSP: *Stratigraphy*, v. 8, p. 125–143.

Ghiold, J., 1982, Observations on the clypeasteroid *Echinocyamus pusillus* (O.F. Müller): *Journal of Experimental Marine Biology and Ecology*, v. 61, p. 57–74.

Giannelli, L., and Salvatorini, G., 1972, I foraminiferi planctonici dei sedimenti terziari dell'Arcipelago maltese: *Biostratigrafia del "Globigerina Limestone" I*, *Atti della Società Toscana di Scienza Naturali, Memorie, Serie A*, v. 82, p. 1–24.

Gregory, J.W., 1891, The Maltese fossil Echinoidea and their evidence on the correlation of the Maltese rocks: *Transactions of the Royal Society of Edinburgh*, v. 36, p. 565–639.

Grun, T.B., and Nebelsick, J.H., 2015, Sneaky snails: How drill holes can affect paleontological analyses of the minute clypeasteroid echinoid *Echinocyamus*, in Zamora, D., and Rábano, I., eds., *Progress in Echinoderm Palaeobiology*: Madrid, Cuadernos del Museo Geominero, 19. Instituto Geológico y Minero de España, p. 71–74.

Grun, T., Sievers, D., and Nebelsick, J.H., 2014, Drilling predation on the clypeasteroid echinoid *Echinocyamus pusillus* from the Mediterranean Sea (Giglio, Italy): *Historical Biology*, v. 26, p. 745–757.

Gruszczynski, M., Marshall, J.D., Goldring, R., Coleman, M.L., Małkowski, K., Gaździcka, E., Semil, J., and Gatt, P., 2008, Hiatal surfaces from the

- Miocene Globigerina Limestone Formation of Malta: Biostratigraphy, sedimentology, trace fossils and early diagenesis: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 270, p. 239–251.
- Harper, E.M., 2003, Assessing the importance of drilling predation over the Palaeozoic and Mesozoic: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 201, p. 185–198.
- Hoffmeister, A.P., Kowalewski, M., Baumiller, T.K., and Bambach, R.K., 2004, Drilling predation on Permian brachiopods and bivalves from the Glass Mountains, west Texas: *Acta Palaeontologica Polonica*, v. 49, p. 443–454.
- Hughes, R.N., and Hughes, H.P.I., 1971, A study of the gastropod *Cassia tuberosa* (L.) preying upon sea urchins: *Journal of Experimental Marine Biology and Ecology*, v. 7, p. 305–314.
- Hughes, R.N., and Hughes, H.P.I., 1981, Morphological and behavioural aspects of feeding in the cassidae (Tonnacea, Mesogastropoda): *Malacologia*, v. 20, p. 385–402.
- Huntley, J.W., and Kowalewski, M., 2007, Strong coupling of predation intensity and diversity in the Phanerozoic fossil record: *PNAS*, v. 104, p. 15006–15010.
- Janssen, A.W., 2012, Systematics and biostratigraphy of holoplanktonic Mollusca from the Oligo-Miocene of the Maltese Archipelago: *Bollettino del Museo Regionale di Scienze Naturali*, v. 28, p. 197–605.
- Kelley, P.H., 1988, Predation by Miocene gastropods of the Chesapeake Group: Stereotyped and predictable: *Palaiois*, v. 3, p. 436–448.
- Kelley, P.H., 1989, Evolutionary trends within bivalve prey of Chesapeake Group naticid gastropods: *Historical Biology*, v. 2, p. 139–156.
- Kelley, P.H., 2001, The role of ecological interactions in the evolution of naticid gastropods and their molluscan prey, in Allmon, W., and Bottjer, D., eds., *Evolutionary Paleocology*: New York, Columbia University Press, p. 149–170.
- Kowalewski, M., and Nebelsick, J.H., 2003, Predation on recent and fossil echinoids, in Kelley, P.H., Kowalewski, M., and Hansen, T.A., eds., *Predator-Prey Interactions in the Fossil Record*: New York, Kluwer Academic/Plenum Publishers, p. 279–302.
- Kowalewski, M., Dulai, A., and Fürsich, A.T., 1998, A fossil record full of holes: The Phanerozoic history of drilling predation: *Geology*, v. 26, p. 1091–1094.
- Kowalewski, M., Hoffmeister, A.P., Baumiller, T.B., and Bambach, R.K., 2005, Secondary evolutionary escalation between brachiopods and enemies of other prey: *Science*, v. 308, p. 1774–1777.
- Kroh, A., 2004, First fossil record of the family Euryalidae (Echinodermata: Ophiuroidea) from the Middle Miocene of the Central Mediterranean, in Heinzeller, T., and Nebelsick, J.H., eds., *Echinoderms*: München: London, Taylor & Francis, p. 447–452.
- Kroh, A., and Nebelsick, J.H., 2006, Stachelige Leckerbissen: *Natur und Museum*, v. 136, p. 6–14.
- Lamarck, C., 1816, *Histoire Naturelle des Animaux sans Vertèbres*: Paris, Verdrière, 586 p.
- Lambert, J., 1909, Description des échinides fossiles des terrains miocéniques de la Sardaigne: *Mémoires de la Société Paléontologique Suisse*, v. 35, p. 73–142.
- Lierl, H.J., 1992, Tenside - ihre Verwendung für die Präparation geologisch-paläontologischer Objekte: *Der Präparator*, v. 38, p. 12–17.
- Lützen, J., and Nielsen, K., 1975, Contributions to the anatomy and biology of *Echineulima* n.g. (Prosobranchia, Eulimidae): *Videnskabelige Meddelelser fra den Naturhistoriske Forening i Kjøbenhavn*, v. 138, p. 171–199.
- Mazzei, R., 1985, The Miocene Sequence of the Maltese Islands: Biostratigraphic and chronostratigraphic references based on nannofossils: *Atti della Società Toscana di Scienze Naturali, Memorie A*, v. 92, p. 165–197.
- Mazzetti, G., 1893, Catalogo degli echini del mar rosso e descrizione di sp. n.: *Atti della Società del Naturalisti die Modena Serie III*, v. 12, p. 239–240.
- Meadows, C.A., Fordyce, R.E., and Baumiller, T.K., 2015, Drill holes in the irregular echinoid, *Fibularia*, from the Oligocene of New Zealand: *Palaiois*, v. 30, p. 810–817.
- Mooi, R., 1989, Living and fossil genera of the clypeasteroidea (Echinoidea: Echinodermata): An illustrated key and annotated checklist: *Smithsonian Contributions to Zoology*, v. 488, p. 1–51.
- Mortensen, T., 1927, *Handbook of the Echinoderms of the British Isles*: London, UK, Humphrey Milford Oxford University Press, 471 p.
- Mortensen, T., 1948, A Monograph of the Echinoidea IV.2 Clypeasteroidea. Clypeasteridæ, Arachnoidæ, Fibulariidae, Laganidae and Scutellidae. Copenhagen, Denmark: C.A. Reitzel, 471 p.
- Müller, O.F., 1776, *Zoologica prodromus, seu animalium Daniae et Norvegiae indigenarum characteres, nomina, et synonyma imprimis popularium: Havniae [Copenhagen], Typis Hallageriis*, 282 p.
- Nebelsick, J.H., 1999, Taphonomic comparison between Recent and fossil sand dollars: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 149, p. 349–358.
- Nebelsick, J.H., 2008, Taphonomy of the irregular echinoid *Clypeaster humilis* from the Red Sea: Implications for taxonomic resolutions along taphonomic grades, in Ausich, W.I., and Webster, G.D., eds., *Echinoderm Paleobiology*: Bloomington, Indiana University Press, p. 114–128.
- Nebelsick, J.H., and Kowalewski, M., 1999, Drilling predation on recent clypeasteroid echinoids from the Red Sea: *Palaiois*, v. 14, p. 127–144.
- Palmer, A.R., 1982, Predation and parallel evolution: Recurrent parietal plate reduction in balanomorph barnacles: *Paleobiology*, v. 8, p. 31–44.
- Pedley, H.M., 1992, Bio-retexturing: Early diagenetic fabric modifications in outer-ramp settings—A case study from the Oligo-Miocene of the Central Mediterranean: *Sedimentary Geology*, v. 79, p. 173–188.
- Pedley, H.M., and Bennett, S.M., 1985, Phosphorites, hard-grounds and syndepositional solution subsidence: A palaeoenvironmental model from the Miocene of the Maltese Islands: *Sedimentary Geology*, v. 45, p. 1–34.
- Pedley, H.M., House, M.R., and Waugh, B., 1978, The geology of the Pelagian Block: The Maltese Islands, in Nairn, A.E.M., Kaness, W.H., and Stehli, F.G., eds., *The Ocean Basins and Margins: The Western Mediterranean*: London, Plenum Press, p. 417–433.
- Pedley, H.M., Hughes, C.M., and Galea, P., 2002, Limestone Isles in a Crystalline Sea—The Geology of the Maltese Islands: San Gwann, Publishers Enterprise Group Ltd., 109 p.
- Rehfeld, U., and Janssen, A.W., 1995, Development of phosphatized hard-grounds in the Miocene Globigerina Limestone of the Maltese archipelago, including a description of *Gamopleura melitensis* sp. nov. (Gastropoda, Euthecosomata): *Facies*, v. 33, p. 91–106.
- Reyment, R.A., 1966, Preliminary observations on gastropod predation in the western Niger Delta: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 2, p. 81–102.
- Rose, E.P.F., 1974, Stratigraphical and facies distribution of irregular echinoids in Miocene limestones of Gozo, Malta, and Cyrenaica, Libya: *Mémoires du Bureau de Recherches Géologiques et Minières*, v. 78, p. 349–355.
- Rose, E.P.F., 1975, Oligo-Miocene echinoids of the Maltese Islands: Proceedings of the VIth Congress of the Regional Committee on Mediterranean Neogene Stratigraphy, v. 1, p. 75–79.
- Rose, E.P.F., Pratt, S.K., and Bennett, S.M., 1992, Evidence for sea-level changes in the Globigerina Limestone Formation (Miocene) of the Maltese Islands: *Paleontologia I Evolutio*, v. 24, p. 265–276.
- Schultz, H., 2006, *Sea Urchins I: A Guide to Worldwide Shallow Water Species* (third edition): Hemdingen, Heinke and Peter Schultz, 495 p.
- Seilacher, A., 1979, Constructional morphology of sand dollars: *Paleobiology*, v. 5, p. 191–221.
- Stefanini, G., 1908, Echinidae mioceni di Malta esistenti nel museo di geologica di Firenze: *Bollettino del Sociedad Geologica d'Italia*, v. 27, p. 435–483.
- Tapanila, L., Roberts, E.M., Bouaré, M.L., Sissoko, F., and O'Leary, M.A., 2008, Phosphate taphonomy of bone and coprolite conglomerates: A case study from the Eocene of Mali, NW Africa: *Palaiois*, v. 23, p. 139–152.
- Warén, A., and Crossland, M., 1991, Revision of *Hypermastus* Pilsbry, 1899 and *Turveria* Berry, 1956 (Gastropoda: Prosobranchia: Eulimidae), two genera parasitic on sand dollars: *Records of the Australian Museum*, v. 43, p. 85–112.
- Warén, A., Norris, D., and Templado, J., 1994, Descriptions of four new eulimid gastropods parasitic on irregular sea urchins: *Veliger*, v. 37, p. 141–154.
- Wisshak, M., Kroh, A., Bertling, M., Knaust, D., Nielson, J.K., Jagt, J.W.M., Neumann, C., and Nielsen, K.S.S., 2015, In defence of an iconic ichnogenus—*Oichnus* Bromley, 1981: *Annales Societatis Geologorum Poloniae*, v. 85, p. 445–451.
- Wright, T.W., 1855, On fossil echinoderms of the Island of Malta: *Annals of Natural History London Ser. 2*, v. 15, p. 101–127.
- Wright, T.W., 1864, On the fossil Echinoidea of Malta: *Quarterly Journal of the Geological Society of London*, v. 20, p. 470–491.
- Young, D.K., 1969, *Okadaia elegans*, a tube-boring nudibranch mollusc from the central and west Pacific: *American Zoologist*, v. 9, p. 903–907.
- Zachos, L., 2015, Holistic morphometric analysis of growth of the sand dollar *Echinarachnius parma* (Echinodermata:Echinoidea:Clypeasteroidea): *Zootaxa*, v. 4052, p. 151–179.
- Zammit-Maempel, G., 1969, A new species of *Coelopleurus* (Echinoidea) from the Miocene of Malta: *Palaeontology*, v. 12, p. 42–47.
- Złotnik, M., and Ceranka, T., 2005, Patterns of drilling predation of cassid gastropods preying on echinoids from the middle Miocene of Poland: *Acta Palaeontologica Polonica*, v. 50, p. 409–428.

Accepted 20 July 2016