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PREDATION-FACILITATED PRESERVATION OF ECHINOIDS IN A TROPICAL MARINE ENVIRONMENT

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ABSTRACT: **Actuopaleontological studies of echinoids and their predators in modern ecosystems can augment our ability to identify and interpret the fossil record of predation. Here, we examine present-day interactions between the spatangoid *Meoma ventricosa* and the drilling gastropod *Cassis tuberosa* from a shallow tropical marine habitat (San Salvador Island, Bahamas) to assess the impact of drilling predation on the fossilization potential of echinoids, estimate drilling frequency, characterize drill hole morphology, and evaluate size and site selectivity of predators. Cassids produced recognizable drill holes ranging from 2–14 mm in diameter. A comparison of drilled versus live individuals suggested that predation was size-selective with preference toward smaller prey ($p << 0.001$), whereas landmark morphometrics revealed no evidence of stereotypy in specific attack site, drill holes were preferentially located on the oral side of the test (85.2%). Although the annual mortality of *M. ventricosa* attributed to *C. tuberosa* was 0.021 individuals per m^2, the drilling frequency in samples of dead echinoid tests was 96.8%. This exceedingly high drilling frequency most likely reflects the fact that echinoids killed by *C. tuberosa*—a predator that immobilizes, drills, kills, and consumes *M. ventricosa* buried in the sediment—have a greater chance of preservation than echinoids that died due to other causes (e.g., fish predation). These results not only suggest that the frequency of drilled prey specimens may greatly exaggerate the importance of certain species of drilling predators, but also indicate that certain predators may play a critical role in enhancing the fossilization potential of their prey.**

INTRODUCTION

Using observations from present-day ecosystems to better interpret paleontological data ("actuopaleontology") has been a remarkably fruitful approach when applied to the fossil record of drilling predation (e.g., Kitchell et al. 1981; Kelley and Hansen 2007; Schiffbauer et al. 2008; Tyler and Schiffbauer 2012; Tyler et al. 2013; Grun 2017). However, with respect to predator-prey interactions this avenue of research, both in modern settings and the fossil record, has primarily focused on drilling organisms that interact with mollusks (e.g., Vermeij 1977, 1983; Vermeij et al. 1980, 1981; Kitchell et al. 1981, 1986; Kelley and Hansen 1993; Kowalewski et al. 1998; Dietl et al. 2000; Hoffmeister and Kowalewski 2001; Kowalewski 2004; Yanes and Tyler 2009). In contrast, other important prey groups such as echinoids have remained understudied from a paleontological perspective (Harper 2016), limiting our understanding of the ichnological and taphonomic aspects of echinoid predation. While there has been a growing interest in traces produced by predators that consume echinoids in modern environments (e.g., Grun et al. 2014; Grun 2017; Sievers and Nebelsick 2018), numerous additional case studies are needed to provide a comprehensive assessment across a full range of predator taxa, prey taxa, and habitats. The project reported here, and similar future studies, are needed to develop an adequate reference baseline for interpreting the fossil record of predation on echinoids.

If echinoids are to be employed to advance our understanding of biotic interactions as an ecological and evolutionary process, the potential for predation traces to introduce taphonomic biases must be rigorously evaluated. The use of drill holes to interpret patterns of predation intensity in fossil assemblages is contingent upon the assumption that the relative abundance of drilled and undrilled specimens accurately reflects that of the community from which they are derived, and that drilled and undrilled specimens accumulate in the same manner. This assumption has been debated and repeatedly tested for mollusks and brachiopods (e.g., Roy et al. 1994; Hagstrom 1996; Kaplan and Baumiller 2000; Zuschin and Stanton 2001; Kowalewski 2002; Kelley 2008; Molinaro et al. 2013). However, comparable evaluations of taphonomic biases affecting predation traces in echinoid fossil assemblages are relatively sparse (but see discussions in Nebelsick 1998; Nebelsick and Kowalewski 1999; Ceranka and Złotnik 2003; Złotnik and Ceranka 2005a; Grun et al. 2014; Grun and Nebelsick 2015). As quantitative assessments of the potential impact of drill holes on echinoid preservation are limited, the effects of drill holes on preservation potential are currently largely anecdotal and speculative. If drill holes weaken echinoid tests, then drilled specimens should be more susceptible to mechanical, chemical, and biological alteration, preferentially removing drilled tests and thus underestimating drilling frequencies. In addition, several other issues hinder the interpretation of predation traces on fossil echinoids. Recognizing traces produced by predation and identifying the predator that produced the trace remains problematic (Ceranka and Złotnik 2003; Donovan and Pickerill 2004; Złotnik and Ceranka 2005b; Meadows et al. 2015). A range of distinct traces found on Recent and fossil echinoids have been attributed to predation, especially drill holes made by cassid gastropods (e.g., Moore 1956; Chesher 1969; Hughes and Hughes 1971, 1981; Beu et al. 1972; Hendler 1977; Gladfelter 1978; Gibson and Watson 1989; McClintock and Marion 1993; McClanahan 1999; Nebelsick and Kowalewski 1999; Ceranka and Złotnik 2003; Kowalewski and Nebelsick 2003; Złotnik and Ceranka 2005a). However, descriptions of the morphology and ecology of drill holes produced by cassids are limited, and identifying cassids as the trace-maker on fossil echinoids remains contentious, due to the paucity of diagnostic

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criteria and modern ecological data (e.g., Donovan and Pickerill 2004; Złotnik and Ceranka 2005b). Modern observations of echinoid predation by known predators, could therefore also improve our ability to identify and interpret these interactions in the fossil record.

Cassid gastropods are found in tropical sand and reef environments around the world, and their diet is typically dominated by echinoids (Hughes and Hughes 1981). For example, echinoids are known prey of the King Helmet, *Cassis tuberosa* (Linnaeus 1758) (e.g., Hughes and Hughes 1981; Grun and Nebelsick 2017), and in sandy substrates cassids tend to feed on burrowing echinoids (Hughes and Hughes 1981), such as *Meoma ventricosa* (Lamarck 1816), a deposit feeding spatangoid echinoid that occurs in tropical nearshore areas at depths of up to 200 m (Chesher 1969; Hughes and Hughes 1981). *Meoma ventricosa* burrows within the top 10 cm of sediment, and may emerge at night (Kier and Grant 1965; Chesher 1969). During predation, cassids frequently produce drill holes that vary in size, morphology, and location on the prey test (see Grun 2017, table 1), providing direct evidence of predator-prey interactions and predator ecology. Cassids have been observed to selectively drill on a preferred location on the tests of some prey, however, observations of site selectivity are highly variable and differ across species (e.g., Abbott 1968; McClintock and Marion 1993; Nebelsick and Kowalewski 1999). Several factors may contribute to site selectivity by gastropod predators, such as specific hunting and handling techniques, targeting weaker portions of the echinoid test that is easier to penetrate, access to high energetic value tissues in a specific region (Kitchell et al. 1981), or avoidance of defensive spines.

Here, we employ a modern tropical marine environment as a natural laboratory to examine predation by the gastropod *C. tuberosa* on *M. ventricosa*. Surveys of the live population of *M. ventricosa* were conducted in conjunction with *in situ* collections of the tests of dead echinoids and laboratory observations of interactions between live cassids and echinoids. This study aims to: (1) assess the impact of drilling predation on the fossilization potential of echinoid tests; (2) characterize drill hole morphology using laboratory feeding trials and drilled tests collected in the field; and (3) quantitatively identify ecological signatures of drilling predation by cassids, such as site and size selectivity. A detailed examination of modern interactions and how they impact the potential for preservation of prey tests should enhance our ability to interpret the paleoecology of fossil echinoids.

MATERIALS AND METHODS

This study was conducted on San Salvador Island, located at the southeast edge of the Commonwealth of the Bahamas (Fig. 1). Sand Dollar Beach is on the northwest side of the island (24.10524°, -74.519195° WGS 84) $\sim$ 1.25 km north of the Victoria Hills Settlement, and live echinoids are abundant along the northern section of the shore. The small, shallow water area ($<$ 5 m depth) is partially protected by a jutting point to the north, and a strip of patchy coral reefs run parallel to the beach, starting $\sim$ 500 m out from the shoreline and extending out to the escarpment roughly 1,400 m from shore. The environment between the reef and the shoreline is composed of fine grained carbonate sand free of seagrasses, and is populated by numerous live individuals of the infaunal echinoid, *M. ventricosa* (Fig. 2A, 2B), often found on the sediment surface, or covered in a thin coating of sediment ($<$ 1 cm) at the terminal end of their feeding tracks (Fig. 2C). The field site consisted of a 250 m $\times$ 100 m ($\sim$ 0.025 km^2) section of this wave protected area.

In 2013, live specimens of *M. ventricosa* visible on or buried in the shallow subsurface were surveyed using SCUBA within a smaller 25 m^2 subset of the field area to estimate prey density. Drilling frequency was quantified from dead tests collected in the study area over five time intervals: 2010 (June–July), 2012 (July–August), 2013 (April), 2014 (April), and 2015 (July). In 2010, all dead *M. ventricosa* tests were

FIG. 1.—Map of the study area (San Salvador Island, Bahamas). The arrow on the inset map in the top left shows location of San Salvador relative to the rest of the Bahamas archipelago. Samples were collected from Sand Dollar Beach (denoted by star).

collected that were visible at or near the sediment surface over the entire field area, and for the following 24 days, surveys were conducted every three days to collect accumulating tests. In 2012–2015, dead tests were collected once a week. All dead tests were examined for evidence of predation by *Cassis,* and the daily mortality due to *C. tuberosa* could thus be estimated and compared with the drilling frequency in the death assemblage. As the diameter of drill holes made by *C. tuberosa* correlates with the size of the predator (Hughes and Hughes 1981), maximum and minimum drill hole diameter was measured, and the relationship between drill hole size and prey size was estimated using a Pearson's product moment correlation in R V3.3.3 (R Development Core Team 2016). All measurements of drill holes and *M. ventricosa* tests were made from photographs using ImageJ (1.46r).

Size selectivity was examined by comparing the size distribution of live *M. ventricosa* with the sizes of drilled tests in the death assemblage. In 2013, 2014, and 2015 all live individuals within the study site were surveyed, photographed and immediately released. Prey size in both the live population and death assemblage was determined using linear measurements of the length and width of *M. ventricosa*. Length was measured as the distance from the anus to the divot in the test above the mouth in ambulacral column III, and width was measured at the maximum distance along the test perpendicular to length. Size differences between the live population and dead tests were compared using a Wilcoxon rank-sum test, a nonparametric alternative to the two-sample t-test in R V3.3.3 (R Development Core Team 2016).

To assess site selectivity, two-dimensional landmark coordinates were acquired using ImageJ for the following landmark and pseudo-landmarks (Fig. 2B): (1) posterior bulge below the anus; (2) point of maximum width on the left side; (3) the anterior edge of the test above the mouth; (4) point of maximum width on the right side; and (5) midpoint of the drill hole. Landmarks were chosen to characterize the shape of the test, so that the location of drill holes could be compared across specimens of different sizes (Roopnarine 1999). Landmark analysis was performed using

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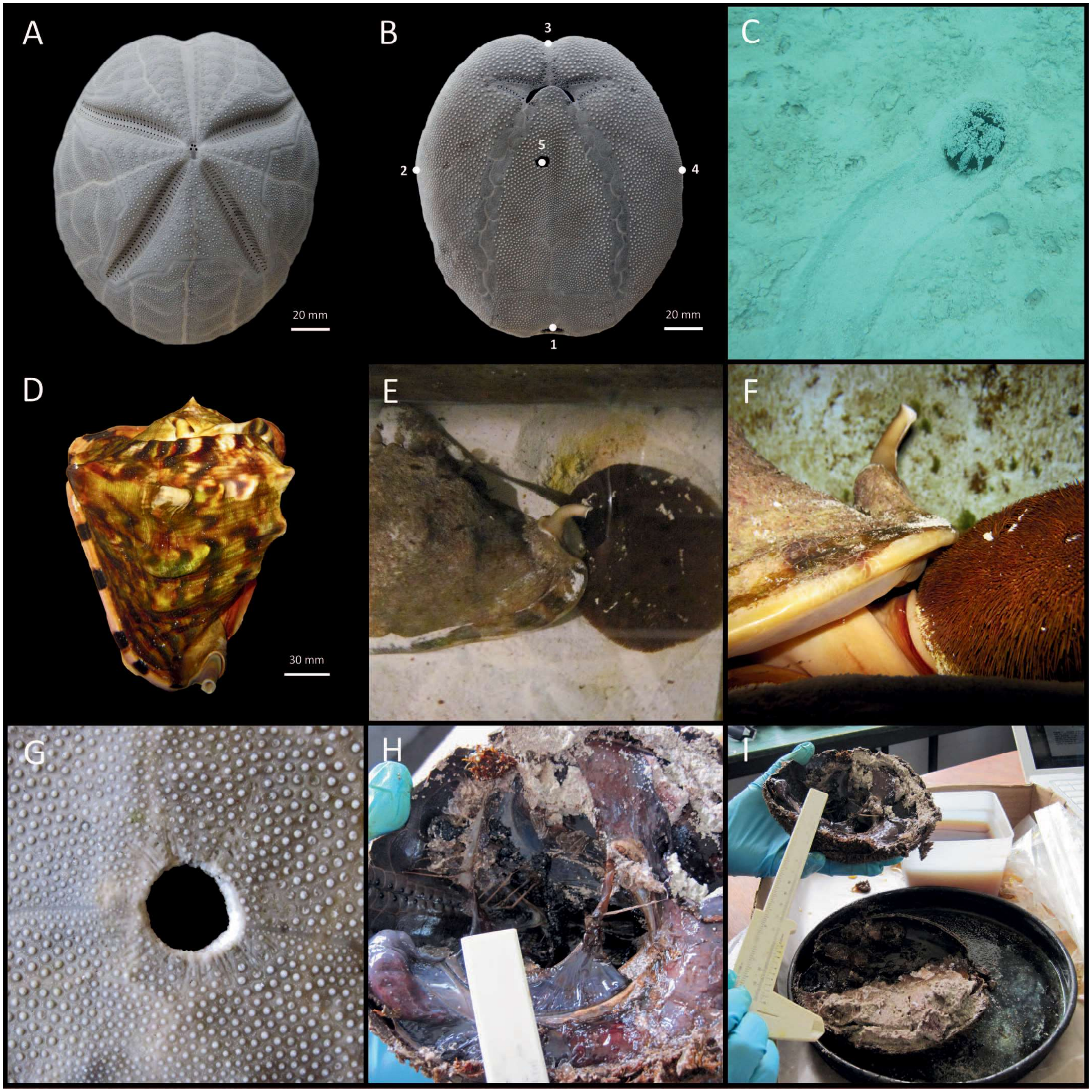

FIG. 2.—Specimens. **A**) Aboral view of *Meoma ventricosa*. **B**) Oral view of *M. ventricosa* showing the positions of landmarks 1–5. **C**) Live *M. ventricosa* from the field area. **D**) *Cassis tuberosa*. **E**) *Cassis tuberosa* attacking *M. ventricosa* in the lab. **F**) *Cassis tuberosa* feeding on *M. ventricosa* in the lab. **G**) The resultant drill hole from E, F. **H**) The internal remains of *M. ventricosa* after feeding by *C. tuberosa*. **I**) Internal cavity of a dead test collected from the field area.

Bookstein scaling and rotation of coordinates (Bookstein 1991) with custom code written by Kowalewski in R, assigning Landmark 1 and Landmark 3 as the baseline (Fig. 2B).

Reports of drill hole shapes produced by cassids vary from cylindrical to irregular in outline. *Cassis tuberosa* penetrates the echinoid test with the aid of a chelating agent secreted by the accessory boring organ (Hughes and Hughes 1971, 1981), and in some cases, evidence of acid etching has been observed (Kowalewski and Nebelsick 2003; Grun 2017). To characterize traces produced by *C. tuberosa* and facilitate the identification of drilling predation on dead echinoid tests, a number of live specimens were brought back to the Gerace Research Center for feeding trials in 2010. Specimens were housed in sea tables with continuous flow of marine water at a depth of 30 cm, which were filled with an $\sim$ 10 cm layer of uniform sand to accommodate the infaunal lifestyle of *M. ventricosa*. One *C. tuberosa* was placed in a sea table with a single *M. ventricosa*, and observations of feeding activity were made periodically during the day and late into evening over the course of a week. The appearance of drill holes produced in feeding trials were compared with drill holes observed on

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TABLE 1.—*Annual specimen collection. The mean specimen length (mm) and number of specimens for both the live and dead* Meoma ventricosa *tests collected in each field season. The mean size and number of dead specimens that were undrilled, drilled on the oral side, and drilled on the aboral side are also shown.*

	2010		2012		2013		2014		2015		Total	
Year	Mean	n	Mean	n	Mean	n	Mean	n	Mean	n	Mean	n
Live	-	-	-	-	169	28	158	76	165	65	163	169
Dead	148	64	170	31	160	22	161	8	-	-	157	125
Undrilled	148	2	0	0	155	2	0	0	-	-	152	4
Drilled Oral	148	50	172	29	155	13	162	6	-	-	157	98
Drilled Aboral	149	12	150	2	171	7	161	2	-	-	157	23

specimens in the death assemblage, to corroborate *C. tuberosa* as the trace-maker.

RESULTS

In 2013, 27 live *M. ventricosa* were observed in the 25 m^2 subset of the field area, an estimated density of 1.08 individuals per m^2. A total of 169 live individuals were collected and measured from the entire field area (0.025 km^2) during the 2014 and 2015 field seasons (Table 1), resulting in a pooled average density estimate from 2014–2015 of 0.007 live individuals per m^2. For data pooled across all field seasons, average test length was 163 mm and 157 mm for live and dead specimens respectively (Table 1, Fig. 3), a difference that was statistically significant (Wilcoxon rank test $W = 6969$, $p << 0.0001$). As pooled samples compare specimens collected in different years, a second comparison was made using only live and dead samples collected during 2013, which is the only year with sufficient sample sizes of both live and dead samples for a meaningful comparison. The difference in mean test length remained significant ($W = 180$, $p = 0.01$) for 2013 samples.

A live *C. tuberosa* specimen was directly observed feeding on *M. ventricosa* in the laboratory feeding trials. The cassid began drilling the prey at approximately 8:00 pm and finished feeding the following morning (Fig. 2E, 2F). The dead *M. ventricosa* specimen was dissected, revealing a small amount of tissue left behind in the test, predominantly most of the digestive tract (Fig. 2H). The drill hole produced by the predator had jagged edges and was circular in shape with perpendicular abrasive markings around the opening, which we interpret as radula rasping traces (Fig. 2G). The drill hole opening did not follow test plate sutures but rather transected plates independent of their boundaries. These characteristics were used to confirm *C. tuberosa* as the predator when examining drill holes on dead tests.

In 2013, the daily mortality rate of *M. ventricosa* was ~ 1.4 individuals per day, or $\sim 5.67 \times 10^{-5}$ individuals per m^2 per day in the field area (Table 2). Over the course of a year, this would result in an annual mortality of 0.021 individuals per m^2. Specimens collected on the first day of sampling ($n = 30$) were removed from the mortality calculation as these specimens represented accumulation of tests over an indeterminate length of time. The dead specimens collected ($n = 34$) subsequently represented a total of 24 collection days. Live *C. tuberosa* were found in the sampling area during every collection season, and empty shells of deceased *C. tuberosa* were recovered in the sampling area during the first and final collection seasons.

A total of 125 tests of deceased *M. ventricosa* were collected over the course of this study (Table 1). Many of these tests were well preserved and appeared to be in the early stages of decomposition, retaining spines and coloration. Of the 125 tests, only four tests (3.2%) were not drilled, whereas 102 (96.8%) possessed distinct drill holes. Interestingly, a single live specimen possessed a distinct, complete drill hole on the oral side of the test, but had apparently survived the predatory encounter (this specimen was measured and photographed in the field and then immediately returned to its habitat). Drill holes were roughly circular in shape, completely penetrated the test, and were predominantly located on the oral side (see below). Multiple holes rarely occurred, and in some cases, radula rasping marks were present around the edges of the drill hole (Fig. 2G). Live *C. tuberosa* were also observed in the sampling area during every collection season, and shells of deceased *C. tuberosa* were collected at the site each year. Drill holes ranged from 2 to 14 mm in diameter, with a mean diameter of 7.1 mm (Fig. 4A), and were highly circular with a strong correlation ($r = 0.84$, $p << 0.0001$) between the maximum and minimum diameter of the drill hole (Fig. 4B). There was a weak negative correlation between maximum drill hole diameter and test length ($r = -0.21$, $p = 0.02$) (Fig. 5). The mean dead test length (Table 1) was significantly different between all pairwise comparisons across field seasons (Tukey's HSD adjusted p values) except 2014–2012, and 2014–2013 (Fig. 6).

Of the drilled specimens, 98 (81%) were drilled on the oral side, and 23 (19%) were drilled on the aboral side. Multiple holes rarely occurred, and only five specimens possessed two drill holes. On four of these individuals both drill holes were located on the oral side, and on one individual, there was a drill hole located on the oral side and another on the aboral side of the test. There was no significant difference in test length between orally and aborally drilled specimens ($W = 1293$, $p = 0.2$). *Meoma ventricosa* varied little in test size and shape, and there is no apparent pattern of drill hole location on either the oral or aboral side of the test (Fig. 7).

DISCUSSION

Laboratory observations confirmed that *C. tuberosa* produced distinctive drill holes that were readily identified on dead tests collected from the study area. The exceedingly high drilling frequency in the death assemblage points to a bias towards preferential preservation of *drilled* specimens. First, the observed frequency is outside the range of drilling frequencies previously reported (1%–94.7%) for other echinoids preyed upon by cassids (McClintock and Marion 1993; Nebelsick and Kowalewski 1999; Grun et al. 2014; Grun and Nebelsick 2015). Second, the overall drilling frequency was high in the context of the low daily mortality estimates, and the discrepancy between the estimated annual mortality at this locality of $\sim 1\%$ (derived from the systematic removal of dead tests in 2013) relative to the 98% drilling frequency is striking. Although echinoid mortality was low, the exceptionally high drilling frequency may generate an inaccurate perception of high predation mortality. Given the similarity between drill holes observed on dead tests and those produced in feeding trials, and given that only two specimens were not drilled, the death assemblage of *M. ventricosa* recorded mortality which can be attributed almost entirely to predation by drilling predators. However, it is improbable that cassids account for 98% of the mortality from predation, and other sources of mortality are likely (e.g., predation by rays and ray pits were observed in the field area; Grun 2016). Moreover, infaunal post-mortem scavenging of dead, decomposing echinoids by cassids may also produce some drill holes when attempting to access internal tissue, and inflate drilling frequency. In taphonomic decay experiments, Greenstein (1991) noted that after only one day, numerous cassid gastropods were present on dead specimens of *Diadema antillarium* (Philippi 1845) buried in the substratum (dead *Diadema* were undamaged at the time of burial). Undrilled tests accumulating on the sediment surface may be removed by other taphonomic processes (transport, physical damage, etc.) and subject to scavenging by fish, crabs, and rays, abundant in the area, destroying tests shortly after death. Furthermore, echinoid preservation is lowest in tropical warm water environments, and tests remaining on the sediment surface would likely disintegrate in only a few days (Kidwell and Baumiller 1990; Greenstein 1991). Consistent with these predictions, recent radiocarbon dating efforts at San Salvador Island

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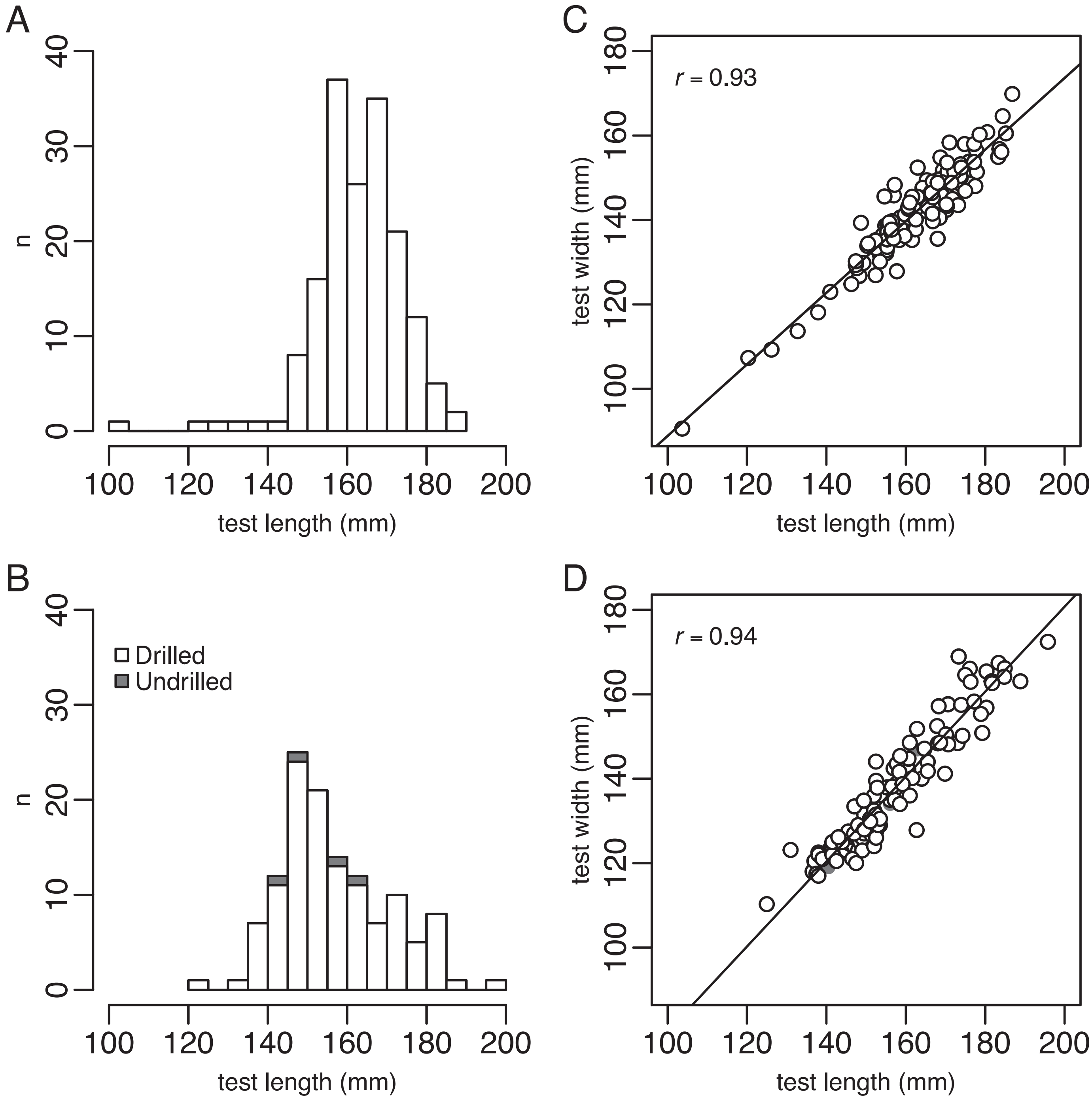

FIG. 3.—Size selectivity. **A**, **B**) Prey-size distributions of live and dead *Meoma ventricosa*, respectively. The live population contained larger individuals on average than the death assemblage (Wilcoxon $p < 0.0001$), indicative of size selectivity by *Cassis tuberosa* for smaller individuals. **C**, **D**) Test length and width plots for live and dead populations, respectively. Strong correlations are evident in both the live population and the dead tests (r = Pearson's correlation coefficient, $p << 0.0001$).

indicate that irregular echinoids last at most only a few years near the sediment surface (Kowalewski et al. 2018).

Predation-facilitated preservation may occur for two reasons. First, in the specific case of *M. ventricosa*, predators frequently immobilize, kill, and consume their echinoid prey under the sediment surface (Hughes and Hughes 1981) resulting in immediate burial upon death, which should greatly improve the probability for the preservation of drilled tests. This process minimizes the post-mortem exposure time on the surface, thus increasing the preservation potential of the test (although a minimum depth of burial may be necessary to protect tests from temperature effects; Kidwell and Baumiller 1990). Second, by penetrating the test and removing the majority of the soft issue (including internal soft tissue covering the anal opening), cassid predators facilitate sediment infill and prevent decay gases from accumulating internally within the test. Indeed, in feeding trials, *C. tuberosa* consumed a significant portion of the internal tissue of the prey, leaving the test cavity largely empty (Fig. 2H).

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TABLE 2.—*Mortality rate. The average daily* Meoma ventricosa *test accumulation was 1.4/day over the course of the first field season (a total of 24 days), and served as a proxy for echinoid mortality. The number of tests collected on the first day represents an unknown period of time, and was therefore excluded from the mortality rate calculation. Rows represent years of field seasons, and columns represent days within each field season.*

	1	2	5	8	10	11	14	15	17	24	25	30	Total
2010	30	2	4	4	-	5	6	-	1	12	-	-	64
2012	-	-	-	-	19	-	-	12	-	-	-	-	31
2013	-	-	-	-	-	1	-	21	-	-	-	-	22
2014	-	-	-	-	-	-	-	-	-	-	6	2	8

Moreover, dead tests collected from the study area, including freshly dead specimens still retaining spines and coloration, were typically filled with sediment (Fig. 2I). In sum, predation by cassids may facilitate the preservation of dead tests by burying dying prey, removing soft tissue, and enabling rapid sediment infill. Whether this process is widespread for echinoids or unique to specific predators, prey, and habitats remains unclear. Additional studies of the role of drill holes in echinoid preservation from a variety of habitats and sedimentation regimes among different taxa are needed to evaluate this hypothesis and the magnitude of the potential impact on the fossil record.

The secretion of acid during feeding weakens the echinoid test (Hughes and Hughes 1981), and test damage associated with drill holes have also been observed in the fossil record (Złotnik and Ceranka 2005a). Nebelsick and Kowalewski (1999), however, found no relationship between the degree of pre-burial taphonomic alteration and the presence of drill holes. In cases where drill holes weaken echinoid tests enough to make drilled specimens more susceptible to mechanical, chemical, and biological alteration, drilled tests should be preferentially destroyed, leading to the underestimation of drilling frequencies. The low number of undrilled tests observed here suggests that drill holes did not weaken the test sufficiently to lead to preferential breakage of drilled specimens in the observed time-frame, which is consistent with other observations that preservation of *M. ventricosa* is not an artifact of coronal strength (Greenstein 1993). Drill holes may also affect the stability of echinoid tests, particularly large holes occurring on small tests (Grun and Nebelsick 2015), and large predators may be more likely to destroy the tests of much smaller prey during handling (Grun et al. 2014), introducing size bias. These taphonomic biases should be considered in conjunction with those potentially introduced by drill holes for a more thorough understanding of the relationship between drilling frequency and predation intensity.

The mean drill hole size of 7 mm is consistent with other observations of cassid drill holes which range from approximately 1–9 mm (Moore 1956; Hughes and Hughes 1981; McClintock and Marion 1993; Grun 2017). The smaller average test size in the death assemblage relative to the live population points to potential size selectivity. Differences in the size frequency distributions of the live prey population and the death assemblage have not been observed previously for cassids, and evidence for cassid size selectivity of echinoid prey is sparse (Grun and Nebelsick 2015). However, size-selective cassid predation was also recognized for cassids preying on Miocene echinoids (Złotnik and Ceranka 2005a). As handling time (the time taken to penetrate and consume the prey) for cassids is not proportional to prey size and the nutritional value of urchins increases with size (Hughes and Hughes 1981), smaller cassids may more frequently attack relatively larger prey at no increased energetic cost, which could account for the weak negative correlation observed between predator and prey size. Cassids also frequently destroy prey tests (Hughes and Hughes 1971, 1981; Levitan and Genovese 1989; Nebelsick and Kowalewski 1999), and large predators may be more likely to destroy the tests of much smaller prey during handling introducing size bias (Grun et al. 2014). However, all dead tests collected from the study area were complete, and echinoid fragments were not observed in the field, indicating that destructive predation by cassids is probably rare for the large *M. ventricosa* individuals studied here. Alternatively, the correlation may be a taphonomic artifact, as the presence of larger drill holes on tests may promote the destruction of small specimens (Nebelsick and Kowalewski

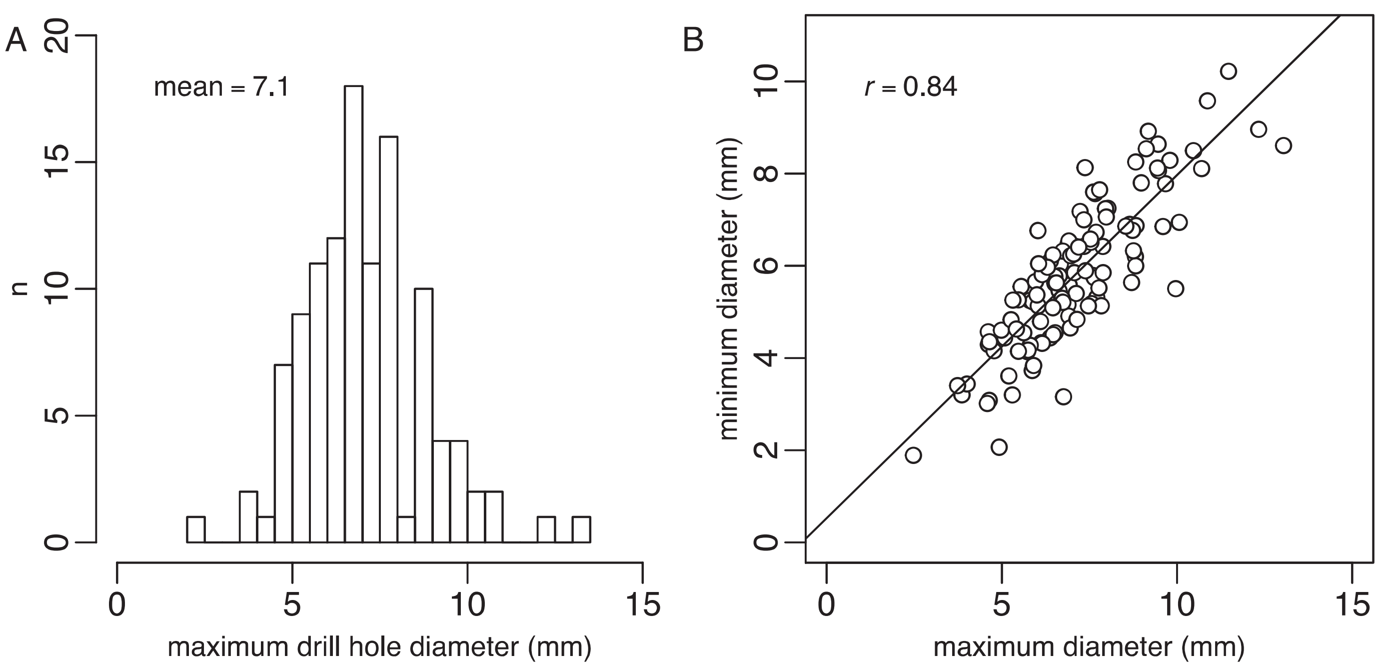

FIG. 4.—Drill hole size distribution. **A**) *Cassis tuberosa* drill holes range from 2 – 14 mm in diameter, with a mean diameter of 7.1 mm. **B**) Holes are generally circular, and the maximum and minimum diameter are strongly correlated (r = Pearson's correlation coefficient, $p << 0.0001$).

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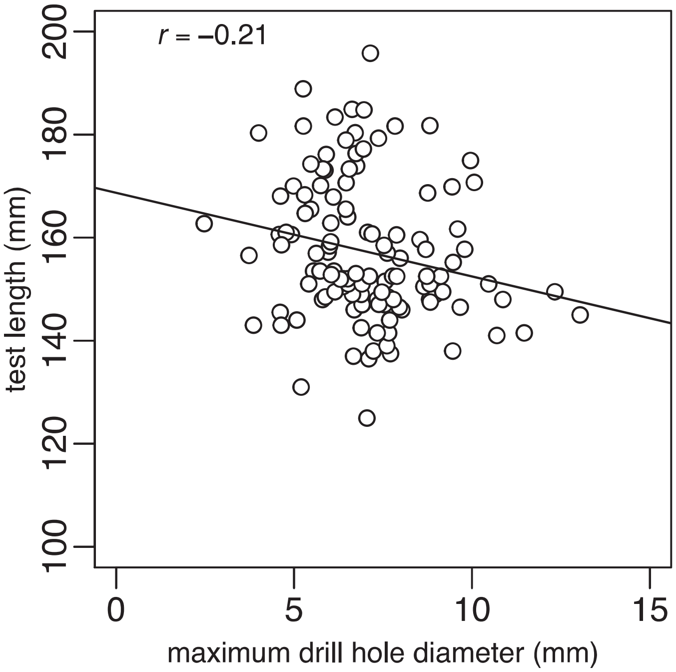

FIG. 5.—Drill-hole length decreases with prey size (test length). There is a weak, but significant relationship between *Cassis tuberosa* drill hole size and prey size. Inferring predator size from drill hole size, smaller predators prey upon larger prey (r = Pearson's correlation coefficient, $p = 0.02$).

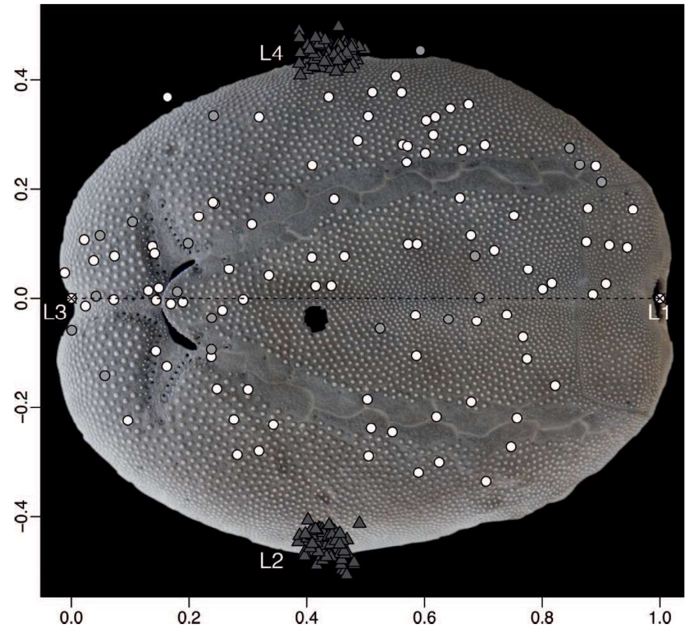

FIG. 7.—Site selectivity. White and light gray points indicate *Cassis tuberosa* drill hole location on the oral and aboral side of the test respectively. White crossed points specify landmarks used to define the baseline (dashed line from landmark 1 to 3) for Bookstein (shape) coordinates. Dark gray triangles denote landmarks 2 and 4, which mark the maximum width on each side of the test (right and left). An oral view of *Meoma ventricosa* is shown in the background for reference.

1999). Experimental studies of handling time and the relationship between the size of the predator and prey are required to directly assess these hypotheses.

The scarcity of multiple drill holes on a single test is consistent with laboratory observations of *C. tuberosa* feeding on *Tripneustes ventricosus*

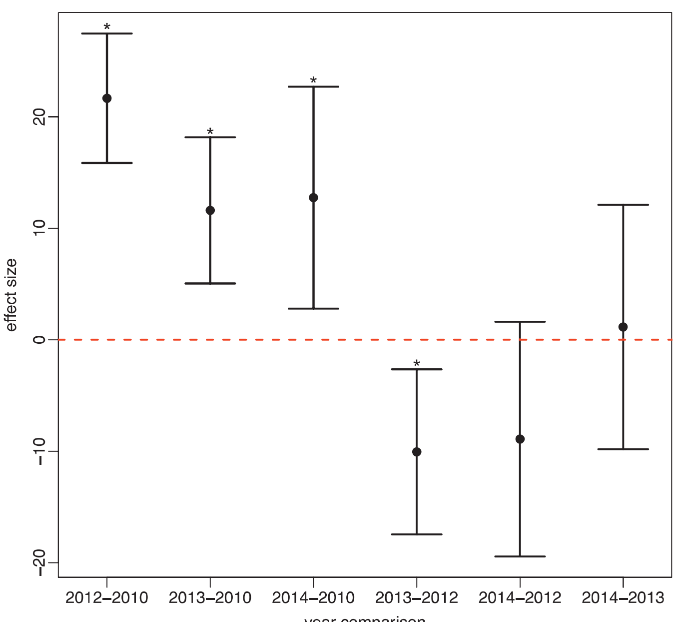

FIG. 6.—Interannual variation in size. Differences in the mean length (mm) of dead tests were significant between all pairwise comparisons across field seasons (Tukey's HSD adjusted p values). 95% confidence intervals for each pairwise comparison, asterisk indicates significant differences for all comparisons ($p << 0.01$) except 2014–2012 ($p = 0.12$), and 2014–2013 ($p = 0.99$).

(Lamarck 1816) and *Echinometra lucunter* (Linnaeus 1758) from Barbados (Hughes and Hughes 1971). As no site specific stereotypy was observed, i.e., drill holes are not preferentially located on the petals or apical disc, *C. tuberosa* does not appear to regularly target specific locations on the test of *M. ventricosa*, and drill hole location could simply be an arbitrary product of prey orientation during individual attacks (Hughes and Hughes 1981). As the proboscis is presumably long enough to reach all inner parts of the prey test regardless of the point of entry (Hughes and Hughes 1981), there may be no selective pressure for stereotypical *C. tuberosa* feeding behaviors targeting specific locations on the prey test, e.g., petals and apical disc. The preferential location on the oral side of the test is also consistent with *C. tuberosa* feeding behavior, which may handle *M. ventricosa* in a habitual way. When preying upon urchins, *C. tuberosa* envelops the prey with the front of its foot and extends its proboscis, which is 1–1.5 times the length of its shell, over the foot and under the prey to begin feeding (personal observation; Hughes and Hughes 1971). The dominance of oral penetration observed here concurs with observations of *C. tuberosa* preferentially drilling on the oral side of *Leodia sexiesperforata* (Leske 1778) also from San Salvador Island (McClintock and Marion 1993; Grun 2017). However, others have observed *C. tuberosa* preferentially drilling through the sides of tests when feeding on *T. ventricosus* and *E. lucunter* (Hughes and Hughes 1971), and drill holes attributed to *Semicassis undulata* (Gmelin 1791) in the Mediterranean were preferentially located on the aboral side of *Echinocyamus pusillis* (Müller 1776) (Grun et al. 2014). The positioning of drill holes may thus vary depending on prey taxa. Although a preference for drilling on the oral side of the test towards the anterior end has been observed on Tertiary spatangoids (Beu et al. 1972), drill holes on fossil echinoid tests attributed to predatory gastropods are often preferentially located on the aboral side of the test, particularly on or near the ambulacra (Gibson and Watson 1989; Donovan and Jagt 2013; Grun and Nebelsick 2015; Donovan et al. 2016; Grun et al. 2017). Preferential drilling on the aboral side of the test of the ambulacra was also recognized for cassids

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preying upon Miocene echinoids (Złotnik and Ceranka 2005a). Predators are thought to have been targeting the gonadal tissue or, in the case of infaunal prey, the part of the test closest to the sediment surface may simply be more accessible to predators (Donovan et al. 2016). Therefore, although providing important insights into the ecology of drilling predators and their prey, preferential drill hole location appears to be highly variable and prey-taxon specific, and thus may not serve as evidence for definitive identification of cassid predation in the fossil record.

CONCLUSIONS

Drill holes made by *C. tuberosa* on tests of *M. ventricosa* from San Salvador Island (Bahamas) were distinct and readily identifiable. In contrast to some previous studies of the drilling behavior of cassids, drill holes examined here occurred preferentially on the oral side of the test, and their spatial distribution on the test appears random. Exceedingly high drilling frequencies were observed consistently across all sampling seasons over the course of the five-year study interval. Given other documented sources of mortality in the study area, the $\sim$ 97% mortality rates from drilling predators estimated from the death assemblage of *M. ventricosa* seems unrealistic. This biased frequency likely reflects the fact that cassids are effective agents of fossilization. Cassid predators can facilitate the initial preservation of echinoid tests by creating an enlarged opening, removing soft tissue, and accelerating sediment infill and burial. Although this bias towards drilled tests may not affect all cassid-echinoid systems, instances of high drilling frequencies have been observed in the fossil record (e.g., Gibson and Watson 1989; McNamara 1994), and death assemblages (e.g., Nebelsick and Kowalewski 1999; this study). These past instances may be potentially attributable to predator-facilitated preservation, rather than intense predator-prey interactions between cassid gastropods and their echinoid prey.

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