Taphonomy of a clypeasteroid echinoid using a new quasimetric approach

TOBIAS B. GRUN and JAMES H. NEBELSICK

A new quasimetric approach is used to statistically analyze taphonomic data from a commonly occurring shallow water clypeasteroid echinoid in order to obtain metric equivalent measurements of taphonomic alteration on an interval-like scale. This technique takes the character condition as well as its proportion into account and translates the taphonomic alteration into data, which behave as interval scaled and thus allows for the use of parametric as well as non-parametric statistics. Tests of *Echinocyamus pusillus* from Giglio Island (Mediterranean Sea, Italy) were analyzed with respect to a suite of taphonomic features including abrasion of the test surface, tubercles, ambulacral and genital pore margins as well as, if present, the outline and cross section of predatory drillholes. The degree of fragmentation and encrustation was also determined. Taphonomic features were analyzed using a semi-quantitative approach with three degrees of test alteration including non-altered, moderately altered, and highly altered which were statistically analyzed using non-parametric statistics due to highly non-normal distributed data. Abrasion intensities vary among different surface characters, with exposed areas of the test showing higher abrasion intensities than sheltered areas. Fragmentation occurs in low frequencies (7%) and fractures in the tests are almost absent (1.7%). Encrustation rates by bryozoans and serpulids can cover up to 80% of the test surface, but vary strongly among individuals and sample sites. Encrustation is independent of test size and prolongs overall test survival by crossing plate boundaries. The presence of drillholes in decreasing test preservation potentials is discussed with respect to analytical parameters.

Key words: Echinoidea, *Echinocyamus*, taphonomy, quasimetric, abrasion, encrustation, drillhole, Mediterranean.

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Introduction

Investigations of Recent environments provide direct insight into the composition and distribution of communities and organisms as well as inter- and intraspecific interactions. In the ancient sedimentary records, however, populations are rarely truly represented because death assemblages of shells can be strongly biased by a whole suite of taphonomic processes such as predation, scavenging, water and sediment agitation, transport, bioturbation, as well as time averaging effects (e.g., Schäfer 1962; Lawrence 1968; Brett and Gordon 1986; Wilson 1988; Fürsich and Aberhan 1990; Kidwell and Bosence 1991; Parsons and Brett 1991; Flessa et al. 1993; Kowalewski 1996; Behrensmeyer et al. 2000; Schein and Lewis 2001; Nebelsick 2004; Hauser et al. 2008). The study of taphonomic processes has been shown to provide important paleoenvironmental signals of both biotic and abiotic origin (e.g., Lawrence 1968; Hauser et al. 2008).

Clypeasteroid echinoids are robust echinoderms due to their interlocking plates and internal support structures and have been the object of several taphonomic studies (e.g., Seilacher 1979; Smith 1984; Donovan 1991; Nebelsick and Kampfer 1994; Nebelsick 1995, 1999a, b, 2008; Schein and Lewis 2001, El-Hedeny 2007; Grun and Nebelsick 2015). *Echinocyamus pusillus*, a minute clypeasteroid species, is used for the present taphonomic analyses because it is abundant in various Recent and Cenozoic environments. This species also occurs in sufficient numbers within samples and thus allows for statistical comparisons among different environments. Restricting the study to a single species additionally alleviates the effects of varying skeletal morphologies on preservation potentials.

The present study employs a new quasimetric approach to (i) evaluate the influence of taphonomic processes such as abrasion and encrustation on test preservation, (ii) compare abrasion effects on surface characters from different areas of the test, (iii) assess the influence of encrustation and predatory drillholes on preservation potential, (iv) correlate

encrustation rate with test size, and (v) compare taphonomic test alterations among sample sites.

Institutional abbreviations.—GPIT/EC, accession number, Department for Geosciences, University of Tübingen, Germany.

Other abbreviations.—N, sample size; p, significance level; r, Pearson's Correlation Coefficient; rho, Spearman's Correlation Coefficient.

Background

Problems of descriptive taphonomic quantification.—Echinoids show different categories of skeletal organization at various hierarchical levels (e.g., Nebelsick et al. 2015). Taphonomic processes can thus result in differential effects on the various characters present on echinoid test surfaces.

This can be problematic with respect to taphonomic analysis because different test features often show varying degrees of alteration and can be differentially distributed on the test, thus making a generalized assignment into specific semi-quantitative categories difficult. Tubercles, for example, are highly abundant on the test surface and feature a whole suite of characters including the mamelon, boss, and the areole which show different morphologies and stereom densities (e.g., Smith 1980, 1981, 1984). In the case of complex and unevenly altered tests, a detailed description of each single test character is thus useful.

One solution to quantifying different alteration grades within single characters, which also takes the frequency of the alteration grade of the whole skeleton into account, is to describe the character alteration in relation to its frequency of occurrence. Since abundant test characters, such as tubercles, occur in such a high number making a quantitative exploration impractical, a more useful approach is preferable, such as the quasimetric approach introduced here. A taphonomic process, such as abrasion, as well as its frequency, can be reduced to a few, recognizable categories. This method is generally sufficient to describe the character alteration accurately with respect to its frequency as well as to a large number of individuals. The Likert-Type scale based model (e.g., Clasen and Dormody 1994) combines both the variation in alteration of a single character as well as the frequency in which the character alteration occurs. This approach not only results in a quasimetric scale, which can be handled as an interval scaled variable, but it also allows for the combination of various taphonomic characters using simple mathematical operations. The method thus allows to describe complex taphonomic alterations of a multifaceted object with a single value. This study illustrates the advantages in data handling based on the described methodology using taphonomic alterations of *Echinocyamus pusillus* tests from the Mediterranean Sea.

Mathematical aspects and limits of the quasimetric method.—The quasimetric method based on the Likert-Type scale is a method to precisely describe complex taphonomic pathways using a numerical approach. The character condition is a pre-defined description which is inherently represented by an ordinal scale. Such ordinal data often do not show the same or similar distances between the character degrees. The taphonomic conditions of the characters are thus defined such that the distances between degrees can be assumed to be roughly equivalent. Deviations from roughly equivalent distances can result in a shift to either lower or higher taphonomic values. These deviations can be reduced by increasing the gradations of a single character description, which, however, would result in a higher number of time-consuming calculations.

Based on the defined number of character conditions, the calculated taphonomic value occurs in a range between the smallest and highest taphonomic grades. The calculated taphonomic value represents a mathematical operation which transforms ordinal into interval scaled data. Since there is no guarantee that all distances between the values within the interval range have the same length, the data are principally not interval scaled, but can be assumed to behave as interval scaled. This behavior as interval scaled data is advantageous in that the generated data can be subjected to sophisticated statistical methods, as opposed to ordinal data, which can only be analyzed using descriptive methods and basic statistics.

This method with its advantages can, however, only be applied to characters where a graduated description is present along with the proportion of the taphonomic degree. Characters that are either absent or present cannot be transformed into a quasimetric value using this method. This new approach allows for a precise taphonomic character description, which can be used for all statistical tests that are applicable to interval scaled data.

Pitfalls of taphonomy in high-energy environments.—The use of taphonomic alterations based solely on recorded features has numerous pitfalls. For example, higher energetic environments can contain well-preserved specimens (e.g., Kelley 2008), while lower-energetic environments may preserve highly altered specimens (e.g., Nebelsick and Kampfer 1994). These counterintuitive results can be explained by the fact that whereas low alteration rates are generally expected in low energy environments, skeletons in such environments have less chance of being destroyed as a whole and thus can show higher rates of alteration over the long term (e.g., Kelley 2008). One method to investigate the offsetting effects of both destructive and constructive taphonomic processes is to compare the effects of abrasion, fragmentation, encrustation, and other processes on different skeletal features.

Study area and fauna.—Giglio is part of the Tuscan Archipelago within the Tyrrhenian Sea (Fig. 1). The island is characterized by generally high-energy environments with coastlines dominated by steep cliffs and rough breaker
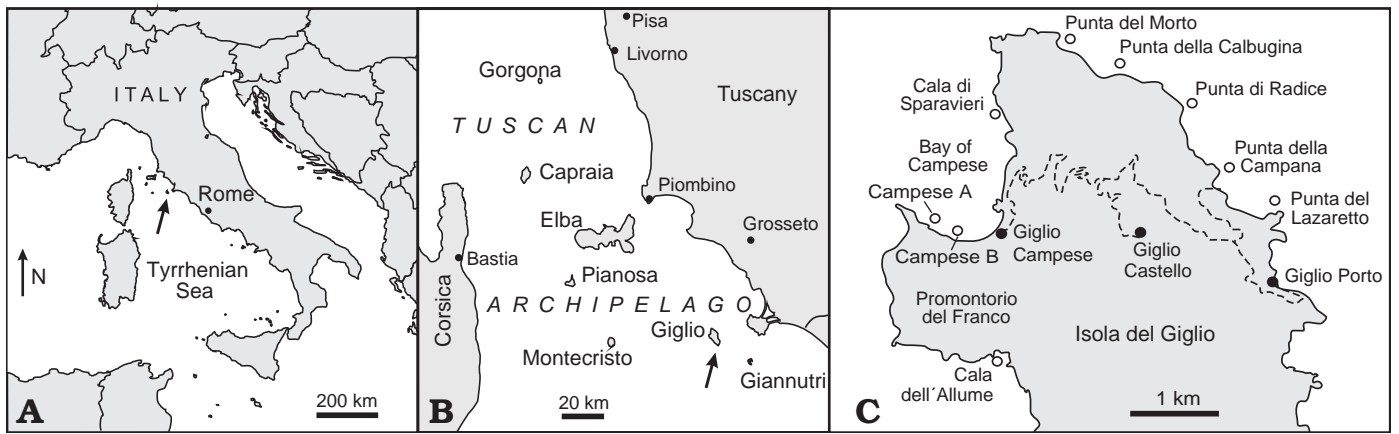
Fig. 1. Location (arrows) of study area on the map of Italy and the Tyrrhenian Sea (**A**) and Giglio Island in the Tuscan Archipelago (**B**). Location of sample points (white circles) around the northern part of the island (**C**). Modified after Grun et al. 2014.

zones. Beaches with low gradient shorelines are rare. The presence of rocky shores, beaches, and sandy slopes results in a variety of habitats in a relatively small area that are easily accessible by snorkeling and scuba diving. Substrates vary from bare rocks and boulders to gravel, coarse sand, and finer sands (e.g., Grun et al. 2014). Seagrass meadows are abundant and mainly consist of *Posidonia oceanica*. Algal meadows (mainly *Caulerpa*) are less abundant and tend to occur in deeper waters.

The irregular echinoid *Echinocyamus pusillus* (Figs. 2, 3) is abundant in a variety of environments in the Atlantic Ocean, the North Sea, and the Mediterranean Sea. The genus *Echinocyamus* has been the subject of numerous studies dealing with morphology (Mortensen 1927, 1948; Nichols 1959; Ghiold 1982; Telford et al. 1983; Telford 1985), behavior (Ghiold 1982; Telford et al. 1983) and drilling predation (Nebelsick and Kowalewski 1999; Kowalewski and Nebelsick 2003; Ceranka and Złotnik 2003; Złotnik and Ceranka 2005; Grun et al. 2014; Grun and Nebelsick 2015).

Echinocyamus pusillus rarely exceeds 15 mm in test length as an adult (Mortensen 1927) and occurs from shallow waters to 1250 m depth (Mortensen 1927). The calcareous test of *Echinocyamus pusillus* is elliptical to sub-elliptical in outline (Figs. 2A$_1$, B$_1$, 3A, B$_1$). The flattened test has internal supports connecting the oral and aboral sides. The test is entirely covered by short spines and podia, which are used by the clypeasteroid to burrow into the sediment (Nichols 1959; Ghiold 1982). The aboral side of the test has five petals with two rows of ca. six to nine ambulacral pore-pairs (Mortensen 1927; Fig. 2A$_1$). The apical disc contains four readily recognizable large genital pores and a tiny hydropore. The aboral side of the test features numerous rows of unipores for lateral podia.

The oral side of the test is characterized by a large and slightly depressed circular to sub-circular peristome (Fig. 2B$_1$, C) and an elliptical periproct near the posterior ambitus margin (Fig. 2B$_1$). Surface structures also include crenulated, sunken tubercles as well as glassy tubercles, which are both easily recognizable at lower magnification (Fig. 2A$_2$, D).

Material and methods

Samples of *Echinocyamus pusillus* were collected around Giglio Island (Fig. 1) in the summer of 2010. The patchy distributed tests were exhaustively sampled and detected by manually picking them from the sediment surface of nine nearshore sites during dives using SCUBA (Fig. 1C). Complete tests and larger fragments were recovered from depths of 2−35 m from exposed areas, near patches of sea grass (*Posidonia*) and algal (*Caulerpa*) meadows, as well as near rocky substrates (Table 1). Sediment types within these sites consist of medium to coarse-grained, mixed carbonate-siliciclastic deposits. The collected specimens were recently analyzed for drilling predation by cassid gastropods (Grun et al. 2014; Grun and Nebelsick 2015).

The echinoids were analyzed using a reflecting light microscope (max. 5× magnification) for abrasion of three surface characters including (i) tubercles, (ii) test surface (apart from the tubercles), (iii) ambulacral and genital pores, and, if present, the outline and cross section of predatory

Table 1. Sites around Giglio according to sample depth and environment.

Sample site	Depth (m)	Environment
Cala dell'Allume	6−10	bordering sea grass meadow, medium sand
Campese A	10−20	bordering sea grass meadow, medium sand
Campese B	3−12	bordering sea grass meadow, coarse sand
Cala di Sparavieri	11−35	base of rock face, sandy slope, coarse sand
Punta del Morto	15−30	sandy slope, coarse sand
Punta della Calbugina	10	bordering sea grass meadow, coarse sand
Punta di Radice	2−30	sandy slope, coarse sand
Punta della Campana	20−30	coarse sand with *Caulerpa racemosa*
Punta del Lazzaretto	25−30	coarse sand

Table 2. Taphonomic description of test surface characters of *Echinocyamus pusillus*.

Alteration	Character	Grade 1	Grade 2	Grade 3
Abrasion	tubercle	mamelon and boss present; mamelon can be partly abraded	boss present; mamelon entirely gone; boss can be partly abraded	stereom visible; mamelon and boss entirely gone; gap indicates former presence of tubercle
	surface	surface intact; no visible signs of abrasion	stereom can be slightly abraded; labyrinthic stereom not visible	stereom abraded; labyrinthic stereom visible
	pores	outline smooth; no visible signs of abrasion	outline irregular due to abrasion	outline ragged due to abrasion or fragmentation
	drillhole outline	margins show no visible signs of abrasion	margins abraded	margins fragmented
	drillhole cross section	present	recognizable	not recognizable
Fragmentation	test	absent	cracks present	parts missing
Encrustation	test surface	absent	present	not applicable

drillholes. The echinoids were also examined for fragmentation and encrustation (see Table 2).

Analyzed characters were assigned to one of three grades of taphonomic alterations: grade 1, non-altered to slightly altered; grade 2, moderately altered; or grade 3, highly altered (Table 2). Additionally, the proportion of the test surface, character, or drillhole affected by each grade of taphonomic alteration was estimated for each specimen. The proportion of alteration was classified into five categories: category 1, taphonomic alteration is virtually not detectable; category 2, up to 25% of the area or character is altered; category 3, 25 to 50% is altered; category 4, 50 to 75% is altered; and category 5, more than 75% of the area or character is altered.

Using the abrasion grade of the test surface (apart from the tubercles), tubercles, and pores, as well as the proportion category of the altered area, a total abrasion value (V_A) is calculated by the following equations:

$$A_t = \frac{1P_{t1} + 2P_{t2} + 3P_{t3}}{P_{t1} + P_{t2} + P_{t3}} \qquad (1)$$

$$A_s = \frac{1P_{s1} + 2P_{s2} + 3P_{s3}}{P_{s1} + P_{s2} + P_{s3}} \qquad (2)$$

$$A_p = \frac{1P_{p1} + 2P_{p2} + 3P_{p3}}{P_{p1} + P_{p2} + P_{p3}} \qquad (3)$$

$$V_A = \frac{A_t + A_s + A_p}{3} \qquad (4)$$

Abrasion values are as follows: A_t = tubercles; A_s = test surface, and A_p = ambulacral and genital pores. P_t = proportion (categories 1 to 5) of altered tubercles (grades 1 to 3); P_s = proportion (categories 1 to 5) of altered test surfaces (grades 1 to 3); and P_p = proportion (categories 1 to 5) of altered ambulacral and genital pores (grades 1 to 3). The coef-

ficients (1, 2, and 3) in front of the abrasion values represent the abrasion grade 1 to 3. V_A is the total abrasion value.

The fragmentation value (V_F) is calculated using the following equation:

$$V_F = \frac{1P_{F1} + 2P_{F2} + 3P_{F3}}{P_{F1} + P_{F2} + P_{F3}} \qquad (5)$$

Proportions for calculating the fragmentation value (V_F) are as follows: P_{F1} = proportion (categories 1 to 5) of non-altered tests surface; P_{F2} = proportion (categories1 to 5) of fractures on the test surfaces; and P_{F3} = proportion (categories 1 to 5) of missing test parts.

The calculated values can be assumed to behave as interval scaled measurements. Although the distances between abrasion grades are not necessarily equal in length, the computational process results in a range of values based on the pre-defined grades and can thus be used for comparative analysis. The quasimetric Likert-Type scale (e.g., Clasen and Dormody 1994) is appropriate because both the definition of abrasion grades and the inclusion of the altered area are included in the analysis. Dispersion of values is always given as the standard deviation (SD). Descriptive statistics include mean values and standard deviations. Although the data are not normally distributed, the arithmetic average is commonly used, as generally in Likert-Type scales.

Spearman's rho is used to detect possible correlations between the abrasion of tubercles, test surface, and pores. Pearson's r is used for analyzing a possible correlation between encrustation rates and test length. The effect of encrustation on test preservation potential is analyzed by a Mann-Whitney U test and visualized using Box-Whisker plots to detect a direction on a possible relation between abrasion and encrustation (Fig. 4). Total abrasion value distributions of drilled and undrilled tests are compared using

Fig. 2. SEM microphotographs of well-preserved *Echinocyamus pusillus* Müller, 1776 (sample GPIT/EC/00740) from Giglio Island, Recent. **A**. Specimen gg-al-1.11, in aboral view, showing petalodium including paired ambulacral pores (A_1); well preserved surface detail of the aboral surface with sunken tubercles, glassy tubercles, and paired ambulacral pores (A_2). **B**. Specimen gg-3t-3.60, in oral view, showing central peristome, periproct situated half way between peristome and the posterior margin as well as a drillhole at the upper left (B_1); well preserved predatory drillhole with internal support still preserved within the skeleton (B_2). **C**. Specimen gg-na-1.1, well preserved peristome on the oral surface, showing tubercles and secondary unipores. **D**. Specimen gg-pm-4.35, very well preserved tubercle showing differential stereom densities of the perforated mamelon, crenulated boss, and sunken areole.
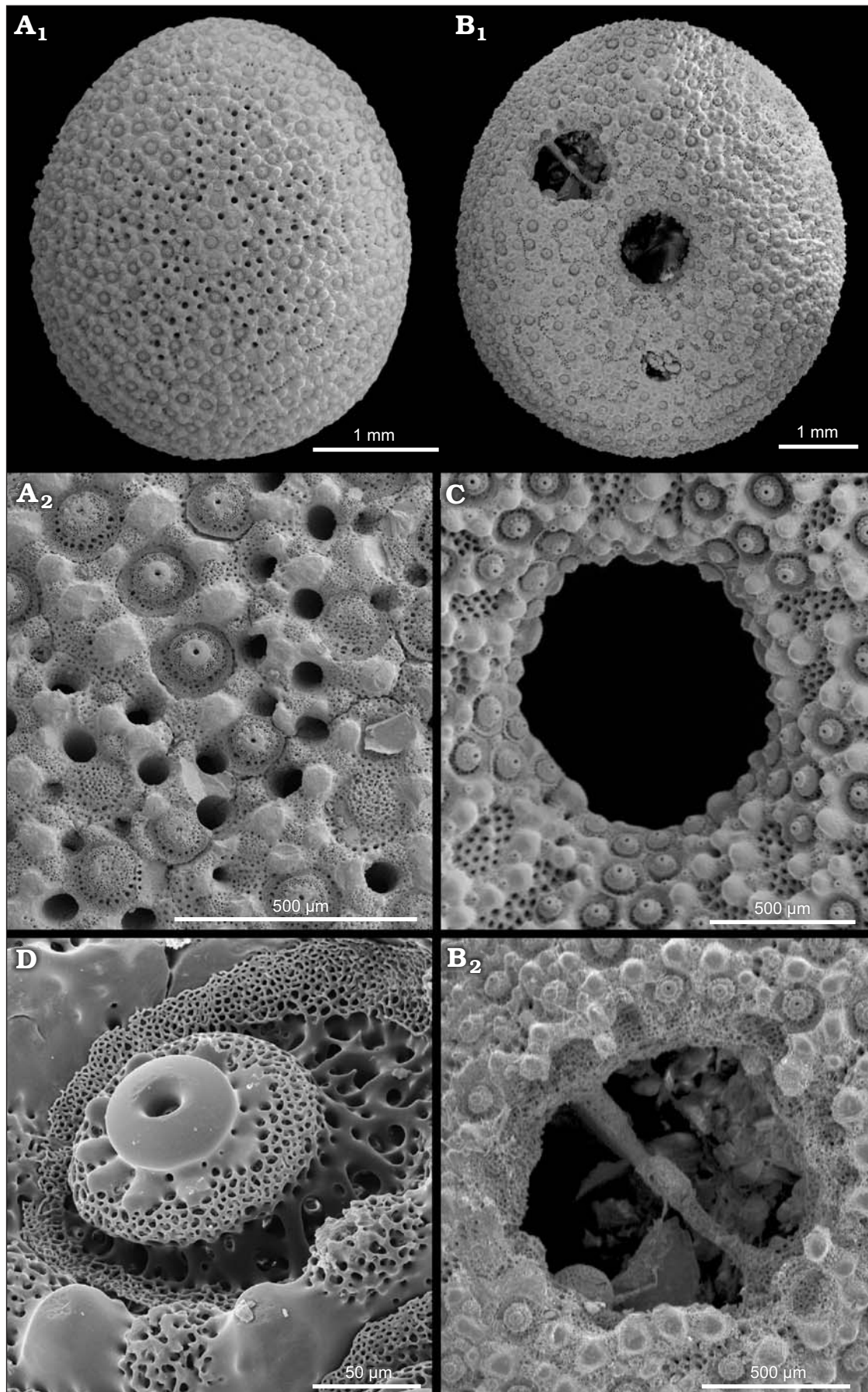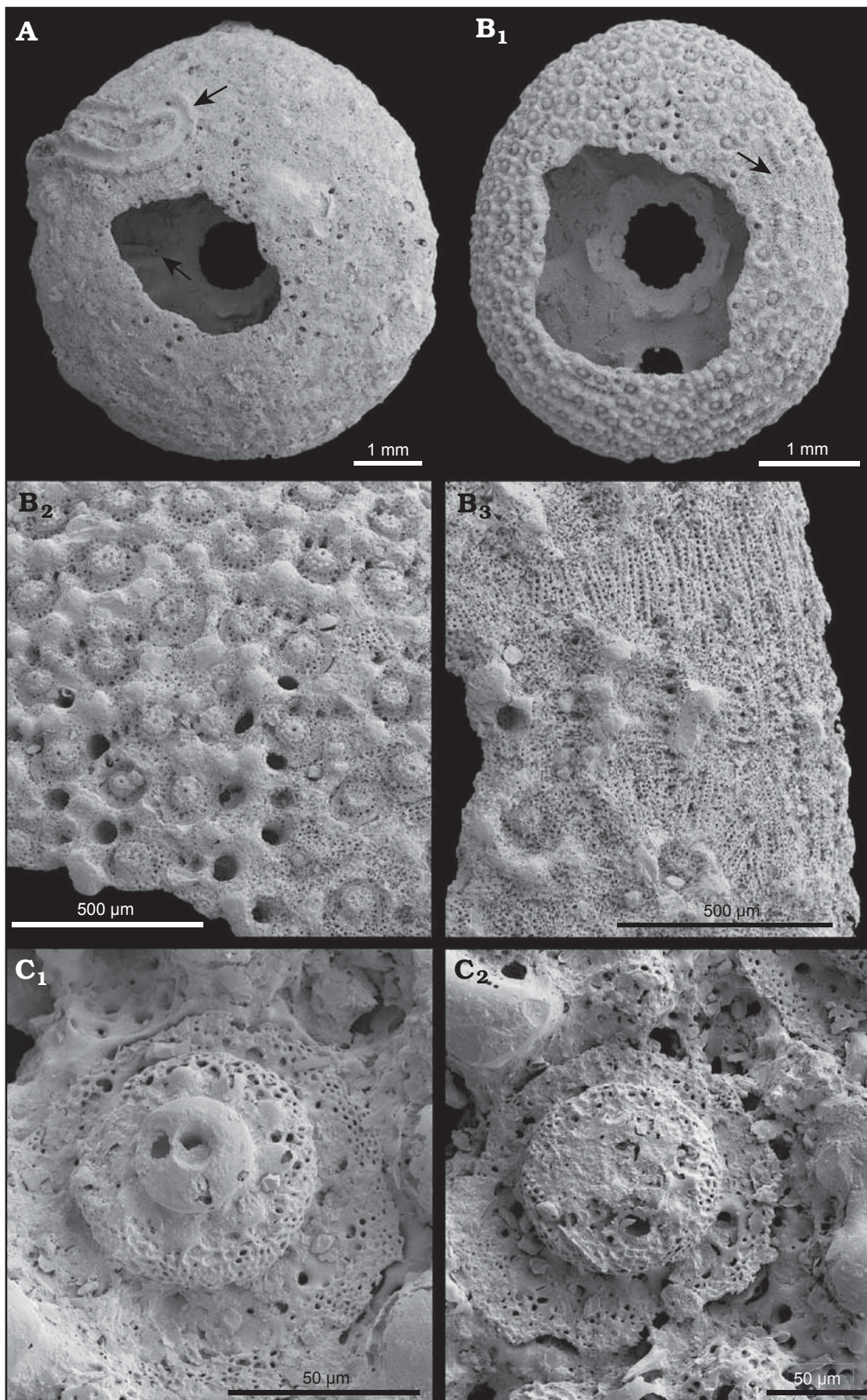
a Mann-Whitney U Test. This non-parametric test is robust with respect to differences in sample sizes (Nachar 2008).

Holes were described as predatory in origin when circular to subcircular in outline and concave in cross section (Grun et al. 2014; Grun and Nebelsick 2015). Holes lacking these features were not recognized as predatory and not included in the analysis. Abrasion was classified by the rate of abrasion and its proportion on the drillhole outline and cross section respectively. The abrasion of the drillhole outline at the test surface was classified into three grades: margins with no visible signs of abrasion (grade 1), margins slightly to moderately abraded (grade 2), and margins highly abraded (grade 3). The concave cross section of the drillhole wall was similarly classified into three grades based on its preservation: concave drillhole wall completely preserved (grade 1), slightly to moderately abraded (grade 2), or highly affected (grade 3). These two characteristics were analyzed with respect to their proportion of the drillhole affected and classified into five categories: category 1, taphonomic alteration not detectable; category 2, up to 25% of the drillhole outline or cross section, respectively, is altered; category 3, 25–50% is altered; category 4, 50–75% is altered; and category 5, more than 75% is altered. A drillhole value (V_D) is calculated based on the abrasion grade of the drillhole margin, the cross section, and their proportions using the following equation:

$$V_D = \left(\frac{(\text{abrasion}) + (\text{cross section})}{2} \right) = \left(\frac{\left(\frac{1P_{m1} + 2P_{m2} + 3P_{m3}}{P_{m1} + P_{m2} + P_{m3}} \right) + \left(\frac{1P_{c1} + 2P_{c2} + 3P_{c3}}{P_{c1} + P_{c2} + P_{c3}} \right)}{2} \right) \quad (6)$$

Symbols are as follows: V_D = drillhole value, P_m = proportion (categories 1–5) of altered drillhole margin (grades 1–3), and P_c = proportion (categories 1–5) of altered drillhole cross section (grades 1–3). The coefficients (1–3) in front of the abrasion values represent the abrasion grade 1–3.

Results

A total of 1051 tests of *Echinocyamus pusillus* were analyzed from nine sites (Fig. 1C, Table 1). All examined tests were denuded, or lacking spines. Individuals range from well preserved, showing little taphonomic alterations of the test (Fig. 2), to highly abraded or highly encrusted specimens (Fig. 3).

Abrasion.—Tubercles show different rates of abrasion (Figs. 2, 3), ranging from pristine preservation, partly abraded mamelons (Fig. 2A$_2$, D), abraded bosses (Fig. 3B$_2$, C) and finally, completely removed tubercles (Fig. 3B$_3$). The remaining test
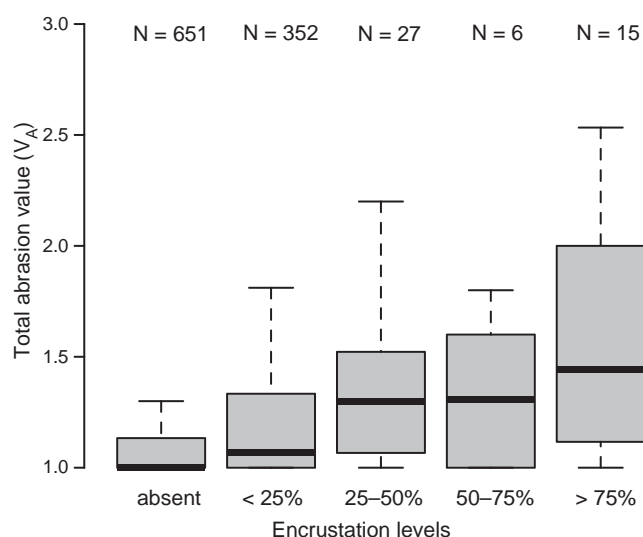

Fig. 4. Box-Whisker plot of the taphonomic value of *Echinocyamus pusillus* samples among the five encrustation levels. Outliers were removed from the graph. N, number of individuals.

surface also shows high variation of preservation including highly abraded surfaces in which the stereom is exposed (Fig. 3B$_3$). The tubercles show the highest abrasion values (mean 1.22 ± 0.5) while the remaining test surface shows slightly lower abrasion values (mean 1.17 ± 0.4). The ambulacral and genital pore margins are the least altered (mean 1.09 ± 0.4 and 1.09 ± 0.3, respectively). Drillhole margins and cross sections are rather well preserved with a mean abrasion value of 1.14 ± 0.4. The abrasion of tubercles on the test surface is greater (mean 1.22 ± 0.5) than of the surrounding, slightly depressed peristome (mean 1.09 ± 0.4). The total abrasion values (V_A) range from pristinely (mean 1.00) to moderately preserved (mean 2.24) (Table 3). 75% of the total abrasion values are lower than 1.20. The total abrasion values among sample sites are generally low ranging from 1.05 to 1.28 (mean 1.12 ± 0.21) indicating well preserved tests (Table 4).

Fragmentation and encrustation.—Test fragmentation ranges from fractures on still intact tests to partially destroyed individuals (Fig. 3A, B$_1$). Fractures are rare (1.7%) while fragmentation is more common (7.5%). Fractures occur exclusively along plate boundaries; intraplate breakage was never observed. Plate loss mostly affects the apical system. Some specimens were also fragmented near the peristome, while the periproct was never affected.

Commonly encrusting organisms on the tests of *Echinocyamus pusillus* include serpulid worm tubes and bryozoans. Worm tubes ranged in length from several millimeters to centimeters depending on the test size and the degree of coiling of the serpulids (Fig. 3A). Bryozoans consisted of small colonies of unidentified unilaminate cheilostomes. These sclero-

← Fig. 3. SEM microphotographs of poorly preserved *Echinocyamus pusillus* Müller, 1776 (sample GPIT/EC/00740) from Giglio Island, Recent. **A**. Highly abraded specimen gg-3b-2.10, in aboral view, showing fragmentation and moderate external and internal encrustation by serpulids (arrows). **B**. Specimen gg-3b-2.17, in aboral view, showing showing fragmentation and high test surface abrasion (arrow) on the right side (B$_1$). Details of B$_1$, showing moderate abrasion of the tubercles and ambulacral pores (B$_2$); high surface abrasion revealing the underlying stereom of the test (B$_3$). **C**. Specimen gg-3t-2.26, moderately abraded tubercle with perforated mamelon and boss still present (C$_1$); highly abraded tubercle with boss present, but the mamelon entirely gone (C$_2$).

bionts cross plate boundaries of the echinoid test. Serpulids and bryozoans are not only present on the outer surface but also occur on the inner surface of the test (Fig. 3A).

Of the 1051 tests examined, 651 (61.9%) do not show any evidence of encrustation, 352 (33.5%) show up to 25% of the test surface covered by encrusting organisms, 27 (2.6%) have between 25 and 50% of the surface covered, only 6 tests (0.6%) between 50 and 75%and 15 tests (1.4%) have more than 75% of their surface covered. Encrustation rates

Table 3. Description of the total abrasion values (V_A) for the studied sample sites.

Sample site	Total abrasion value		
	mean	minimum	maximum
Cala dell'Allume	1.28	1.00	2.06
Campese A	1.19	1.00	1.87
Campese B	1.10	1.00	2.04
Cala di Sparavieri	1.07	1.00	1.49
Punta del Morto	1.14	1.00	2.01
Punta della Calbugina	1.05	1.00	2.24
Punta di Radice	1.09	1.00	1.44
Punta della Campana	1.18	1.00	1.98
Punta del Lazzaretto	1.14	1.00	1.92

Table 4. Mean taphonomic values of test characteristics with respect to sample sites.

Sample site	Tubercle abrasion	Surface abrasion	Pore abrasion	Total abrasion
Cala dell'Allume	1.53	1.47	1.30	1.28
Campese A	1.36	1.36	1.17	1.19
Campese B	1.20	1.15	1.06	1.10
Cala di Sparavieri	1.08	1.08	1.06	1.07
Punta del Morto	1.25	1.24	1.19	1.14
Punta della Calbugina	1.09	1.07	1.06	1.05
Punta di Radice	1.16	1.19	1.10	1.09
Punta della Campana	1.39	1.35	1.16	1.18
Punta del Lazzaretto	1.31	1.29	1.13	1.14
Mean	1.24	1.21	1.11	1.12
Standard deviation	0.36	0.38	0.28	0.21
Minimum	1.08	1.07	1.06	1.05
Maximum	1.53	1.47	1.30	1.28
Number of individuals	1049	1049	1041	1041

around Giglio Island vary widely among localities ranging from 20.5% of samples encrusted at Cala dell'Allume to 78.4% at Punta del Lazzaretto (Table 5).

Comparison of taphonomic signatures.—Spearman's rho indicates a high correlation between the values of tubercle abrasion and surface abrasion (rho = 0.73, p < 0.001, N= 1049). Abrasion values of tubercles and pores as well as of the test surface and pores, respectively, are positively correlated (rho = 0.56, p < 0.001, N = 1041 and rho = 0.60, p < 0.001, N = 1041, respectively). Correlations between tubercle abrasion and test fragmentation as well as between surface abrasion and fragmentation, respectively, are lower (rho = 0.21, p < 0.001, N = 1049, and rho = 0.22, p < 0.001, N = 1049, respectively).

The Mann-Whitney U test shows a significant difference of the total abrasion values among the five encrustation categories (Mann-Whitney U = 2090.00, p = 0.01, N = 660). The Box-Whisker plots of the total abrasion among encrustation rates show a slight increase in the total abrasion with increasing encrustation category (Fig. 4). The Pearson's Correlation Coefficient shows that encrustation rates are similar among test length (r = 0.132, p < 0.001, N = 400) (Fig. 5).

The Mann-Whitney U test suggests that the total abrasion value of drilled and undrilled specimens are significantly different (Mann-Whitney U = 53606, p = 0.01, N = 996). The first bar in the histogram of undrilled tests contains 62.0% of the specimens, while that of drilled tests contains 74.1% (Fig. 6). The mean abrasion value for undrilled tests is 1.183 and for drilled tests 1.138. The median abrasion value for undrilled tests is 1.067 and for the drilled tests 1.000. Drilled tests show lower total abrasion values, while undrilled tests shows more abraded tests (Fig. 6).

Discussion

The method based on the quasimetric Likert-Type scale represents a technique that allows a precise assessment of the preservation state of a multi-character shell due to the implementation of both the grade of taphonomic alteration and its proportional distribution on the surface.

Table 5. Encrustation rates of *Echinocyamus pusillus* with respect to sample sites.

Sample site	Number of individuals			Encrustation rate (%)	Number of individuals within an encrustation range			
	total	non-encrusted	encrusted		< 25%	25−50%	50−75%	>75%
Cala dell'Allume	88	70	18	20.5	18	0	0	0
Campese A	40	15	25	62.5	22	1	0	2
Campese B	525	393	132	25.1	111	12	3	6
Cala di Sparavieri	35	21	14	40.0	14	0	0	0
Punta del Morto	127	33	94	74.0	86	5	1	2
Punta della Calbugina	104	72	32	30.8	30	0	0	2
Punta di Radice	33	12	21	63.6	19	2	0	0
Punta della Campana	48	24	24	50.0	22	1	1	0
Punta del Lazzaretto	51	11	40	78.4	30	6	1	3
Total	1051	651	400	38.1	352	27	6	15

Abrasion of the test is generally low and occurs in a narrow range, which is, as previously mentioned, counter-intuitive since the habitats around Giglio Island are generally high-energy environments and might be expected to be dominated by poorly preserved individuals. Tests in these environments, however, are likely to be largely destroyed before they become highly altered (see Kelley 2008).

Tubercle abrasion shows the highest values, followed by the remaining surface abrasion and then the pore abrasion with the lowest values. Differences in abrasion values of the characters can be explained by their relief relative to the test surface. The tubercles, although sunken, are elevated above the test surface and represent the most exposed features of the test while the pore margins are well sheltered within the test. Drillholes are larger than both the ambulacral and genital pores which can explain the difference in abrasion between these two features. The lesser abrasion of peristome relative to other tubercles may likewise be due to the fact that the former occur in a slightly depressed area. There is no significant difference with respect to abrasion among sites although they are at different depths and are characterized by different environmental conditions. The similar abrasion signatures among the different environments can be due to the fact that the environmental conditions are in average similar over the year.

Fragmentation and test destruction.—Sampled tests around Giglio Island show low rates of fragmentation. This can be due to their rapid destruction. Fragmentation can result from a variety of factors such as abiotic processes including tumbling or water and sediment agitation, which can decrease plate integration and lead to a loss of single or multiple plates as well as larger fragments (Kidwell and Baumiller 1990). Test fracturing can occur along plate sutures (interplate disarticulation) or within plates (intraplate fragmentation). As soft tissues decay, fragmentation along plate structures become more common (Kidwell and Baumiller 1990). Once the structural integrity of the test is disturbed, complete tests disarticulation can be rapid as has been shown for larger clypeasteroids by Nebelsick and Kampfer (1994).

Encrustation and test strength.—Echinoids, with their highly variable test surface, area common substrate for encrusting organisms including serpulids and bryozoans (e.g., Nebelsick et al. 1997; Santos and Mayoral 2008; Borszcz 2012; Borszcz et al. 2013; Belaústegui et al. 2013). All encrustation of *Echinocyamus* from Giglio occurred post-mortem, after spine denudation. These echinoids, with lightweight tests not exceeding 15 mm in length (Nebelsick et al. 2015), can be considered as short-termed, unstable substrates and are thus expected to show low rates of encrustation with infrequent encounters between organisms (e.g., McKinney and Jackson 1989).

In our analysis, we show that the abrasion values increase with increasing encrustation rates. Encrustation is highly likely to increase the test preservation potential since it can slow the decrease in shell strength due to taphonomic processes (e.g., Stachowitsch 1980). The high energy environ-
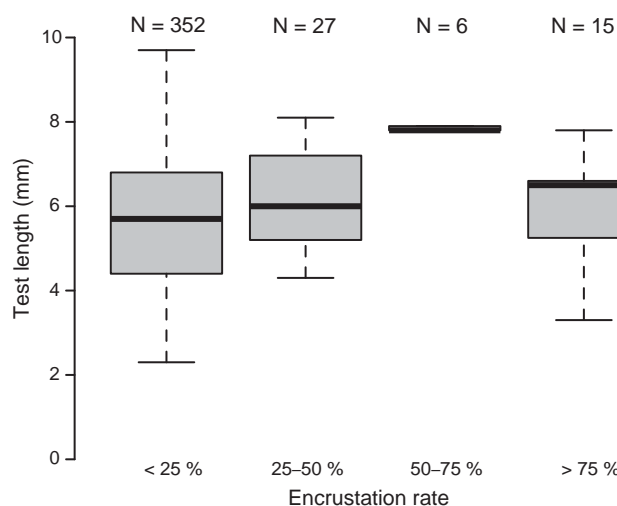

Fig. 5. Box-Whisker plot of the encrustation rates of *Echinocyamus pusillus* samples among the tests size. Outliers were removed from the graph. N, number of individuals.
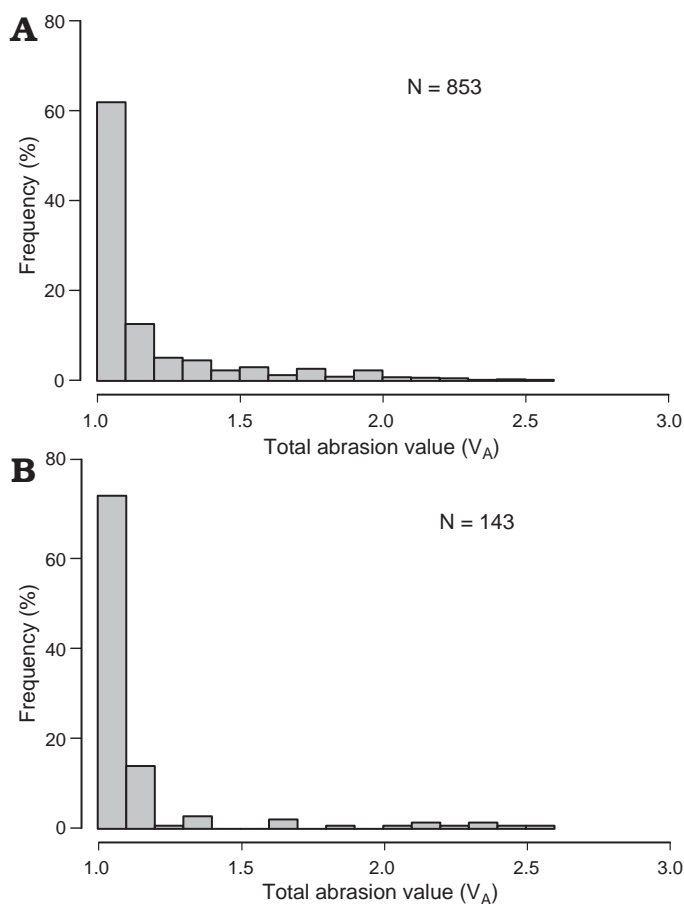

Fig. 6. Histograms of undrilled (**A**) and drilled (**B**) tests of *Echinocyamus pusillus* with respect to the total abrasion value. N, number of individuals.

ments around Giglio are characterized by low encrustation rates. Unlike in low energy settings, surface residence times in these high energy environments are not long enough for high rates of encrustation (e.g., Daly and Mathieson 1977; Meldahl and Flessa 1990; Parsons and Brett 1991; Perry 2000). It is, however, difficult to determine if encrustation

rates increase the preservation potential by crossing plate boundaries, or if variation in energy categories among the environments results in longer surface residence times and thus higher encrustation rates. The results show furthermore that encrustation rates are independent of test size. In general, small substrates show relatively low rates of encrustation (McKinney and Jackson 1989) in contrast to larger substrates which show increasing encrustation rates with increasing shell size (e.g., Rodland et al. 2004).

Taphonomic biasing and drillholes.—The effect of predatory drillholes on the preservation potential of shells has been extensively discussed for both mollusks (e.g., Kelley 2008; Klompmaker 2009 and literature cited therein) and echinoids (Nebelsick and Kowalewski 1999). Kelley (2008) found that shells with fossil predatory drillholes of *Oichnus* Bromley, 1981 are more resistant to taphonomic processes and survive more often than undrilled individuals. The present study shows that the distribution of drilled and undrilled tests are statistically different. It must be stated, however, that the sample size of 1041 tests is large and statistical tests based on such high sample sizes can even detect minor differences in the compared distributions. The overall distribution of both drilled and undrilled distributions is similar, but the high accumulation of pristinely preserved tests (74.1%) of individuals showing drillholes compared to the much lower number without drillholes (62.0%) indicate that a shift in tests featuring drillholes to more pristine preservation is present (Fig. 6) although the difference in medians and means of the test abrasion values for drilled and undrilled specimens is minor. Nonetheless, these results indicate that drilled specimen show a lower preservation potential than undrilled tests.

Studies of predatory drillholes in *Echinocyamus crispus* Mazzetti, 1983 and *Fibularia ovulum* Lamarck, 1816, a minute clypeasteroid lacking internal supports, by Nebelsick and Kowalewski (1999) from the Red Sea showed that drilling predation did not influence test preservation in either *Echinocyamus crispus* or *Fibularia ovulum*. The analysis of *Echinocyamus pusillus* from Giglio may suggest taphonomic filtering against tests with drillholes. Differences between the findings of Nebelsick and Kowalewski (1999) and the results presented here can be due to environmental differences including temperature and exposure. The Northern Bay of Safaga, Red Sea represents various tropical environments, while the Mediterranean Island of Giglio (*E. pusillus*) represents a warm temperate, higher energy setting. These two species also differ in morphology, making a direct comparison of test strength difficult (e.g., Allison 1990).

Conclusions

The semi-quantitative, quasimetric Likert-Type scale method allows for comparisons between complex taphonomic characters. It is, however, limited to combined measurements of taphonomic conditions and the proportion of surface area

affected. Results show that abrasion grades can vary due to the character's position on the test. Exposed features such as tubercles are more likely to abrade on the aboral side than on the slightly depressed peristomal area. The alterations on tests of *Echinocyamus pusillus* from Giglio Island are low due to rapid test destruction in the high energy environments around the island. The test abrasion among the nine sample sites around Giglio are similar, regardless of the environments and depths where the samples were collected. Fragmentation rates are low due to a high structural integrity based on interlocking plates and internal supports, preventing rapid test disaggregation. Encrustation rates are generally low with few highly encrusted individuals reflecting the high energy levels of the environments. Encrustations increase the test integrity by crossing and strengthen plate connections. Predatory drillholes are seen to slightly lower preservation potentials in higher energy environments.

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References

Allison, P.A. 1990. Variation in rates of decay and disarticulation of Echinodermata: Implications for the application of actualistic data. *Palaios* 5: 432–440.

Belaústegui, Z., Gibert, J.M. de, Nebelsick, J.H., Domènech, R., and Martinell, J. 2013. Clypeasteroid echinoid tests as benthic islands for gastrochaenid bivalve colonization: Evidence from the Middle Miocene of Tarragona (North-East Spain). *Palaeontology* 56: 783–796.

Behrensmeyer, A.K., Kidwell, S.M., and Gastaldo, R.A. 2000. Taphonomy and paleobiology. *Paleobiology* 26: 103–147.

Borszcz, T. 2012. Echinoids as substrates for encrustation: review and quantitative analysis. *Annales Societatis Geologorum Poloniae* 82: 139–149.

Borszcz, T., Kuklinski, P., and Zatoń, M. 2013. Encrustation patterns on Late Cretaceous (Turonian) echinoids from southern Poland. *Facies* 59: 299–318.

Brett, C.E. and Gordon, C.B. 1986. Comparative taphonomy: A key to paleoenvironmental interpretation based on fossil preservation. *Palaios* 1: 207–227.

Bromley, R.G. 1981. Concepts in ichnotaxonomy illustrated by small round holes in shells. *Acta Geològica Hispànica* 16: 55–64.

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

Clasen, D.L. and Dormody, T.J. 1994. Analyzing data measured by individual Likert-Type items. *Journal of Agricultural Education* 35: 31–35.

Daly, M.A. and Mathieson A.C. 1977. The effects of sand movement on intertidal seaweeds and selected invertebrates at Bound Rock, New Hampshire, USA. *Marine Biology* 43: 45–55.

Donovan, S.K. 1991. The taphonomy of echinoderms: calcareous multi-element skeletons in the marine environment. *In*: S.K. Donovan (ed.), *The Process of Fossilization*, 241–269. Belhaven Press, London.

El-Hedeny, M. 2007. Encrustation and bioerosion on Middle Miocene bivalve shell and echinoid skeletons: Paleoenvironmental implications. *Revue de Paléobiologie* 26: 381–389.

Flessa, K.W., Cutler, A.H., and Meldahl, K.H. 1993. Time and taphonomy: Quantitative estimates of time-averaging and stratigraphic disorder in a shallow marine habitat. *Paleobiology* 19: 266–286.

Fürsich, F.T. and Aberhan, M. 1990. Significance of time-averaging for palaeocommunity analysis. *Lethaia* 23: 143–152.

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

Grun, T.B. and Nebelsick, J.H. 2015. Sneaky snails: How drillholes can affect paleontological analyses of the minute clypeasteroid echinoid *Echinocyamus*? *In*: S. Zamora and I. Rábano (eds.), *Progress in Echinoderm Paleobiology*, 71–73. Publicaciones del Instituto Geológico y Minero de España, Madrid.

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

Hauser, I., Oschmann, W., and Gischler, E. 2008. Taphonomic signatures on modern Caribbean bivalve shells as indicators of environmental conditions (Belize, Central America). *Palaios* 23: 586–600.

Kelley, P.H. 2008. Role of bioerosion and taphonomy: Effect of predatory drillholes on preservation of mollusc shells. *In*: M. Wisshak and L. Tapanila (eds.), *Current Developments in Bioerosion*, 451–470. Springer, Berlin.

Kidwell, S.M. and Baumiller, T. 1990. Experimental disintegration of regular echinoids: Roles of temperature, oxygen, and decay thresholds. *Paleobiology* 16: 247–271.

Kidwell, S.M. and Bosence, D.W.J. 1991. Taphonomy and time-averaging of marine shelly faunas. *In*: P.A. Allison and D.E.G. Briggs (eds.), *Taphonomy: Releasing Data Locked in the Fossil Record, Topics in Geobiology, Volume 9*, 115–209. Plenum Press, New York.

Klompmaker, A.A. 2009. Taphonomic bias on drill-hole predation intensities and paleoecology of Pliocene mollusks from Langenboom (Mill), The Netherlands. *Palaios* 24: 772–779.

Kowalewski, M. 1996. Time-averaging, overcompleteness, and the geological record. *Journal of Geology* 104: 317–326.

Kowalewski, M. and Nebelsick, J.H. 2003. Predation on recent and fossil echinoids. *In*: P.H. Kelley, M. Kowalewski, and T.A. Hansen (eds.), *Predator-Prey Interactions in the Fossil Record*, 1–20, Kluwer Academic/Plenum Publishers, New York.

Lawrence, D.R. 1968. Taphonomy and information losses in fossil communities. *Geological Society of America Bulletin* 79: 1315–1330.

McKinney, F. and Jackson, J. 1989. *Bryozoan Evolution*. 238 pp. Unwin Hyman, Boston.

Meldahl, K.H. and Flessa, K.W. 1990. Taphonomic pathways and comparative biofacies and taphofacies in Recent intertidal/shallow shelf environment. *Lethaia* 23: 43–60.

Mortensen, T.H. 1927. *Handbook of the Echinoderms of the British Isles*. 498 pp. Humphrey Milford Oxford University Press, London.

Mortensen, T.H. 1948. *A Monograph of the Echinoidea IV.2 Clypeasteroida*. 471 pp. C.A. Reitzel. Copenhagen.

Nachar, N. 2008. The Mann-Whitney U: A test for assessing whether two independent samples come from the same distribution. *Tutorials in Quantitative Methods for Psychology* 4: 13–20.

Nebelsick, J.H. 1995. Comparative taphonomy of clypeasteroids. *Ecological Geology of Helvetia* 88: 685–693.

Nebelsick, J.H. 1999a. Taphonomic comparison between Recent and fossil sand dollars. *Palaeogeography, Palaeoclimatology, Palaeoecology* 149: 349–358.

Nebelsick, J.H. 1999b. Taphonomy of *Clypeaster* fragments: preservation and taphofacies. *Lethaia* 32: 241–252.

Nebelsick, J.H. 2004. Taphonomy of echinoderms: Introduction and outlook.

In: T. Heinzeller and J.H. Nebelsick (eds.), *Echinoderms–München*, 471–477. Taylor and Francis Group, London.

Nebelsick, J.H. 2008. Taphonomy of the irregular echinoid *Clypeaster humilis* from the Red Sea: Implications for taxonomic resolutions along taphonomic grades. *In*: W.I. Ausich and G.D. Webster (eds.), *Echinoderm Paleobiology*, 114–128. Indiana University Press, Bloomington.

Nebelsick, J.H. and Kampfer, S. 1994. Taphonomy of *Clypeaster humilis* and *Echinodiscus auritus* from the Red Sea. *In*: B. David, A. Guille, J.P. Féral, and M. Roux (eds.), *Echinoderms Through Time*, 803–808. Balkema, Rotterdam.

Nebelsick, J.H. and Kowalewski, M. 1999. Drilling predation on recent clypeasteroid echinoids from the Red Sea. *Palaios* 14: 127–144.

Nebelsick, J.H., Dynowski, J.F., Grossmann J.N., and Tötzke, C. 2015. Echinoderms: hierarchically organized light weight skeletons. *In*: C. Hamm (ed.), *Evolution of Lightweight Structures: Analyses and Technical Applications, Biologically-Inspired Systems*, 141–156. Springer Verlag, Heidelberg.

Nebelsick, J.H., Schmid, B., and Stachowitsch, M. 1997. The encrustation of fossil and recent sea-urchin tests: Ecological and taphonomic significance. *Lethaia* 30: 271–284.

Nichols, D. 1959. The histology and activities of the tube-feet of *Echinocyamus pusillus*. *Quarterly Journal of Microscopical Science* 100: 539–555.

Parsons, K.M. and Brett, C.E. 1991. Taphonomic processes and biases in modern marine environments: An actualistic perspective on fossil assemblage preservation. *In*: S.K. Donovan (ed.), *The Processes of Fossilization*, 22–65. Columbia University Press, New York.

Perry, C.T. 2000. Factors controlling sediment preservation on a north Jamaican fringing reef: a process-based approach to microfacies analysis. *Journal of Sedimentary Research* 70: 633–648.

Rodland, D.L., Kowalewski, M., Carroll, M., and Simões, M.G. 2004. Colonization of a "Lost World": encrustation patterns in modern subtropical brachiopod assemblages. *Palaios* 19: 381–395.

Santos, A.G. and Mayoral, E.J. 2008. Colonization by barnacles on fossil *Clypeaster*: an exceptional example of larval settlement. *Lethaia* 41: 317–332.

Schäfer, W. 1962. *Aktuopaläontologie nach Studien in der Nordsee*. 666 pp. Waldemar Kramer, Frankfurt.

Schein, J.P. and Lewis, R.D. 2001. The relationship between living echinoid populations and their skeletal remains in the sea-floor sediment, San Salvador, Bahamas. *In*: B.J. Greenstein and C.K. Carney (eds.), *Proceedings of the 10th Symposium on the Geology of the Bahamas and other Carbonate Regions*, 163–174. Gerace Research Center, San Salvador Island.

Seilacher, A. 1979. Constructional morphology of sand dollars. *Paleobiology* 5: 191–221.

Smith, A.B. 1980. The structure and arrangement of echinoid tubercles. *Philosophical Transactions of the Royal Society, London, Series B* 289: 1–54.

Smith, A.B. 1981. The stereom microstructure of the echinoid test. *Special Papers in Palaeontology* 25: 1–85.

Smith, A.B. 1984. *Echinoid palaeobiology*. 190 pp. George Allen and Unwin, London.

Stachowitsch, M. 1980. The epibiotic and endolithic species associated with the gastropod shells inhabited by the hermit crabs *Paguristes oculatus* and *Pagurus cuanensis*. *Publicazioni della Stazione Zoologica di Napoli: Marine Ecology* 1: 73–101.

Telford, M. 1985. Structural analysis of the test of *Echinocyamus pusillus* (O.F. Müller). *In*: B.F. Keegan and B.D.S. O'Conner (eds.), *Proceedings of the Fifth International Echinoderm Conference, Ireland 1984*, 353–360. Balkema, Rotterdam.

Telford, M., Harold, A.S., and Mooi, R. 1983. Feeding structures, behavior, and microhabitat of *Echinocyamus pusillus* (Echinoidea: Clypeasteroida). *Biological Bulletin* 165: 745–757.

Wilson, M.V.H. 1988. Taphonomic processes: information loss and information gain. *Geoscience Canada* 15: 131–148.

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* 50: 409–428.