

CHARACTERIZATION OF TRACES OF PREDATION AND PARASITISM ON FOSSIL ECHINOIDS

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ABSTRACT: Interactions with predators and parasites can result in traces found on Recent and fossil echinoids. However, identifying specific trace makers, particularly on fossil echinoids, remains contentious. To document the range of trace morphologies present on echinoids and improve our ability to identify and quantify biotic interactions affecting echinoids, we characterized traces found on fossil echinoids using museum collections and field sampling spanning the Jurassic to Recent worldwide. Using light microscopy, 8,564 individual echinoid specimens were examined including 130 species, and 516 traces of potential biotic interactions identified. Morphological characteristics were recorded for each trace, including the shape of the trace outline, maximum diameter and cross-section profile. Based on shared morphological characteristics, it was possible to classify all traces into eight categories: circular, subcircular, elongated, irregular, rectangular, figure-eight, notched, and linear. Cross-section characteristics provided additional insights into the identity of potential trace makers. To further evaluate the proposed biotic origins of these traces, trace diversity was examined through time and compared with anticipated ecological trends associated with the diversification of echinoids, and their predators and parasites. Trace diversity increased over time, starting in the late Eocene, coincident with the proliferation of echinoid-drilling gastropods, an indication that biotic interactions intensified through evolutionary time, as predicted by several macroevolutionary hypotheses previously tested using mollusks. The morphological descriptions provided here enhance our understanding of biotic traces on fossil echinoids, and the potential to identify temporal trends in the intensity and diversity of biotic interactions that have affected echinoids throughout their evolutionary history.

INTRODUCTION

Predation is thought to be an important evolutionary (Vermeij 1987; Kelley et al. 2003; Huntley and Kowalewski 2007; Sallan et al. 2011) and regulatory (Paine 1966; Pianka 1966; Bertness and Cunningham 1981; Navarrete and Menge 1996; Yamada and Boulding 1996; Burrows et al. 1999; Guidetti 2007; Schemske et al. 2009; Molinaro et al. 2014; Tyler et al. 2014) force. Although the evolutionary importance of biotic interactions remains contentious (e.g., Kelley et al. 2003; Tyler and Leighton 2011; Tyler et al. 2013), several macroevolutionary hypotheses are consistent with the idea that ecological interactions are an important evolutionary force, such as Escalation Theory (Vermeij 1977, 1987), and the Red Queen Hypothesis (Van Valen 1973). Traces of biotic interactions preserved on skeletal remains, such as drill holes and repair scars, provide direct evidence of biotic interactions in the fossil record (Kowalewski and Kelley 2002), and have been widely used to infer the intensity of interactions, particularly on molluscan prey (Dudley and Vermeij 1978; Vermeij 1978, 1993; Vermeij and Dudley 1982; Leighton 2002; Kelley and Hansen 2003; Huntley and Kowalewski 2007; Chattopadhyay and Dutta 2013; Tyler et al. 2013; Molinaro et al. 2014; Stafford et al. 2015; Tyler et al. 2015; Leonard-Pingel and Jackson 2016; Smith et al. 2018; Klompmaker et al. 2019; Tyler et al. 2019). Because the fossil record of predation has been especially well documented for drilling organisms that interact with benthic 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), our current understanding of the

evolutionary role of biotic interactions remains predominantly centered around mollusks. If biotic interactions are an important evolutionary driver for other groups such as echinoids, temporal changes in the nature and intensity of those interactions recorded by fossils should link to long-term temporal evolutionary trends, including, for example, diversity, body size, or functional traits. Although echinoids are common in the fossil record (Kowalewski and Nebelsick 2003), they have received far less scrutiny in this regard compared to mollusks. Organisms interacting with echinoids today are widespread and abundant and produce diverse traces which are often distinctive and can be preserved in the fossil record, particularly traces of predation and parasitism (see Table 1 for a summary of traces previously described in the literature, and discussions elsewhere, e.g., Kier 1982; Kowalewski and Nebelsick 2003; Coppard et al. 2012; Donovan 2015). However, studies to date have predominantly focused on single echinoid species, regions, or stratigraphic units (e.g., Gibson and Watson 1989; Nebelsick and Kowalewski 1999; Ceranka and Złotnik 2003; Meadows et al. 2015), and large-scale analyses comparable to those available for mollusks are lacking.

Predators of echinoids documented in the literature include gastropods (Moore 1956; Chesher 1969; Hughes and Hughes 1971, 1981; Hendler 1977; Gladfelter 1978; Kier 1981; Levitan and Genovese 1989; McClintock and Marion 1993; Nebelsick and Kowalewski 1999; McClanahan 1999; Ceranka and Złotnik 2003; Złotnik and Ceranka 2005; Grun et al. 2014, 2017; Meadows et al. 2015; Tyler et al. 2018), crustaceans (e.g., Smith 1984), sea stars (e.g., Smith 1984), fishes (e.g., Smith 1984; Borszcz and Zaton 2013; Wilson et al. 2015), turtles (e.g.,

TABLE 1.—Previous reports of trace morphologies found on modern and fossil echinoids. TM = Trace maker. Length is reported in mm, and dashes indicate missing data (i.e., data not reported). Morphotype indicates the trace outline categorizations used in this study equivalent to the trace shapes reported in the literature.

Ecology	Inferred Trace Maker	Echinoid Species	Geologic Occurrence	Trace freq. %	Trace length	Site selectivity	N	TM length	Echinoid length	Reported trace shape	Morpho-class	References
Predation	<i>Semicassis miclaevigata</i>	<i>Echinocyamus linearis</i>	M. Miocene	4	0.28	Ambulacra	7324	—	2.4	Circular	Circular	Zlotnik and Ceranka 2005
	<i>Phallium zeylanica</i>	<i>Echinodiscus bisporforatus</i>	Modern	—	—	—	—	—	—	Circular	Circular	Day 1969
	<i>Phallium granulatum</i>	<i>Mellitia quinquiesperforata</i>	Modern	—	—	—	—	—	—	Circular	Circular	Moore 1956
	Gastropods	<i>Micraster corangitum</i>	L. Cretaceous	10	—	Dorsal	420	—	—	Circular	Circular	Rose and Cross 1993
	<i>Cypracaassis testiculus</i>	<i>Toxopneustes variegatus</i>	Modern	—	—	—	—	—	—	Circular	Circular	Lynnan 1937
	<i>Cassis tuberosa</i>	<i>Echinometra lucunter</i>	Holocene	70	5	Ambial	109	140–200	—	Circular	Circular	Hughes and Hughes 1971
	—	<i>Triopneustes ventricosus</i>	Holocene	81	5	Ambial	100	140–200	—	Circular	Circular	Hughes and Hughes 1971
	—	<i>Cassidulus caribbeorum</i>	Modern	53	4–5	Ventral	823	15–18	<35	Oval, jagged	Elongated	Gladfelter 1978
	—	<i>Meoma ventricosa</i>	Modern	96.8	2–14	Ventral	125	—	157	Circular	Circular	Tyler et al. 2018
	—	<i>Triopneustes ventricosus</i>	Modern	—	—	—	—	—	—	Circular	Circular	Moore 1956
	—	<i>Triopneustes variegatus</i>	Modern	—	—	—	—	—	—	Circular	Circular	Lynnan 1937
	—	<i>Diadema antillarum</i>	Modern	—	—	—	—	—	—	Circular	Circular	Schroeder 1962
	<i>Cassis madagascariensis</i>	<i>Leodia sexiesperforata</i>	Holocene	59.5	3.92–5.33	Ventral	289	—	66.9	Subcircular, Irregular	Subcircular, Irregular	Grun 2017
	<i>spinella</i>	<i>Plagiobrissus grandis</i>	Modern	—	—	—	—	—	—	Circular	Circular	Moore 1956
	<i>Cassis madagascariensis</i>	<i>Toxopneustes variegatus</i>	Modern	—	—	—	—	—	—	Circular	Circular	Lynnan 1937
	—	Spatangoid indet.	Modern	—	—	—	—	—	—	Circular	Circular	Schroeder 1962
	—	<i>Brissus unicolor</i>	Modern	—	—	—	—	—	—	Circular	Circular	Kier and Grant 1965
	Cassids	<i>Echinocyamus linearis</i>	M. Miocene	4	0.28	Dorsal	7290	—	—	Circular	Circular	Ceranka and Zlotnik 2003
	—	<i>Echinocyamus stellatus</i>	Miocene	11	0.69	Dorsal	1053	—	2.8	Circular	Circular	Grun et al. 2017
	—	<i>Echinocyamus pusillus</i>	Holocene	10	0.24–0.55	Dorsal	1016	—	5.1–5.2	Circular, Irregular	Circular, Irregular	Grun et al. 2014
	—	<i>Echinocyamus crispus</i>	Holocene	71	0.89	Dorsal	294	—	5.1	Circular	Circular	Nebelsick and Kowalewski 1999
	—	<i>Fibularia ovulum</i>	Holocene	46	—	Dorsal	782	—	4.5	Circular	Circular	Nebelsick and Kowalewski 1999
	—	<i>Echinocyamus pusillus</i>	M. Miocene	11	0.24	Ambulacra	402	—	2.7	Circular	Circular	Ceranka and Zlotnik 2003
	—	<i>Echinocyamus pseudopusillus</i>	M. Miocene	15	0.18	Ambulacra	197	—	2.59	Circular	Circular	Zlotnik and Ceranka 2005
	—	<i>Fibularia</i>	Oligocene	7	0.5	Dorsal	813	—	—	Circular to subcircular	Subcircular	Meadows, Fordyce, and Baumiller 2015
Parasitism	—	<i>Echinocorys scutata</i>	L. Cretaceous	—	1.8	Dorsal	—	—	38	Incomplete circular	Circular	Donovan and Jagt 2004
	—	<i>Hemipneustes striatoradiatus</i>	Maastrichtian	—	3.35–5.23	Dorsal	—	—	73.1	Circular	Circular	Donovan and Jagt 2002
	—	<i>Oligopygus wetherbyi</i>	Eocene	50	1	Dorsal	32	—	—	Circular, Irregular	Circular, Irregular	Gibson and Watson 1989
	—	<i>Oligopygus haldemani</i>	Eocene	19	2	Ventral	21	—	—	Circular, Irregular	Circular, Irregular	Gibson and Watson 1989
	—	<i>Weisbordella cubae</i>	Eocene	14	1.05	Dorsal	14	—	—	Figure-Eight	Figure-Eight	Gibson and Watson 1989
	—	<i>Neolaganum archerensis</i>	Eocene	66	1.68	Dorsal	6	—	—	Circular, Irregular	Circular, Irregular	Gibson and Watson 1989
	—	<i>Schizaster ocalanus</i>	Eocene	100	3.6	Dorsal, Ventral	1	—	—	Sinuuous tunnel	Linear	Gibson and Watson 1989
	—	Cidaroids	Modern	—	—	Periproct	—	—	—	Spindle, Teardrop	Elongated, NA	Waren 1981
	<i>Sabinella infrapatula</i>	<i>Arachnoides placenta</i>	Holocene	13	—	Dorsal	723	4.8	—	Circular	Circular	Crossland et al. 1991
	<i>Hypermastus</i>	<i>Echinocorys</i>	L. Cretaceous – E. Paleocene	—	0.8–19	Ventral	7000	—	—	Circular	Circular	Neumann and Wissiak 2009
	Eulimids	—	—	—	—	—	—	—	—	—	—	—
	—	<i>Echinoderms</i>	Modern	—	—	—	—	—	—	Circular	Circular	Jangoux 1984
	—	<i>Echinodiscus tenuissimus</i>	Modern	—	0.49–0.9	Ventral	1	3.9–5.68	34.5	Circular, Subcircular	Circular, Subcircular	Waren and Crossland 1991
	Cassids	<i>Meoma ventricosa</i>	Modern	—	—	—	—	—	—	Circular	Circular	Chesher 1969
	—	<i>Echinocorys ovata</i>	E. Maastrichtian	—	3.4	Ventral	1	—	97	Linear	Linear	Wissiak and Neumann 2006
	Boring polychaete	<i>Cardiaster granulatus</i>	Maastrichtian	100	1.0–2.0	Dorsal	1	—	—	<i>Rogeria</i> isp.	NA	Donovan et al. 2016

Smith 1984), birds (e.g., Smith 1984; Sievers et al. 2014), and sea otters (e.g., Smith 1984). Trace-producing parasites of echinoids documented to date also include a variety of organisms including gastropods (Chesher 1969; Warén 1980, 1981; Warén et al. 1984; Fujioka 1985; Alekseev and Endelman 1989; Warén and Moolenbeek 1989; Warén and Mifsud 1990; Warén and Crossland 1991; Crossland et al. 1993; Rinaldi 1994; Warén et al. 1994; Cross and Rose 1994; Oliverio et al. 1994; Vaitilingon et al. 2004; Campos et al. 2009; Neumann and Wisshak 2009; Britayev et al. 2013; Matsuda et al. 2015; Yamamori and Kato 2017), worms (Wisshak and Neumann 2006; Campos et al. 2009; Britayev et al. 2013), barnacles (Madsen and Wolff 1965; Cross and Rose 1994; Donovan and Jagt 2013; Donovan et al. 2016), shrimps (Britayev et al. 2013), crabs (Campos et al. 2009; Britayev et al. 2013), and copepods (Margara 1946; Roman 1952). Although these morphologically and behaviorally diverse predators and parasites produce a wide range of different traces, we currently lack a comprehensive assessment of trace morphologies preserved on fossil echinoid tests. The most common traces reported in the fossil record are circular holes attributed to cassid and eulimid gastropods (Kowalewski and Nebelsick 2003), which range as far back as the Cretaceous (Kier 1981; Alekseev and Endelman 1989; Neumann and Wisshak 2009). Parasitic traces produced by eulimids are often differentiated from predation traces made by cassids by their smaller size, the absence of dissolution halos, or the presence of multiple traces on one test (Kowalewski and Nebelsick 2003). However, descriptions of cassid drill-hole morphology on echinoid tests vary greatly from circular (e.g., Nebelsick and Kowalewski 1999) to irregular and highly jagged (e.g., Grun et al. 2014, 2017; Grun 2017), and predatory and parasitic gastropods are not often found in conjunction with their hosts in the fossil record (Neumann and Wisshak 2009). Thus, identifying trace makers on fossil echinoids remains challenging.

Documenting the known diversity of trace morphologies present on fossil echinoids represents a first step in assembling diagnostic criteria differentiating traces of predation and parasitism. Gibson and Watson (1989) examined 65 specimens representing five species of irregular echinoid from the Eocene of Florida, and described five trace morphologies: circular, figure-eight, spindle, sinuous tunnel, and teardrop. These morphologies were further differentiated by their size, surface characteristics, and interior walls, resulting in eight unique trace ‘types’. However, given the limited geographic, temporal, and taxonomic ranges they examined, the ubiquity of these types is unclear. In addition, the suitability of their eight types as the basis for a schema for identifying potential trace makers is uncertain. Post-mortem and *in vivo* traces were not clearly differentiated, and the authors describe holes penetrating encrusting bryozoan colonies, suggesting that at least some traces were likely post-mortem. Furthermore, recent discoveries regarding interpretations of potential trace makers are difficult to resolve with the trace makers attributed to their eight types. For example, although only single penetrating holes are typically attributed to predation today, the authors describe multiple examples occurring on a single test in the case of three of the four circular trace types, despite their being attributed to predation by gastropods. Spindle shaped traces were also interpreted as consistent with those produced by predatory gastropods; however, spindle shaped traces are now believed to be created by barnacles attaching to the test post-mortem (Donovan et al. 2016), and fall under the ichnogenus *Rogerella*. Teardrop traces were similarly ascribed to predation by gastropods, but were described as ‘non-penetrative excavations’, which is terminology more typically applied to domiciles or attachment scars. The aggregation of traces based on shared morphological characteristics could provide a broadly applicable trace classification scheme. However, a more extensive classification of trace types systematically applied across numerous echinoid species from a broad spatiotemporal range is necessary to improve our ability to identify biotic traces on fossil echinoids, and enhance our understanding of the evolution and paleoecology of organisms that interact with echinoids as well as echinoids themselves.

Ultimately a set of diagnostic criteria distinguishing types of biotic traces, such as predation from parasitism, would prove useful in expanding our understanding of echinoid ecology. Documenting the diversity of traces found on fossil echinoids represents an important first step toward this goal. Therefore, traces of biotic interactions found on fossil echinoid tests from around the world ranging in geological age from the Jurassic to Recent were described and quantified. The morphological characteristics of inferred biotic traces were systematically described to document the diversity of trace morphotypes present on fossil echinoids, and to assess the potential feasibility of assembling a widely applicable set of morphological diagnostic criteria for ecological interpretations (i.e., infer trace makers). As the latter relies on the accurate identification of traces of predation and parasitism, the distribution of trace frequencies and morphologies were also examined through time to independently assess the reliability of the putative biotic origin of the identified traces. As cassids and eulimids first diversified in the Late Cretaceous, becoming increasingly diverse through the Cenozoic (Bandel 1993), traces attributed to gastropod predation and parasitism were expected to appear in the late Mesozoic, and became more common in the Cenozoic in concert with the proliferation of gastropod trace makers (Baumiller and Gahn 2002; Coppard et al. 2012). Similarly, the infaunalization of echinoids may have led to an increase in the diversity or abundance of traces if predators and/or parasites evolved specialized behaviors or associations to exploit infaunal prey. Therefore, the diversity of epifaunal and infaunal echinoids through time were also examined.

MATERIALS AND METHODS

Fossil echinoids were examined from collections in the Florida Museum of Natural History (FLMNH), Alabama Museum of Natural History (ALMNH), Muséum national d'Histoire naturelle (MNHN), Natural History Museum London (BM), Natural History Museum of Basel (BNHM), Jackson School Museum of Earth History (UTNV) and the Mississippi Museum of Natural Science (MMNS). Lots representing at least 10 individuals were utilized to include samples from underrepresented time periods, and as this study does not test ecological hypotheses, no additional filters were applied to exclude small samples (see Online Supplemental File). All specimens were examined for traces of biotic interactions using light-microscopy. In addition, field sampling was conducted in Florida, Texas, and Mississippi, resulting in the collection of 761 specimens from seven localities (Online Supplemental File). Collected specimens were repositied in the Florida Museum Invertebrate Paleontology Division of the FLMNH. Any traces present on specimens interpreted as originating *in vivo* from biotic interactions were described and measured, and the morphology of each trace was then classified into discrete categories based on shared characteristics. Evidence for abiotic trace origins was broad given the number of localities and species examined, and the variability of abiotic damage. Such damage was typically distinguished from traces produced by gastropods based on a comprehensive assessment of reports of biotic traces on echinoid tests in the literature including modern studies and the appearance of biotic traces on modern echinoids (see Table 1). Characteristics of abiotic damage included dissolution holes produced by groundwater which were often highly irregular and associated with discoloration or paired holes on either side of the test, holes with fresh, ragged edges indicative of damage made post-recrystallization, and holes penetrating through the test and continuing into the internal matrix. As size may be a diagnostic criterion for determining biological and ecological identity of a trace maker (Nebelsick and Kowalewski 1999; Kowalewski and Nebelsick 2003; Zlotnik and Ceranka 2003; Grun et al. 2014; Grun 2017), the size of each trace was measured as the maximum length (the longest axis of the trace), and maximum width (the longest axis perpendicular to the trace length), using digital calipers (± 0.01 mm) with the aid of a light microscope when necessary.

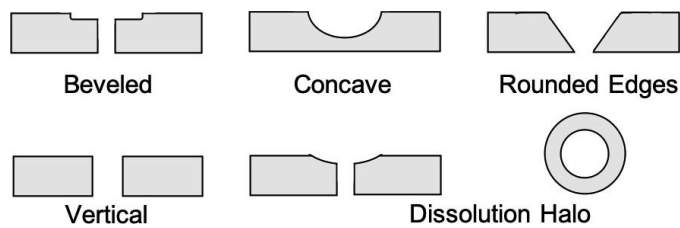


FIG. 1.—Conceptual drawings of trace characteristics. Top row represents outlines of trace shapes in plan view (serrated and irregular), and the dissolution halo is shown in profile (left) and plan view (right). All other perspectives are in cross-section (beveled, concave, rounded edges, and vertical).

The shape of each trace outline was recorded following the nomenclature of Gibson and Watson (1989), where applicable, and the published literature. In addition, characteristics of the cross-section, such as the smoothness of the intersection of the walls with the test surface, the steepness of the cross-section and evidence of dissolution on the area surrounding the trace due to the application of acid were also recorded. Characteristics of the cross-section of traces were anticipated to be potentially useful in differentiating between trace makers. For example, beveled drill holes occurring on bivalves can be produced by predatory naticid gastropods (e.g., Kitchell et al. 1981), whereas holes produced by muricids are typically cylindrical (Carriker and Yochelson 1968; Carriker 1981; Bromley 1981, 2004). Similarly, concave trace profiles can characterize drill holes made by cassids on echinoid tests (e.g., Grun 2017).

Cross-section characteristics were defined as follows (Fig. 1): (1) beveled—a horizontal shelf was present in cross-section; (2) concave—the profile curved inward; (3) rounded edges—the intersection of the trace with the test surface was uniform and typically rounded; and (4) vertical—the interior walls of the trace were perpendicular to the test surface, creating a sharp intersection with the surface of the test.

We also noted dissolution halos—the appearance of a smoothed or engraved region on the test surface around a trace that appeared to have been produced by dissolution due to the secretion of acid. In addition, at the intersection of the trace surface and interior walls, edges may have been serrated, i.e., in plan view the interior walls appear serrated with marginal ‘teeth’ pointing towards an apex, or whether the intersection was irregular, i.e., could not be uniformly characterized. Traces with corresponding descriptions of their characteristics were then aggregated into morphotypes based on their similarity. All of the above trace characteristics were used to infer trace ecology (predation, parasitism, or commensalism), and traces interpreted to originate via the activities of encrusters, or post-mortem interactions (e.g., sponge borings, bivalve borings, and barnacle attachment scars) or abiotic processes (e.g., diagenesis) were not included in the data.

To examine traces in greater detail, representative examples from the resultant morphotypes were selected for imaging using scanning electron microscopy (SEM). Specimens were cleaned using a sonicator in a bath of deionized water for 30–90 seconds, depending on the size and level of accumulated dirt and dust, to remove surface debris. They were then air dried in a fume hood for four hours before being stored in sealed containers. Specimens were coated with 20 μm of gold for 90 seconds and mounted on an aluminum SEM stage using conductive carbon tape immediately prior to imaging. Traces were then examined via secondary electron imaging using a SUPRA 35VP-24-01 field-emission gun scanning electron microscope. Imaging was conducted in a high-vacuum chamber with an electron beam acceleration voltage of 5 kV and a working distance between 10.1 and 22.8 mm.

To assess the reliability of our interpretations of traces as biotic in origin, temporal trends in the abundance and diversity of trace morphotypes were evaluated in relation to the fossil record of the

inferred trace makers. Cassid and eulimid gastropods are the most common and widespread trace producing predators and parasites of echinoids today, therefore, it seems likely that their interactions with echinoids would be the most reliable and least speculative to examine in conjunction with traces. That is, they are known to produce traces today, and have been inferred to be responsible for the majority of reports of traces on fossil echinoids in the literature. Thus, if cassids and eulimids were the most frequent trace makers, and we have correctly identified biotic traces, their diversity should be positively correlated with trace frequency and diversity. Gastropod and echinoid range-through diversity was obtained from the Paleobiology Database to compare trace frequency with inferred trace maker diversity (downloaded June 20, 2019). Overall, the diversity and frequency of traces should correspond to the diversity of trace makers (Baumiller and Gahn 2002; Coppard et al. 2012) as echinoid predators and parasites diversified and, presumably, specialized behaviors evolved (Kier 1974; Vermeij 1977, 1987, 1994). Cassids and eulimids were expected to be absent or rare prior to the Late Cretaceous, and become increasingly diverse following the K/Pg extinction (Bandel 1993). Therefore, if traces ascribed to predation and parasitism were reliably identified, we hypothesized that traces similarly would be absent in the Early Cretaceous, occur with low frequency in the Late Cretaceous, and become increasingly common in the Cenozoic. Trends in trace diversity may alternatively be associated with the infaunalization of echinoids, which may have led to the subsequent coevolution of their predators and parasites (Kier 1982), and an associated diversification of traces. Therefore, in addition, regular and irregular echinoid range-through diversity data were also obtained from the Paleobiology Database (downloaded June 20, 2019). Echinoid life mode classifications (infaunal or epifaunal) were based on vetted Paleobiology Database assignments. In cases where life mode was unassigned or assigned based on taxonomic breadth (e.g., identified to genus), life mode was assigned based on general morphology, with irregular echinoids classified as infaunal and regular echinoids as epifaunal. As both the semi-infaunal and infaunal life modes would offer escape from predators, or require parasites to adapt to tolerating echinoid hosts spending time in the sediment, semi-infaunal life modes were considered infaunal, and no distinction was made between shallow and deep infaunal life modes. Classifying semi-infaunal taxa as epifaunal taxa did not notably change the outcome of the analysis. A Pearson's correlation coefficient was used to assess whether the number of trace morphotypes in a given time interval co-varied with sample size. All analyses were conducted in R 3.3.1 (R Core Team 2017).

RESULTS

Morphological Descriptions

The examined 8,564 specimens originated from 193 different localities in 20 countries (Online Supplemental File), predominantly from the U.S.A. (Fig. 2). The specimens represented 33 stratigraphic stages that ranged from the Jurassic to Recent and included 137 species, including 25 regular and 112 irregular species. Traces inferred to be of biological origin were found on 443 echinoids, 516 traces total. All 516 traces could be classified into one of the following eight qualitative morphological categorizations of trace outline shape (Fig. 3): circular, subcircular, elongated, irregular, rectangular, figure-eight, notched, and linear. The size range of each morphotype varied (Fig. 4), and the size distributions of circular, subcircular, elongated, and irregular traces were unimodal and right skewed.

The three rounded trace outline morphologies (circular, subcircular, elongated) overlapped and differed subtly in the ratio of trace length to width (Fig. 5). Traces were classified as circular if had a nearly equal ratio of length to width (i.e., approximating 1), traces classified as

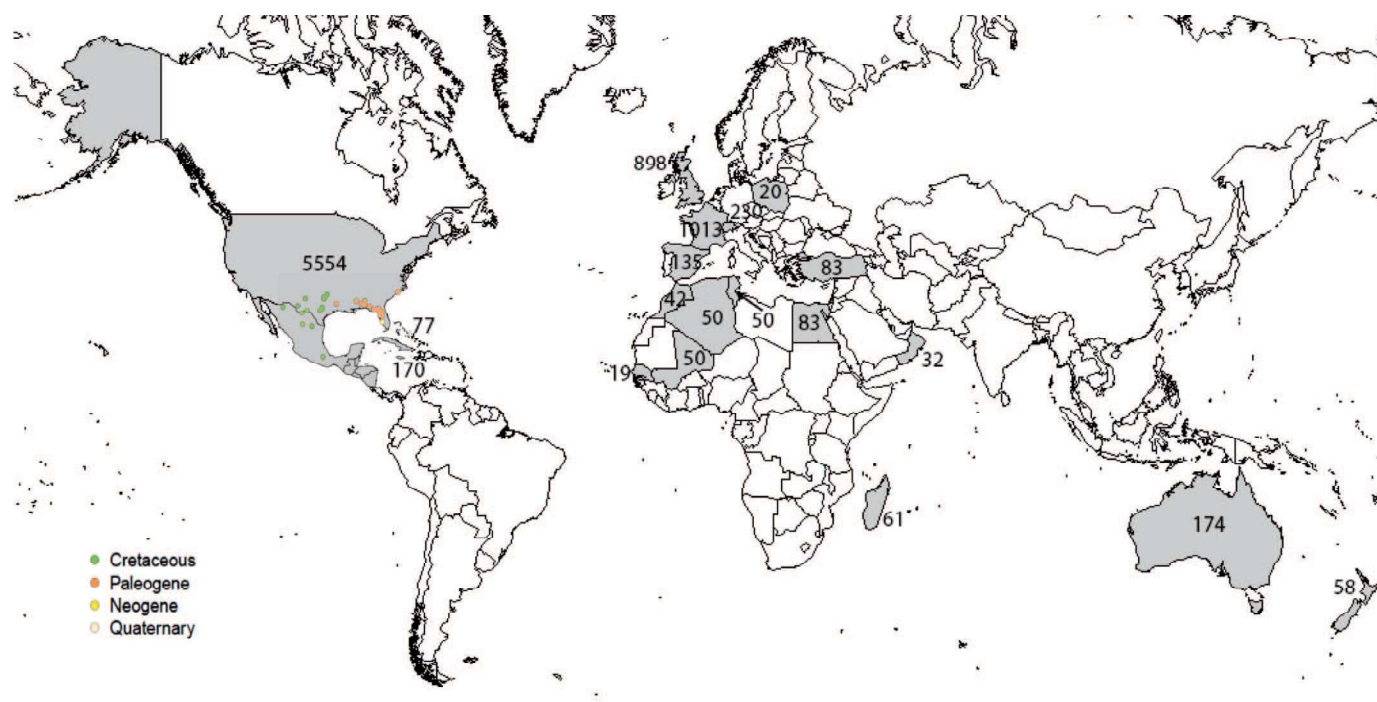


FIG. 2.—Geographic distribution of samples. Samples originated from countries highlighted in dark gray. Numbers denote the total number of specimens for a given country. Colored circles indicate sampling localities in the southeastern U.S.A., and colors correspond to geologic periods.

subcircular were overall marginally longer than wide and with a minimum width to length ratio of 1.6, and traces classified as elongated were more distinctly longer than wide (Fig. 5). To assess the reliability of differentiating the three morphotypes, a linear discriminant analysis (LDA) was performed to distinguish among the three predefined groups, and trace length and width were used to predict group membership (circular, subcircular, or elongated). Length and width were log transformed prior to analysis. The dataset was then randomly partitioned, and 80% of the data were used to train the discriminant function, and 20% of the data were used to test the model. The LDA correctly predicted morphotype (circular, subcircular, or elongated) based on trace length and width 67% of the time. The analysis was then repeated after grouping circular and subcircular traces into a single morphotype, and re-run with two groups (circular + subcircular, elongated). The LDA correctly predicted morphotype with 87% accuracy.

Scanning electron microscopy (SEM) was used to obtain high-resolution images of each morphotype (Fig. 6). A description of each morphotype, their cross-sections, range of maximum lengths and widths, and proposed ecologies (Table 2) are summarized below:

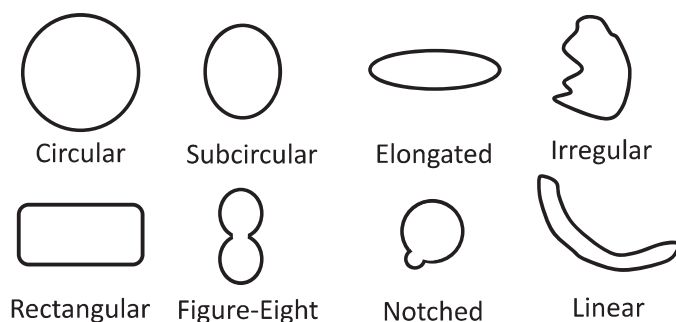


FIG. 3.—Conceptual drawings of each trace morphotype.

Circular.—Circular traces ($n = 289$) had an outline shape that was approximately circular; that is, the length and width of the trace were approximately equal to each other and the circumference was equidistant from the center (Fig. 7A). Length ranged from 0.17 mm to 9.32 mm, and width from 0.15 mm to 7.44 mm. The cross-sections of circular traces varied and included beveled ($n = 14$), rounded edges ($n = 229$), vertical walls ($n = 47$) and dissolution halos ($n = 3$), as well as irregular ($n = 30$) and serrated ($n = 87$) interior walls. These traces included holes representing the ichnogenus *Sedilichnus* (Bromley 1981), and the ichnospecies *Sedilichnus parabolides* (Bromley 1981), *Sedilichnus simplex* (Bromley 1981), *Sedilichnus gradatus* (Nielsen and Nielsen 2001) and *Sedilichnus spongiophilus* (Müller 1977).

Subcircular.—Subcircular traces ($n = 120$) were defined as traces for which the outline approximated a circle, but which were modestly elongated in one dimension, such that the trace appeared to be nearly, but not perfectly, circular (Fig. 7B). Consequently, the maximum length and width of this trace were not equal. The maximum length ranged from 0.35 mm to 7.35 mm, and maximum width ranged from 0.21 mm to 5.46 mm. The cross-sections of this trace included beveled ($n = 13$), rounded edges ($n = 68$) or vertical walls ($n = 25$) and dissolution halos ($n = 1$), and irregular ($n = 14$) and serrated ($n = 31$) interior walls. The proposed ecologies of this morphotype included predation (Hughes and Hughes 1971; Nebelsick and Kowalewski 1999; Złotnik and Ceranka 2005; Grun et al. 2014), parasitism (Meadows et al. 2015) and domiciles (Donovan and Jagt 2002). These traces included holes representing the ichnogenus *Sedilichnus*, and the ichnospecies *Sedilichnus parabolides*, *Sedilichnus simplex*, *Sedilichnus gradatus*, and *Sedilichnus spongiophilus*.

Elongated.—Elongated traces ($n = 67$) consisted of an oval shape (Fig. 7C), with maximum length notably greater than width. The maximum length ranged from 0.32 mm to 12.77 mm. The maximum width ranged from 0.21 mm to 7.80 mm. The cross-sections of this morphotype included rounded edges ($n = 71$) or vertical walls ($n = 7$) and dissolution halos ($n =$

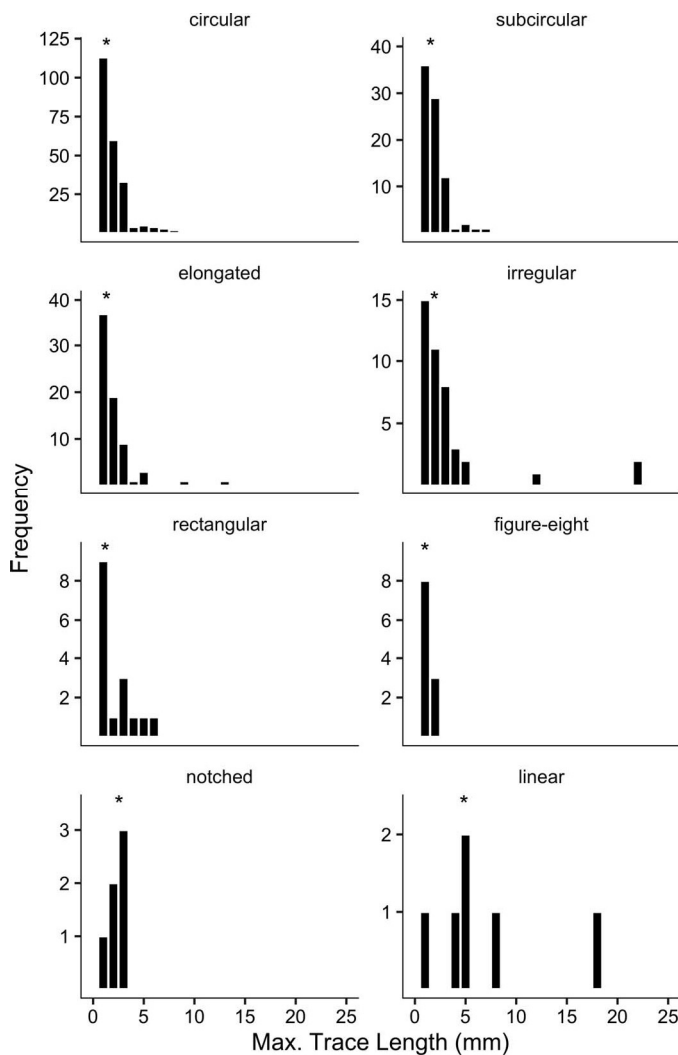


FIG. 4.—Distribution of maximum trace length for each morphotype. Stars indicate median trace length. Circular, $n = 257$; subcircular, $n = 91$; elongated, $n = 79$; irregular, $n = 48$; rectangular, $n = 16$; figure-eight, $n = 13$; notched, $n = 6$; linear, $n = 6$.

1), and irregular ($n = 6$) and serrated ($n = 13$) interior walls. These traces included holes representing the ichnogenus *Sedilichnus*, and the ichnospecies *Sedilichnus asperus* (Nielsen and Nielsen 2001) and *Sedilichnus ovalis* (Bromley 1993).

Irregular.—Irregular traces ($n = 59$) had outlines that could not be systematically characterized (Fig. 7D). The maximum lengths and widths of these traces had no systematic relationship to each other. The maximum lengths ranged from 0.66 mm to 26.61 mm, and maximum widths ranged from 0.56 mm to 19.01 mm. This morphotype included cross-sections that were beveled ($n = 8$), rounded edges ($n = 13$) or vertical walls ($n = 6$), with dissolution halos ($n = 1$), and irregular ($n = 10$) and serrated ($n = 30$) interior walls. The outlines of these traces were too irregular to assign to the ichnogenus *Sedilichnus*.

Rectangular.—Rectangular traces ($n = 15$) were described as traces for which the outline consisted of four linear sides where the opposite sides were approximately parallel and of equal length (Fig. 7E). The maximum length was longer than width, and the sides intersected at 90° angles. The maximum length ranged from 0.56 mm to 6.48 mm. The maximum width

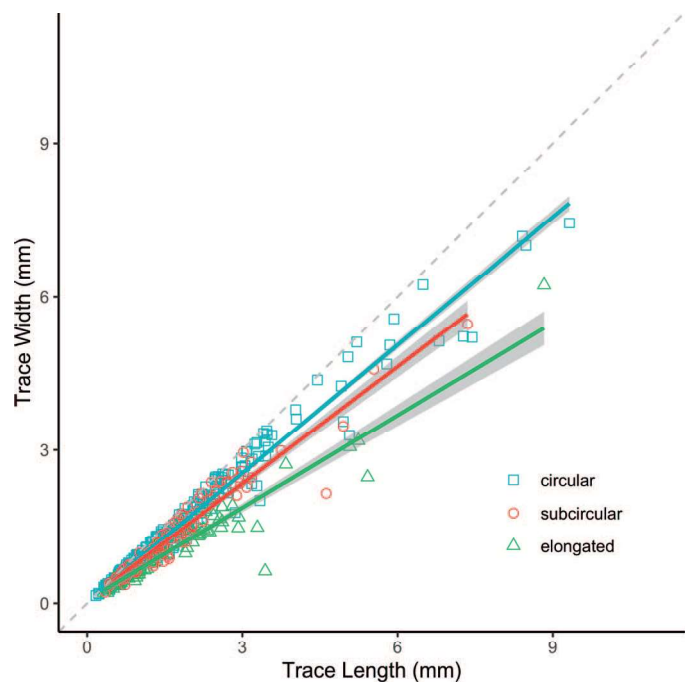


FIG. 5.—Rounded trace morphotypes. Circular, subcircular, and elongated trace morphotypes formed overlapping categories of shapes with increasing length relative to width. Although traces classified as circular or subcircular were often similar in their dimensions, elongated traces were somewhat more distinct. A linear discriminant function correctly differentiated between the three morphotypes 67% of the time. When circular and subcircular are combined, together they were correctly predicted by the discriminant function with 87% accuracy. Gray bands represent 95% confidence intervals, and the dashed line shows the 1:1 ratio (i.e., a perfect circle).

ranged from 0.39 mm to 5.56 mm. Additional characteristics of this trace included rounded edges ($n = 7$), and vertical ($n = 6$), irregular ($n = 7$), and serrated ($n = 5$) interior walls. These traces could not be ascribed to an existing ichnogenus.

Figure-Eight.—Figure-eight traces ($n = 13$) included two connected circles of similar diameter (Fig. 7F). The maximum length ranged from 0.38 mm to 2.23 mm. The maximum width ranged from 0.21 mm to 1.39 mm. The cross-sections of this morphotype included rounded edges ($n = 19$) and vertical ($n = 3$), irregular ($n = 1$) and serrated ($n = 3$) interior walls. These traces included holes representing the ichnogenus *Sedilichnus*.

Notched.—Notched traces ($n = 8$) consisted of an incised circle (Fig. 7G). These traces were characterized by a large circular trace with equal length and width, and a circumference equidistant from the center that was intersected by a single smaller notch. The maximum length ranged from 0.69 mm to 3.75 mm, and maximum width ranged from 0.44 mm to 2.98 mm. The cross-section of this morphotype included rounded edges ($n = 5$) and vertical ($n = 2$) and irregular ($n = 1$) and serrated ($n = 3$) interior walls. These traces included holes representing the ichnogenus *Sedilichnus*.

Linear.—Linear traces ($n = 6$) had approximately parallel sides along the longitudinal axis that extended in a straight (linear) or curved (curvilinear) line. The maximum length was notably longer than width (Fig. 7H). The maximum length ranged from 0.89 mm to 18.16 mm. The maximum width ranged from 0.54 mm to 5.99 mm. This morphotype included rounded edges ($n = 3$) and irregular ($n = 1$) interior walls. These traces included holes representing the ichnogenus *Caulostrepsis* (Wisshak and Neuman 2006).

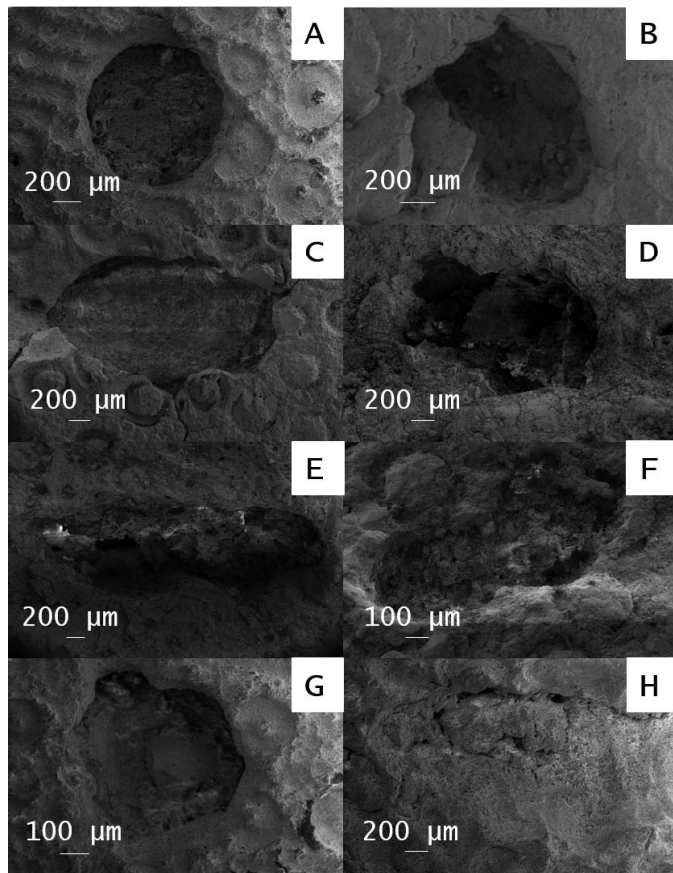


FIG. 6.—SEM micrographs of trace morphotypes. A) Circular. B) Subcircular. C) Elongated. D) Irregular. E) Rectangular. F) Figure-eight. G) Notched. H) Linear.

Trace Diversity and Frequency through Time

No traces were observed until the latest Early Cretaceous, and were first seen in the Bathonian (Fig. 8). Prior to the Maastrichtian (Late Cretaceous), only three morphotypes were present (elongated, subcircular, and circular) with circular traces being the most common, and the

frequency and diversity of trace morphologies remained low until the Eocene, at which point all trace morphologies were present. Trace frequency was weakly but significantly correlated with sample size ($df = 231$, Pearson $r = 0.30$, $p < 0.001$). However, despite the high number of Cretaceous specimens, both the number of traces and trace diversity remained low in this time period. Cassids radiated in the Paleocene, and again in the Miocene and Pliocene, while eulimid diversity increased gradually from the Late Cretaceous onward. The diversity of epifaunal echinoids remained relatively consistent from the Jurassic onwards. In contrast, the diversity of infaunal echinoids increased gradually from the Jurassic to Cretaceous, with a rapid decline in the Maastrichtian, continuing through the Paleocene, followed by a second radiation from the Eocene through to the middle Miocene (Fig. 8).

DISCUSSION

Despite the geographic and temporal breadth of the echinoids examined, all 516 traces could be classified into one of only eight morphotypes, of which 93% ($n = 482$) were interpreted as originating via either predation or parasitism. All of the trace morphologies previously described by Gibson and Watson (1989) were observed, however, as our analyses are restricted to traces that we interpret as being made *in vivo*, we did not document spindle, sinuous tunnels, and teardrop shaped traces. In addition to circular and figure-eight shaped traces, we observed three additional *in vivo* trace morphotypes: rectangular, notched, and subcircular. Furthermore, although our classification was qualitative, these trace morphotypes were repeatedly identifiable on 137 different species of echinoids despite differences such as test microstructure and thickness, and body size. Given the number of echinoids examined, and the spatiotemporal breadth of the samples employed, we propose that these morphotypes likely reflect the diversity of consistently identifiable morphologies of biotic traces on the tests of fossil echinoids produced by *in vivo* interactions.

Overall, rounded traces were inferred to have been produced by parasitic and predatory gastropods. The trace morphologies produced by predatory gastropods, such as cassids, is highly variable in modern environments (Hughes and Hughes 1971; Nebelsick and Kowalewski 1999; Ceranka and Zlotnik 2003; Donovan and Pickerill 2004; Grun et al. 2014; Meadows et al. 2015; Grun 2017). Predatory gastropods typically create large circular or subcircular holes in the test using the radula, often in conjunction with the application of acid secreted by the accessory boring organ to weaken the test (Hughes and Hughes 1971, 1981; Kowalewski and Nebelsick

TABLE 2.—Eight trace morphotypes and their characteristics, such as outline, maximum dimensions, and proposed ecology. Proposed ecology was determined based on the size and shape of the trace.

Trace morphology		Circular	Subcircular	Elongated	Irregular	Rectangular	Figure-eight	Notched	Linear
N		257	91	79	48	16	13	6	6
Size	Min. trace length (mm)	0.17	0.35	0.32	0.6	0.56	0.38	0.69	0.89
	Max. trace length (mm)	9.32	7.35	12.77	21.82	6.48	2.23	3.16	18.16
	Min. trace width (mm)	0.15	0.22	0.21	0.53	0.39	0.21	0.44	0.54
	Max. trace width (mm)	7.44	5.46	7.8	9.73	5.56	1.39	2.2	5.99
Surface characteristics	Dissolution halo	15	2	6	5	2	2	0	0
	Serrated	45	16	12	20	5	1	1	0
	Irregular	5	4	2	5	3	0	1	1
Cross-section	Beveled	14	12	2	2	0	0	0	0
	Rounded edges	158	48	54	16	5	12	1	1
	Vertical	46	22	8	6	7	3	2	0
	Concave	0	0	1	0	0	0	0	3
Ecology	Predation	145	52	41	33	9	0	0	0
	Parasitism	104	31	27	13	5	12	6	0
	Commensal	3	1	2	0	0	0	0	6

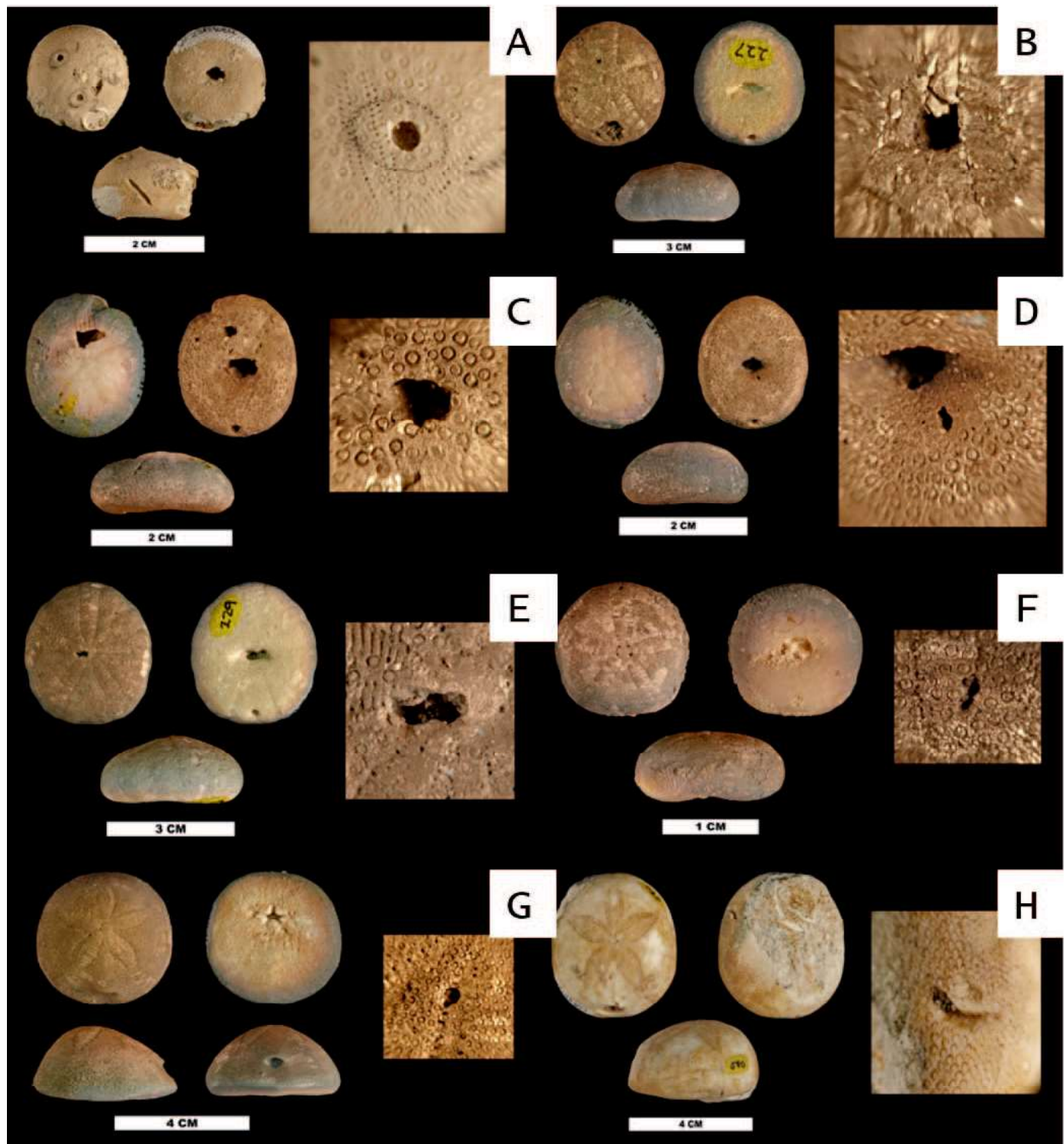


FIG. 7.—Images of the eight different trace morphotypes. A) Circular, *Echinolampas*, UF 226652. B) Subcircular, *Oligopygus haldemani*, UF 46115. C) Elongated, *Oligopygus haldemani*, UF 46105. D) Irregular, *Oligopygus haldemani*, UF 46430. E) Rectangular, *Oligopygus haldemani*, UF 46305. F) Figure-eight, *Oligopygus haldemani*, UF 187590. G) Notched, *Rhyncholampas gouldii*, UF 128805. H) Linear, *Rhyncholampas gouldii*, UF 128807.

2003; Grun 2017). This can result in a serrated hole, and in some cases dissolution from the application of a chelating agent or radula rasping traces may be present (Grun et al. 2014; Grun 2017; Tyler et al. 2018). Large circular, subcircular, irregular, and rectangular holes with dissolution halos, rounded edges, concave or beveled profiles or irregular and serrated

interior walls were, therefore, interpreted as produced by predation (Hughes and Hughes 1971; Nebelsick and Kowalewski 1999; Ceranka and Złotnik 2003; Donovan and Pickerill 2004; Meadows et al. 2015; Tyler et al. 2018; but note caveats in Donovan 2015). In modern settings small holes (2–5 mm in diameter) made by juvenile or small adult cassids have

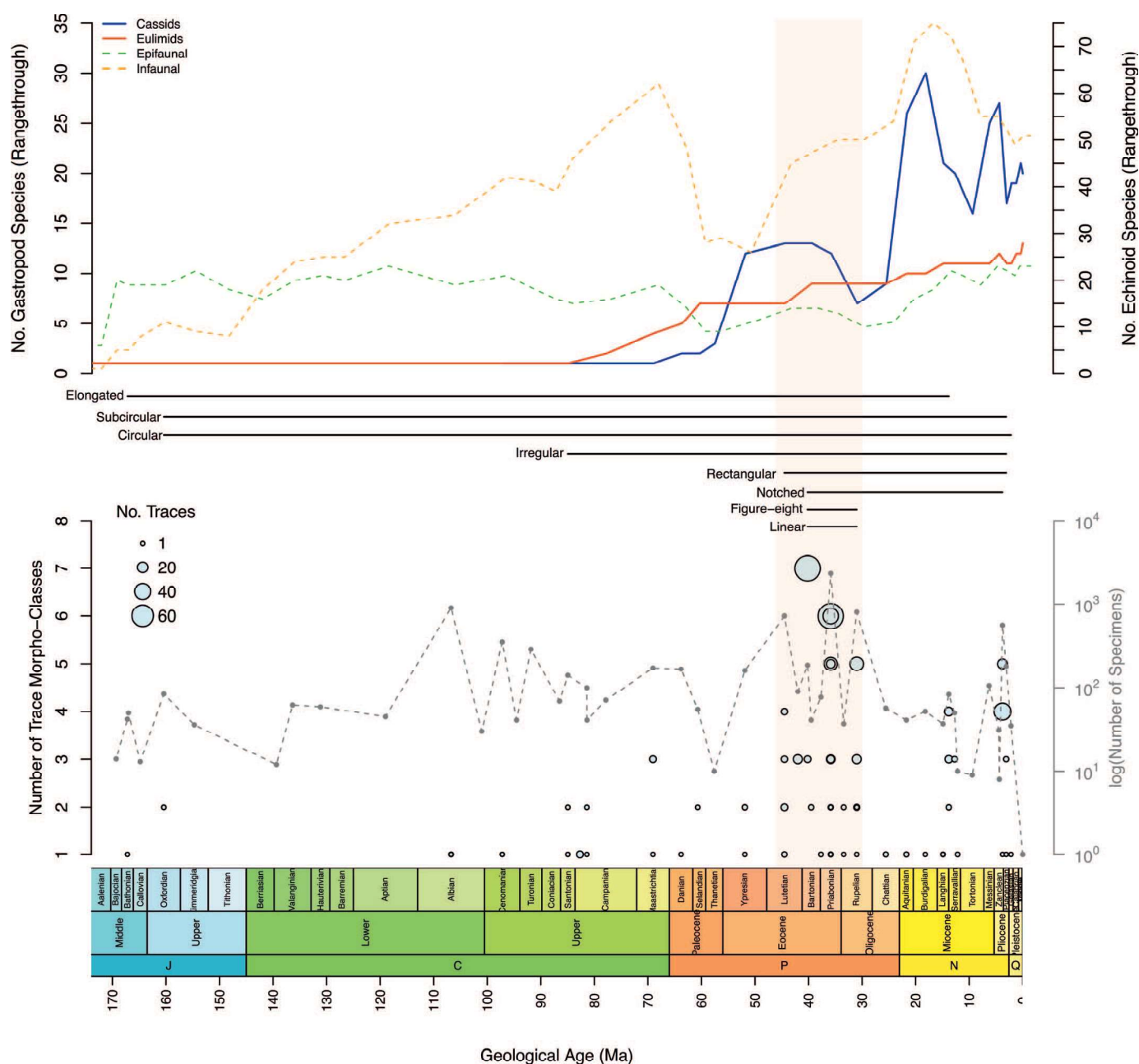


FIG. 8.—Trace diversity through time. The upper panel shows cassid and eulimid diversity through time, and the diversity of epifaunal and infaunal echinoids. The horizontal bars indicate the geologic range of each trace morphotype. The lower panel shows both the number of trace morphotypes per species at each locality (blue circles), and the number of traces (represented by circle size) increased during the Eocene, and coincided with an increase in cassid diversity (shaded area). Trace diversity did not increase as a function of increasing sample size (dashed gray line), however, samples with greater numbers of traces ($n \geq 50$) included a higher diversity of morphotypes ($n \geq 5$).

been observed on both small and large echinoids (e.g., Tyler et al. 2018), thus the size of the echinoid is likely not useful in differentiating between predation and parasitism for smaller traces. However, in the absence of additional evidence, predation may be inferred when trace size notably exceeded the reported diameter of known eulimids. Small rounded type traces > 1 mm in diameter were ascribed to predation when represented by only a single penetration on the test, as such holes may be produced by juvenile predators or small adults. This may have led to an overestimation of predatory traces. However, this would not change the overall findings of this paper. A detailed investigation of predator-prey size ratios within

echinoids is needed to shed more light on the potential relationship between trace size and echinoid size.

Here we used multiple criteria to infer eulimid parasitism, including the number of traces on the test, the trace size and shape, and the trace cross-section and interior walls. Traces were attributed to parasitism in cases with multiple occurrences of small (< 5 mm in diameter) circular, subcircular, elongated, irregular, and rectangular traces with vertical, concave, rounded edges or beveled cross-sections and irregular or serrated interior walls (Warén 1981; Bromley 2004; Donovan and Pickerill 2004; Neumann and Wisshak 2009; Meadows et al. 2015). As multiple holes can occasionally

result from predation, this may have led to the misinterpretation of the ecology of a small number of traces, however, they would still nevertheless be biotic in origin. Figure-eight traces were also inferred to be a result of parasitic eulimids, as a male-female eulimid pair creates two holes in close enough proximity that the holes become connected, and are synonymous with previous descriptions of overlapping circles (Warén and Carney 1981; Warén et al. 1984; Meadows et al. 2015). Parasitic eulimids are thought to create small circular holes by dissolving the surrounding test and then inserting their proboscis into the weakened area of the test, however the method of dissolution remains unknown (Warén and Crossland 1991). Although features resembling dissolution halos associated with eulimid traces have been reported (e.g., Neumann and Wisshak 2009), no definitive cases of *Sedilichnus halo* (Neuman and Wisshak 2009), which is characterized by a circular groove, were observed in this study, suggesting that this trace is rare in the fossil record.

Irregular shaped traces may also be produced by gastropods drilling holes in the test with the use of acid, weakening the plates around the hole, which then collapse inward resulting in an irregularly shaped penetration (Hughes and Hughes 1971; Nebelsick and Kowalewski 1999; Grun 2017; Tyler et al. 2018). It has been previously suggested that irregular traces are defined by the presence of surface structures such as ambulacral pores, or when solid surface structures such as tubercles don't allow circular drillings (e.g., Grun et al. 2014). However, cassid predation can also result in breakage that does not follow plate sutures and transects plate boundaries (Tyler et al. 2018). The shapes of elongated and rectangular traces may reflect dissolution or breakage of the surrounding test by predatory gastropods during drilling (Hughes and Hughes 1971; Nebelsick and Kowalewski 1999; Grun et al. 2014). Notched traces can also be caused by drilling predation (Złotnik and Ceranka 2005; Grun 2017).

It is also possible that some subcircular traces may have originated as a circular shape, and were later altered by taphonomic processes such as abrasion widening or lengthening the trace resulting in smooth or rounded openings (Nebelsick and Kowalewski 1999; Grun et al. 2014), or breakage producing irregular or serrated openings. Therefore, while the ultimate shape may have been influenced by taphonomic overprint, the trace's origins were, nevertheless, inferred here to be biological based on the overall characteristics of the trace which maintained characteristics associated with biotic origins (Ceranka and Złotnik 2003; Złotnik and Ceranka 2005). However, an assessment of the potential effects of taphonomy on traces found on fossil echinoids requires testing in future studies.

Despite uncertainty in the nuanced distinctions between potential trace origins—differentiating between predation and parasitism, in particular—the interpreted biotic origin of traces appears to be consistent with the fossil record of putative trace makers. Both the frequency of traces and the number of trace morphotypes did not increase until the Eocene, when biotic interactions may have intensified due to diversification of the most likely trace makers: cassid and eulimid gastropods. Interestingly, five of the eight trace morphotypes first appear in the Eocene, suggesting the evolution of new ecological behaviors, but not coinciding with the increasing infaunalization of echinoids which occurs in the Late Cretaceous and again in the Eocene. As the radiation of infaunal echinoids did not correspond to a notable increase in trace diversity or frequency, we propose that increases in the diversity and frequency of traces most likely corresponded with increasing predation pressure, and the evolution of new ecological behaviors. However, additional studies examining macroevolutionary trends and echinoid predator-prey interactions are needed to test these hypotheses.

Linear traces formed a distinct morphological category, and were relatively straightforward to identify. Although far more than six linear traces were observed, only six were not classified as traces created post-mortem, and were interpreted as polychaete burrows and assigned to the ichnospecies *Caulostrepsis taeniola* (Wisshak and Neumann 2006) or

Caulostrepsis cretacea (Wisshak and Neumann 2006), based on their overall morphological similarity. These traces were attributed to a commensal symbiotic relationship between echinoids and polychaetes by Wisshak and Neumann (2006).

Distinct patterns differentiating potential trace makers did not emerge from the aggregation of trace morphologies, particularly with regard to distinguishing predation and parasitism. The inclusion of additional lines of evidence such as the co-occurrence of echinoids and potential trace makers at a given locality, and the number of traces (multiple circular holes typically being attributed to eulimid parasitism) remain the most prudent approach to differentiating between predation and parasitism. As the size of holes produced by predatory cassids range from 1–9 mm (Moore 1956; Hughes and Hughes 1981; McClintock and Marion 1993; Grun 2017; Tyler et al. 2018), while those produced by eulimids are typically < 1 mm (Warén et al. 1994; Kowalewski and Nebelsick 2003), size may be a useful diagnostic. However, small rounded traces can be produced both by parasitic eulimids, and by juvenile or small adult predatory gastropods, therefore, size alone is not sufficient to determine trace ecology. The absence of definitive diagnostic morphological criteria may be partly due to the overlap between the characteristics of the three rounded morphotypes. Traces classified here as circular, subcircular, and elongated, appeared to more accurately represent one category of rounded traces, and variation between these three morphotypes may reflect structural heterogeneity of the stereom, angle of penetration, test surface curvature, driller identity, or some combination of these. While the three rounded morphotypes (circular, subcircular, and elongated) overlapped in the maxima and minima of their length to width ratios, there was nevertheless reasonable discrimination among the three groups, and relatively high discrimination between groups when circular and subcircular traces were aggregated. Thus, the distinct classification of circular traces and subcircular traces may be unnecessary, while the elongated morphotype may prove more easily recognizable. Both circular and subcircular traces also included the same four ichnospecies within *Sedilichnus*, all of which can be produced by either predatory or parasitic gastropods.

Given the large number of echinoids examined, and their broad spatiotemporal range, we provide three lines of evidence supporting our assertion that the data consist largely of the accurate identification of *in vivo* biotic traces based on the examination of temporal trends in trace occurrences: (1) The inclusion of a substantial number of abiotic and/or post-mortem traces would increase the noise in the data, likely generating a highly variable dispersion pattern with no significant associations. This is not what we observe: trace abundance and diversity was low for ~ 120 million years and then increased substantially; (2) Some traces produced by abiotic processes could have been erroneously interpreted as of biotic origin. However, despite consistent sampling, Jurassic and Cretaceous traces were rare; and (3) The abundance and diversity of traces were closely associated with that of cassid and eulimid gastropods, the most common and widespread trace producing predators and parasites of echinoids today, and most frequently reported trace makers on fossil echinoids in the literature. Although cassids and eulimids are the most commonly cited as producing traces on fossil echinoids, we do not claim that these were the only organisms producing traces, but only identify them as the most likely culprits. Twenty-two traces were observed prior to the documented appearance of cassids and eulimids, some or all of which may have been produced by other unknown predators or parasites. The alternative is that these early traces were misidentified, and instead were abiotic in origin. However, only three traces were present on Jurassic echinoids, followed by an ~ 50 million year time interval during which no traces were observed despite adequate sampling coverage. A total of ~ 3,000 specimens were examined from the Jurassic and lower Cretaceous, and processes capable of producing abiotic rounded traces that resemble biotic traces should be present in samples throughout this interval. It is difficult to account for a 50 million year absence of abiotic traces on thousands of specimens.

CONCLUSIONS

Traces of predation and parasitism were observed on fossil echinoids from the Jurassic to the Recent, and all 516 traces identified could be aggregated into only eight morphotypes. Changes in the abundance and diversity of traces were associated with the diversification of gastropods that prey upon and parasitize echinoids. The trace categorizations provided here contribute to a growing literature on echinoid associated traces and echinoid paleoecology. The systematic description of the range of trace morphologies observed on fossil echinoids should facilitate future comparative analyses across phyla (particularly echinoids and mollusks). In particular, the improved understanding of morphology and distribution of traces should enable us to carry out in future echinoid-based (i.e., non-molluscan) assessments of ecological and evolutionary importance of biotic interactions in marine benthic ecosystems.

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SUPPLEMENTAL MATERIAL

Data are available from the PALAIOS Data Archive:
<https://www.sepm.org/supplemental-materials>.

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