

# Contributions

from the Museum of Paleontology, University of Michigan

VOL. 34, NO. 11, PP. 148–157

APRIL 27, 2022

## FISH PREDATION ON *CLYPEASTER HUMILIS* FROM THE RED SEA: POTENTIAL FOR RECOGNITION IN THE FOSSIL RECORD

BY

JAMES H. NEBELSICK<sup>1</sup> AND ANDREA MANCOSU<sup>2</sup>

*Abstract* — Fish predation on *Clypeaster humilis* produces characteristic traces on the test. The predatory attacks are lethal, removing much of the oral surface and exposing the internal organs of the animal. There are various stages of test removal, generally expanding from the peristome to the ambitus. In some cases, the wound can be highly irregular and even extend to the aboral surface. In a few instances, accompanying scratch marks are found on the oral surface. In others, discrete indentations can be correlated to bite marks at the rim of the wound. Intraplate fragmentation is mostly prevalent, though interplate breakage along plate boundaries also occurs. Intraplate fragmentation often results in oblique breakage planes reaching toward the oral surface. The potential for recognizing such events in the fossil record depends on the preservation of these specific features. The described predation events can compromise the fossilization potential of such traces unless rapidly buried or encrusted by bioinfestation.

### INTRODUCTION

Recognizing predation events in the fossil record is an important tool for studying synecological interactions through time (e.g., Walker and Brett, 2002; Huntley and Kowalewski, 2007; Klompmaker et al., 2019). Detecting these interactions, however, can be problematic as the act of predation itself is inherently destructive. Predation events on skeletonized organisms lead not only to the death of the

prey, but also to the demolition of protective or associated hard parts (e.g., Nebelsick, 1999a). This circumstance thus compromises the potential recognition of these events in fossil ecosystems, as well as affecting the completeness of the fossil record as a whole, because predation is pervasive in most ecosystems.

Gastropod predation on invertebrates leave neat round holes that may or may not affect the preservation potentials of the shelly remains (e.g., Nebelsick and Kowalewski, 1999; Grun et al., 2014; Harper, 2016; Farrar et al., 2020),

<sup>1</sup>Department of Earth Sciences, University of Tübingen, Schnarrenbergstraße 94-96, 72076 Tübingen, Germany (nebelsick@uni-tuebingen.de).

<sup>2</sup>Dipartimento di Scienze Chimiche e Geologiche, Università degli studi di Cagliari, “Citadella Universitaria di Monserrato, 09127, Cagliari, Italy (andrea.mancosu@gmail.com).

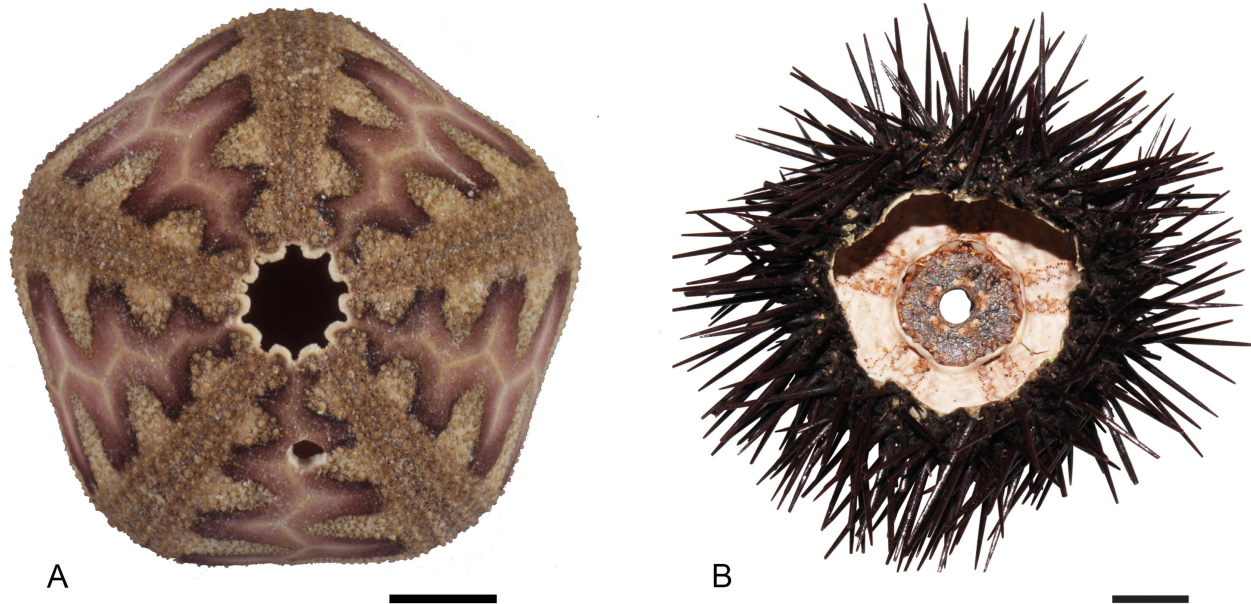


FIGURE 1 — Comparison of predation scars from gastropod and fish predation. **A**, Predatory gastropod bore hole on the regular echinoid *Microcyphus rousseaui* from the Northern Bay of Safaga, Red Sea. The round bore hole is clearly placed within an interambulacral plate row, which in this species is largely devoid of tubercles (Sample JS87-162) **B**, Predation by sparid fish removing the aboral surface of *Paracentrotus lividus*. Spines and peristomal membrane are still preserved indicating a recent predation event. Mediterranean Sea, Torre del Porticciolo, Sardinia (TP-PL-001). Scale bars = 1 cm.

predation by durophagous organisms is usually destructive. The resulting damage to the skeleton may be difficult to differentiate with respect to specific predators as well as from other destructive taphonomic processes such as fragmentation resulting from transport and sediment agitation. Furthermore, such massive wounds potentially weaken the skeletons such that the predated-upon skeletons have poorer preservation potentials. Gastropod predation on echinoids has been studied with respect to changes through deep time (e.g., Kowalewski and Nebelsick, 2003; Farrar et al., 2020; Petsios et al., 2021; and literature therein). Predation by other predators including fish, crustaceans, birds, and mammals can also be common (e.g., Estes et al., 1978; Andrew and MacDiarmid, 1991), although they have received comparatively little attention with respect to their preservation in the fossil record (see Belaústegui et al., 2017). There have been a few specific actualistic studies on predator-prey interactions on echinoids with respect to their preservation potentials besides those concerning gastropods including investigations involving shorebirds, stingrays, and bony fish (Sievers et al., 2014; Grun, 2016; Sievers and Nebelsick, 2018). Variations in the wounds found on sea urchins are consistent with the different types of predators that attack echinoids (see Fig. 1). The degree to which predatory attacks can be recognized and attributed to specific predators depends on the careful analysis of not only wound morphologies but also of the architecture of the prey skeletons.

In the echinoid fossil record, reports of predation on echinoids is again dominated by gastropod drilling in the

form of drill holes (see literature in Złotnik and Ceranka, 2005; Meadows et al., 2015; Grun et al., 2017; Farrer et al., 2020; Petsios et al., 2021). Publications concerning other types of predation on echinoids are less common and have been restricted to fish predation on regular echinoid spines and tests (Borszcz and Zatoń, 2013; Wilson et al., 2015) and predation on echinoids from marine reptiles (Neumann and Hampe, 2018). The preservation potential of echinoids is influenced by a wide range of factors (e.g., Allison, 1990; Donovan, 1991; Kidwell and Baumiller, 1990; Greenstein, 1991; Kowalewski et al., 2018; Nebelsick and Mancosu, 2021). Although durophagous predation may be intuitively destructive, Kidwell and Baumiller (1990) showed in tumbling experiments on regular echinoids that collagenous ligaments continue to connect test plates after death until they fully decay. Breakage crossing plate boundaries thus does not necessarily imply predation events. In addition, some predation events have shown to enhance preservation potentials (Tyler et al., 2018).

In this study, predation by fish on a recent clypeasteroid echinoid, *Clypeaster humilis* (Leske, 1998) from the Red Sea, is described with respect to the wounds and potential recognition in the fossil record. *Clypeaster humilis* is a common Indo-Pacific echinoid in shallow water carbonate sediments typically reaching lengths of 5 to 8 cm (Clark and Rowe, 1971; Nebelsick 1992a, b, 1995b, c, 2008; Nebelsick and Kampfer, 1994). As a clypeasteroid, it has a flattened test with a prominent petalodium on the aboral side containing modified respiratory ambulacral tube feet (Fig. 2). The oral

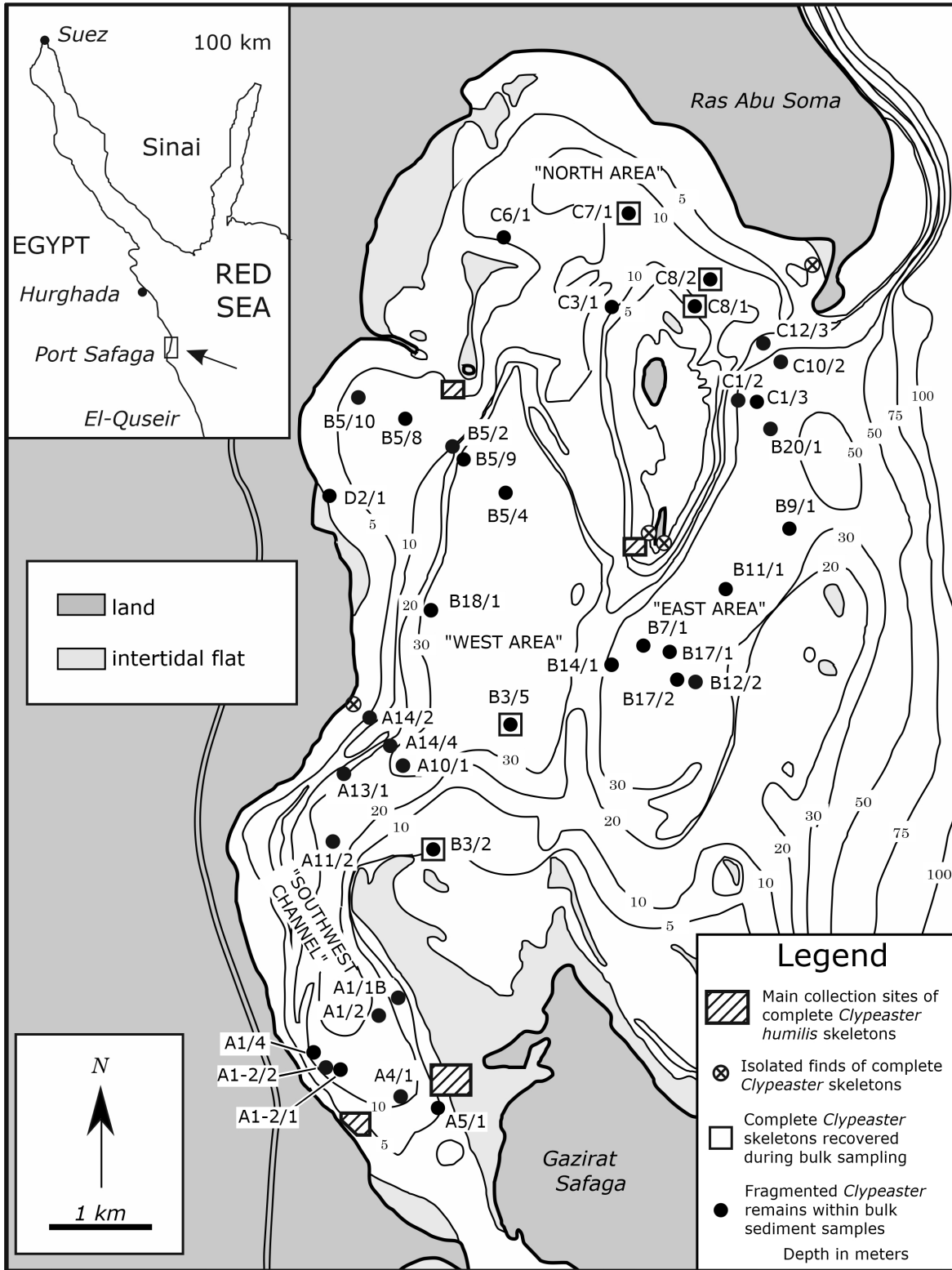


FIGURE 2 — Northern Bay of Safaga, Egypt showing 4 main areas of collection of *Clypeaster humilis* specimens. Specimens found separately as well as those recovered during bulk sampling are also indicated. In addition, bulk samples containing *Clypeaster* fragments are shown.



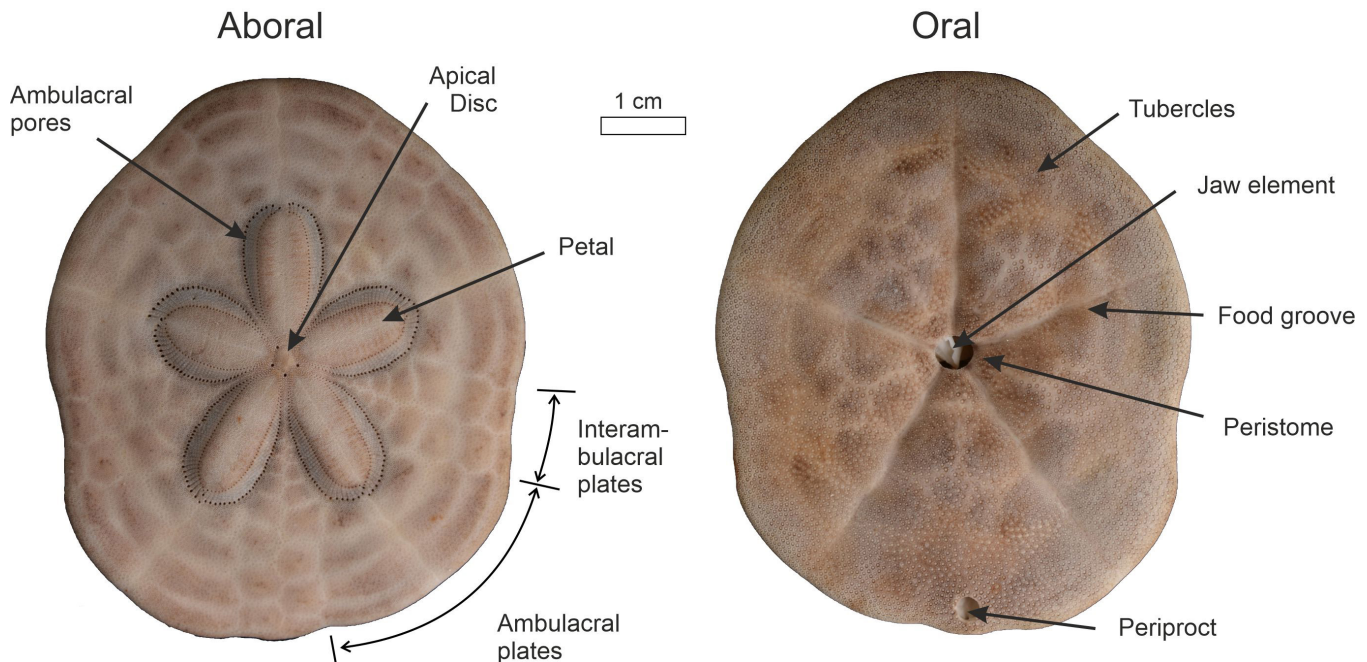


FIGURE 3 — *Clypeaster humilis* from the Northern Bay of Safaga, Red Sea, Egypt. Scale bar = 1 cm. **A** and **B**, Complete, well preserved tests showing plate boundaries and tuberculation. Note that slightly differential length of the left- and right-hand side of the test. The aboral side **A**, shows the central apical system and five petals of the petalodium containing the ambulacral pores in which the modified respiratory tube feet are found during life. The oral side **B**, shows the centrally positioned mouth (peristome), the posterior anus (periproct) and straight food grooves leading to the mouth. Elements of the jaw apparatus are just visible within the peristome. Sample RS-CL2/13.

side of the test is characterized by a central peristome, posteriorly placed periproct, and straight food grooves leading to the mouth. The external test surface is covered by small tubercles that support the spines. The test is stabilized by internal supports that conjoin the oral and aboral sides consisting of more central pillars and peripheral supports near the ambitus. For a detailed morphological description of test features in *Clypeaster* see Durham (1966) and Mihaljević et al. (2011).

#### MATERIAL AND METHODS

*Clypeaster humilis* is a shallow burrower living just underneath the sediment surface. This species belongs to the most widely distributed irregular echinoids in shallow environments of the Red Sea (Clark and Rowe, 1971). Distribution and taphonomy of echinoid remains in general and their correlation to sediment parameters within the Northern Bay of Safaga, Egypt (26°48'9.46"N, 33°58'11.64"E) was analyzed in detail by Nebelsick (1992a, b, 1995a, c). *Clypeaster* is the most widely distributed echinoid genus in the study area (Fig. 3). Three species of *Clypeaster* were recognized in the Northern Bay of Safaga, Egypt, which were totally dominated in shallow water by *Clypeaster humilis*. Rare examples of *Clypeaster fervens* Koehler, 1922 were restricted to deeper water, while only few dead tests of *Clypeaster*

*reticulatus* (Linnaeus, 1758) were recovered. The taphonomy of complete tests as well as fragments of *Clypeaster* has also been studied (see Nebelsick and Kampfer, 1994; Nebelsick, 1999a, c, 2008). Nebelsick (1999c) showed the distribution of taphofacies based on *Clypeaster* fragments and correlated the preservation styles (abrasion, interplate fragmentation, and encrustation) to environmental factors such as exposure and surface residence times. Finally, Nebelsick (2008) recognized a taphonomic gradient from: 1) tests still retaining spines; to 2) well preserved, denuded tests; 3) tests showing initial abrasion of tubercles and loss of the apical discs; 4) highly abraded, encrusted and bioeroded tests; and finally 5) highly corroded tests that could just be recognized as belonging to the genus *Clypeaster*.

*Clypeaster humilis* was common throughout the study area in shallow coarse sands, as well as in small sand patches within seagrass meadows and within sand veneers on reef flats (Fig. 3). Living specimens were found either completely or slightly covered by sediment. Numerous tests and fragments were recovered during scuba diving trips conducted in order to collect sediment cores as well as samples of micro- and macrofauna. Living specimens were collected following visual identification of their outlines if shallowly buried, or recovered by raking the sediment by using a modified rake revealing densities of ca 1.5 to 2 specimens/m<sup>2</sup>. The main areas where complete specimens of *Clypeaster humilis* were



FIGURE 4 — Oral views of predated specimens of *Clypeaster humilis*. **A**, Massive wound restricted to the central area of the oral surface. Internal supports surrounding the petals are broken. The wound is dominated by intraplate fragmentation. The remaining oral surface is well preserved as well as the internal surface of the aboral surface with a slight encrustation by coiled serpulid worm tubes (JS87-321). **B**, Wound dominated by intraplate fragmentation with slanting surfaces. The remaining well-preserved oral surface has some marks (upper right) that could be interpreted as tooth marks. The wound reaches the ambitus on the left-hand side revealing the marginal buttresses that are present near the edge of the test (JS87-318). **C**, Poorly preserved test surface showing abrasion of tubercles and high irregular wound showing indentation (JS87-312). **D**, Specimen showing almost complete removal of the oral surface with breakage predominantly along plate edges (JS87-230). **E**, Highly irregular wound reaching the ambitus. The test surface and interior show encrustation by serpulids (JAE-45). **F**, Larger fragments showing broken oral surfaces which resemble wound found on more complete tests (West Safaga Island).

collected (Fig. 3) were screened for predation scars and compared with respect to the position and the extent of the wound, as well as details of the wound borders.

#### WOUND MORPHOLOGY

All specimens were collected on and in the sediment surface in the Northern Bay of Safaga. The predation events were never observed, despite numerous (daytime) scuba

dives in the environments in which dead tests were collected. All predation events represent lethal attacks as the prey was eviscerated removing the internal organs and jaw apparatus. Predation events were recorded on tests showing a wide range of taphonomic grades (see Nebelsick, 2008) from echinoids still retaining spines, to denuded, well preserved tests, to tests with slight abrasion and encrustation. Heavily abraded tests show few such predation events.

The wounds are mostly restricted to the oral surface, the



peristome is not preserved. Successive stages of destruction are shown by the wounds (see Fig. 4) including: 1) A large central oral wound, removing a number of both ambulacral and interambulacral plates (Fig. 4A). Internal interambulacral pillars that abut the ambulacral petals are destroyed such that only the top halves of these pillars attached to the aboral side of the test are still present. 2) More extensive wounds extend toward the test rim exposing the marginal buttresses that run parallel to the ambitus (Figs. 4B, D, E, F, 5). The periproct, which is adjacent to the posterior rim of these sea urchins, can also be included or fully removed in this stage. 3) Damage extending beyond the oral surface to the aboral side of the test (Figs. 4C, 5). These are intervening stages between those listed above; and, in some cases, the wounds are quite irregular in shape. The wound borders are dominated by intraplate fractures, though interplate fracturing can also occur.

These wounds can be accompanied by the following features: 1) Shallow scratch marks up to 1 mm wide up and 5 mm long can faintly be discerned in a few examples (Fig. 5). These marks radiate away from the wound rim toward the ambitus and are only present on those surfaces in which areas are still intact. 2) The wound borders not only have intraplate fragmentation, but also reveal common highly oblique fracture surfaces that are visible on the outside of the test (Fig. 5). 3) Some highly irregular wound outlines have constrained indentations of skeletal removal extending from the wound toward the ambitus (Figs. 4B, C, E, F, 5). In some cases, these indentations occur along interambulacral plate rows.

Following the above-mentioned characteristics, wound damage can also be recognized in larger fragments representing broken *Clypeaster* tests (Fig. 4F). These fragments also have interplate fragmentation of the oral surface and more completely preserved aboral surfaces. Scratch marks on *Clypeaster* fragments from the study area have already been reported by Nebelsick (1999c).

### INTERPRETATION AS FISH PREDATION

Based on the size and morphology of the wound, the cause of this type of test damage is very likely due to fish predation. A large number of fish species are known to prey on echinoids, and they play an important role in controlling sea urchin populations and further ramification for herbivory and bioerosion (see review in Sievers and Nebelsick, 2018; Nebelsick, 2020).

Similar wound morphologies are described and figured by Kier and Grant (1965: pl. 15, fig. 8) on the Caribbean *Clypeaster subdepressus* (Gray, 1825), which is larger than the *Clypeaster humilis* specimens studied herein, but similar in having a flattened test and an endobenthic lifestyle. The authors report (Kier and Grant, 1965: p. 55) that “Several dead tests of *Clypeaster subdepressus* were collected, in which the ventral surface was almost completely excavated, and the remaining rim marked by numerous short radiating scratches... The organism that preyed upon the urchin was not observed, but presumably it was a fish.”

In Indo-Pacific reefal environments, Fricke (1971, 1974, 1975) analyzed the ethology of predator-prey relationship involving labrids and triggerfish prey on regular echinoids. Detailed accounts of hunting and handling techniques are given along with the observation that these fish hunt infaunal prey by blowing away the sediment. Fricke (1971) described how labrids carry regular echinoids in their mouths to rocky substrates where the prey is smashed open, whereas trigger fish snip off the spines of diademed echinoids, before the fish plunge into the test exposing the inner organs. The echinoid tests are completely consumed, leaving a pile of broken spines behind. Opened sea urchins then attract numerous fish other than the few species that are able to open the specimen.

By studying gray triggerfish feeding on *Mellita*, *Leodia*, and *Encope* in the Gulf of Mexico, Frazer et al. (1991) described in detail the hunting procedures and resulting damage on sand dollars. Foraging behavior with the fish directing a jet of water at the sand with enough force to reveal the sand dollars. The edge of the prey item is exposed by repeated jetting action. The triggerfish then dart in and grasps the sand dollar between the teeth releasing it 2m off the sediment surface. If the sand dollar does not land on its oral surface, the process is repeated. With jaws closed, the triggerfish crushes the center of the overturned sand dollar consuming the soft tissues in the damaged area. The feeding action is then modified in order to access remaining tissue along irregular edges of the broken test leaving distinct teeth marks.

Kurz (1995) documented triggerfish attacking four different species of sand dollars (*Clypeaster*, *Encope*, *Mellita* and *Leodia*) in the Gulf of Mexico in a study analyzing predator-prey interactions and foraging strategies. The possibility for recognizing these interactions using the distinct marks left on the test was emphasized. Stingray predation on the spatangoid *Meoma ventricosa* and the sand dollar *Leodia sexiesperforata* was described by Grun (2016). The sand dollar is crushed with most of the oral side missing with bite marks across thin test and half of the test missing.

McClanahan (1995) found a wide variety of species off the coast of Kenya preying on the common regular echinoid *Echinometra mathaei*, including eight outright predators including triggerfish, wrasses, and an emperor fish. An additional seven species were placed into an attempted predator guild that failed to prey on the echinoid (although potentially could prey on juveniles) and finally a larger number of fish (18 in all) in a scavenger guild. When studying fish predation on regular sea urchins on the Great Barrier Reef Australia, Young and Bellwood (2012) found four fish predators of adult sea urchins including triggerfish, an emperor fish, and a wrasse with clear differences with respect to attack frequencies and handling duration.

Following the above described observations, the central wound on the oral surface of echinoids studied here, together with the accompanying scratch marks, strongly suggests that trigger fish are responsible for the wounds. Massive test destruction as to be expected from predation by stingrays (Grun, 2016) is not present. The scratch marks, as also

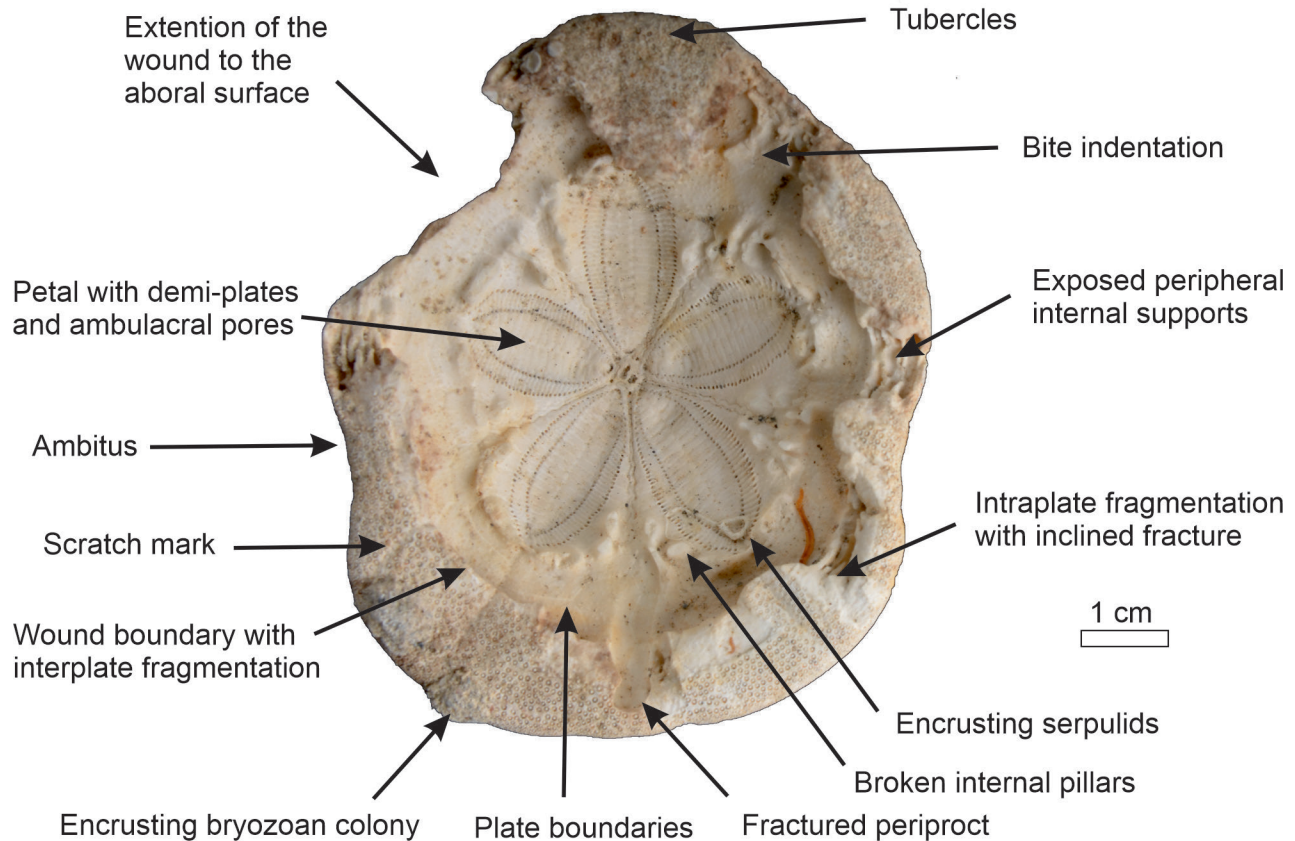


FIGURE 5 — Detailed oral view of predated *Clypeaster humilis* from the Northern Bay of Safaga, Red Sea, Egypt showing test morphology and characteristic wound features. The extensive wound removed much of the oral surface and extends to the aboral surface leading to an irregular outline with a damaged ambitus. The inner surface of the aboral skeleton shows plate boundaries (poorly visible from the outer view) and ambulacral pores. The preserved outer surface of the test shows numerous well-preserved tubercles. Wound features include irregular outline, intra- and interplate fragmentation, bite indentations, fractured periproct and scratch marks on the oral surface. Internal pillars and peripheral internal supports are exposed. Post-mortem encrustation by bryozoans and serpulids are present (JS87-2).

described by Kier and Grant (1965) and Fraser et al. (1991) are not as prominent in *Clypeaster humilis* as in *Sculpisitechinus auritus* (Leske, 1778), which has a broader more flattened test, from the study area (see Nebelsick and Kampf, 1994; Nebelsick, 1999b). These differences may be due to prey handling techniques and the morphology of the prey skeletons. The oblique breakage on intraplate fractures may also represent a handling effect. These fractures are clearly visible from the outside and may be a result of manipulation by fish teeth breaking the test open from the center of the test toward the rim.

The sole presence of the wound on the oral surface and the extension of the wound toward the ambitus suggests a stereotypic behavior of the predators. The oral test surface is evidently weaker than that of the aboral surface. The area around the peristome lack internal supports, and it is here that the fish first destroy the test surface before expanding the wound. Highly irregular outlines as well as the fact that the wound can unnecessarily extend toward the aboral surface suggests that variation in this behavior can occur. These may

be due to the fact that predation events commonly attract the attention of other predators and/or scavengers, thus disturbing the predation event and leading to an irregular outline.

#### RECOGNITION OF FISH PREDATION IN THE FOSSIL RECORD

Predation events described here were successful despite a number of morphological features that support the structural integrity of the test of *Clypeaster humilis*. These consist of both soft and hard parts: 1) The epidermis covering both internal and external surfaces of the plates (echinoderm skeletons are mesodermal in origin). 2) Collagenous fibers crossing plate boundaries. 3) Skeletal connections consisting of stereomic projections between the plates, and 4) Internal supports in the form of both central pillars and marginal buttresses (Seilacher, 1979; Mihaljević et al., 2011; Grun and Nebelsick, 2018a, b; Grun et al., 2018). High energy stress events are thus needed to break open the test. These are provided by the ballasted fish plunging with their snouts into the weaker oral side of

test. This instantly produces fragments and produces the characteristic wound.

The collected examples have been taken out of their taphonomic context in this warm water, well oxygenated environment. Attached spines will invariably be lost, and it is to be expected that these attacks will weaken the test. After the structural integrity of the *Clypeaster humilis* test is compromised, it can readily break apart into separate plates (e.g., Nebelsick and Kampf, 1994). Preservation of specimens damaged by predation could be enhanced if included in sedimentation events rapidly burying the specimens, a process that can occur in near shore environments (e.g., Mancosu and Nebelsick, 2017). In addition, surface encrustation can cross plate boundaries and help preserved specimens (see discussion in Nebelsick and Kampf, 1994; Nebelsick and Mancosu, 2021).

Differentiating these wounds from other possible non-predatory mediated fragmentation in *Clypeaster* and other clypeasteroids in the fossil record should be based on the presence of: 1) accompanying scratch marks, 2) oblique surfaces of intra-plate fragmentation, and/or 3) specific bite marks leading to highly irregular wounds. Larger fragments can also show such wounds that can be associated with predation events. The predation produces fragmented plates by wound production and probably weaken the test as well.

#### AKNOWLEDGEMENTS

We thank Jeffrey Thompson, Adiël Klompmaker and William Ausich for significantly improving upon an earlier version of this manuscript.

#### LITERATURE CITED

- ANDREW, N. L. and A. B. MACDIARMID. 1991. Interrelations between sea urchins and spiny lobsters in northeastern New Zealand. *Marine Ecology Progress Series*, 70: 211–222.
- ALLISON, P. A. 1990. Variations in rates of decay and disarticulation of Echinodermata, implications for the applications of actualistic data. *Palaios*, 5: 432–440.
- BELAÛSTEGUI, Z., F. MUÑIZ, J. H. NEBELSICK, R. DOMÈNECH, and J. MARTINELL, J. 2017. Echinoderm ichnology: bioturbation, bioerosion and related processes. *Journal of Paleontology*, 91: 643–661.
- BORSZCZ, T. and M. ZATOŃ. 2013. The oldest record of predation on echinoids: Evidence from the Middle Jurassic of Poland. *Lethaia*, 46: 141–145.
- CLARK, A. M. and F. W. E. ROWE. 1971. *Monograph of Shallow-Water Indo-West Pacific Echinoderms*. London, Trustees of the British Museum (Natural History). 238 pp.
- DONOVAN, S. K. 1991. The taphonomy of echinoderms: Calcareous multielement skeletons in the marine environment. In S. K. Donovan (ed.), *The Processes of Fossilization*. London: Belhaven Press, pp. 241–269.
- DURHAM, J. W. 1966. Clypeasteroids. In R. G. Moore (ed.), *Treatise on Invertebrate Paleontology. Part U, Echinodermata 3.*, Geological Society of America, University of Kansas Press, Lawrence Kansas, pp. U450–U491.
- ESTES, J. A., N. S. SMITH, and J. F. PALMISANO. 1978. Sea otter predation and community organization in the western Aleutian Islands, Alaska. *Ecology*, 59: 822–833.
- FARRAR, L., E. GRAVES, E. PETSIOS, R. W. PORTELL, T. B. GRUN, M. KOWALEWSKI, and C. L. TYLER. 2020. Characterization of traces of predation and parasitism on fossil echinoids. *Palaios*, 35: 215–227.
- FRAZER, T. K., W. J. LINDBERG, and G. R. STANTON. 1991. Predation on sand dollars by gray triggerfish *Balistes capriscus*, in the northeastern Gulf of Mexico. *Bulletin of Marine Science*, 48: 159–164.
- FRICKE, H. W. 1971. Fische als Feinde tropischer Seeigel. *Marine Biology*, 9: 328–338.
- \_\_\_\_\_. 1974. Möglicher Einfluß von Feinden auf das Verhalten von *Diadema*-Seeigeln. *Marine Biology*, 27: 59–64.
- \_\_\_\_\_. 1975. Lösung einfacher Probleme bei einem Fisch (Freiwasserversuche an *Balistes fuscus*). *Zeitschrift für Tierpsychologie*, 38: 18–33.
- GREENSTEIN, B. J. 1991. An integrated study of echinoid taphonomy: Predictions for the fossil record of four echinoid Families. *Palaios*, 6: 519–540.
- GRUN, T. B. 2016. Echinoid test damage by a stingray predator. *Lethaia*, 49: 285–286.
- \_\_\_\_\_. and J. H. NEBELSICK. 2018a. Biomechanics of an echinoid's trabecular system. *PLoS ONE*, 13(9): e0204432.
- \_\_\_\_\_. 2018b. Structural design analysis of the minute clypeasteroid echinoid *Echinocyamus pusillus*. *Royal Society Open Science*, 5: 171323.
- \_\_\_\_\_, D. SIEVERS, and J. H. NEBELSICK. 2014. Drilling Predation on the Clypeasteroid Echinoid *Echinocyamus pusillus* from the Mediterranean Sea (Giglio, Italy). *Historical Biology*, 26: 745–757.
- \_\_\_\_\_, A. KROH, and J. H. NEBELSICK. 2017. Comparative drilling predation on time-averaged phosphatized and non-phosphatized specimens of the minute clypeasteroid echinoid *Echinocyamus stellatus* from Miocene offshore sediments (Globigerina Limestone Fm., Malta). *Journal of Paleontology*, 91: 633–642.
- \_\_\_\_\_, A. MANCOSU, Z. BELAÛSTEGUI, Z., and J. H. NEBELSICK. 2018. Clypeaster Taphonomy: a paleontological tool to identify stable structures in natural shell systems. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, 288: 189–202.
- HARPER, E. 2016. Uncovering the holes and cracks: from anecdote to testable hypotheses in predation studies. *Palaeontology*, 59: 597–609.
- HUNTLEY, J. W. and M. KOWALEWSKI. 2007. Strong coupling of predation intensity and diversity in the Phanerozoic fossil record. *Proceedings of the National Academy of Sciences of the United States of America*,



- 104(38): 15006–15010.
- KIDWELL, S. M. and T. BAUMILLER. 1990. Experimental disintegration of regular echinoids: Roles of temperature, oxygen, and decay thresholds. *Paleobiology*, 16: 247–271.
- KIER, P. M. and R. E. GRANT. 1965. Echinoid distribution and habits, Key Largo Coral Reef Preserve. Florida Smithsonian Miscellaneous Collections, 149(6): 1–68.
- KLOMPMAKER, A. A., P. H. KELLEY, D. CHATTOPADHYAY, J. C. CLEMENTS, J. W. HUNTLEY, and M. KOWALEWSKI. 2019. Predation in the marine fossil record: Studies, data, recognition, environmental factors, and behavior. *Earth–Science Reviews*, 194: 472–520.
- KOWALEWSKI, M. and J. H. NEBELSICK. 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*. Topics in Geobiology Series, Plenum Press, Kluwer, pp. 279–302.
- \_\_\_\_\_, S. CASEBOLT, Q. HUA, K. E. WHITACRE, D. S. KAUFMAN, and M. A. KOSNIK. 2018. One fossil record, multiple time resolutions: Disparate time–averaging of echinoids and mollusks on a Holocene carbonate platform. *Geology*, 46: 51–54.
- KURZ, R. C. 1995. Predator–prey interactions between gray triggerfish (*Balistes caprisacus* Gmelin) and a guild of sand dollars around artificial reefs in the northeastern Gulf of Mexico. *Bulletin of marine science*, 56: 150–160.
- McCLANAHAN, T. R. 1995. Fish predators and scavengers of the sea urchin *Echinometra mathaei* in Kenyan coral–reef marine parks. *Environmental Biology of Fishes*, 43: 187–193.
- MANCOSU, A. and J. H. NEBELSICK. 2017. Ecomorphological gradient of clypeasteroid–dominated echinoid assemblages along a mixed siliciclastic–carbonate shelf from the Early Miocene of northern Sardinia, Italy. *Acta Palaeontologica Polonica*, 62: 627–646.
- MEADOWS, C. A., R. E. W. FORDYCE, and T. K. BAUMILLER. 2015. Drill holes in the irregular echinoid, *Fibularia*, from the Oligocene of New Zealand. *Palaios*, 30: 810–817.
- MIHALJEVIĆ, M. I. JERJEN, and A. B. SMITH. 2011. The test architecture of *Clypeaster* (Echinoidea, Clypeasteroidea) and its phylogenetic significance. *Zootaxa*, 2983: 21–38.
- NEBELSICK, J. H., 1992a. Echinoid distribution by fragment identification in the Northern Bay of Safaga; Red Sea, Egypt. *Palaios*, 7(2): 316–328.
- \_\_\_\_\_. 1992b. The Northern Bay of Safaga (Red Sea, Egypt): An actuopalaeontological approach. III Distribution of echinoids. *Beiträge zur Paläontologie von Österreich*, 17: 5–79.
- \_\_\_\_\_. 1995a. The uses and limitations of actuopalaeontological investigations on Echinoids. *Geobios, M.S.*, 18: 329–336.
- \_\_\_\_\_. 1995b. Comparative taphonomy of Clypeasteroids. *Eclogae geologicae Helvetiae*, 88: 685–693.
- \_\_\_\_\_. 1995c. Actuopalaeontological investigations on echinoids: The potential for taphonomic interpretation. In R. H. Emson, A. B. Smith, and A. C. Campbell (eds.), *Echinoderm Research*, Balkema, Rotterdam, pp. 209–214.
- \_\_\_\_\_. 1999a. Taphonomic legacy of predation on echinoids. In M. D. Candia Carnevali and F. Bonasoro (eds.), *Echinoderm Research, Proceedings of the Fifth European Conference on Echinoderms*: Balkema, Rotterdam, pp. 347–352.
- \_\_\_\_\_. 1999b. Taphonomic comparison between recent and fossil sand dollars. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 149: 349–358.
- \_\_\_\_\_. 1999c. Taphonomy of *Clypeaster* fragments: preservation and taphofacies. *Lethaia*, 32: 241–252.
- \_\_\_\_\_. 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*. Indiana University Press, pp. 114–128.
- \_\_\_\_\_. 2020. Clypeasteroids. In J. M. Lawrence (ed.), *Biology and Ecology of Sea Urchins* (4th Edition). Elsevier, Amsterdam, pp. 315–332.
- \_\_\_\_\_, and S. KAMPFER. 1994. Taphonomy of *Clypeaster humilis* and *Echinodiscus auritus* from the Red Sea. In B. David, A. Guille, A., J.–P. Féral, and M. Roux, (eds.), *Echinoderms through time*, Balkema, Rotterdam, pp. 803–808.
- \_\_\_\_\_, and M. KOWALEWSKI. 1999. Drilling predation on recent clypeasteroid echinoids from the Red Sea. *Palaios*, 14: 127–144.
- \_\_\_\_\_, and A. MANCOSU. 2021. The taphonomy of echinoids: Skeletal morphologies, environmental factors and preservation pathways. (*Elements of Paleontology*). Cambridge: Cambridge University Press. doi:10.1017/9781108893411.
- NEUMANN, C. and O. HAMPE. 2018. Eggs for breakfast? Analysis of a probable mosasaur biting trace on the Cretaceous echinoid *Echinocorys ovata* Leske, 1778. *Fossil Record*, 21: 55–66.
- PETSIOS, E. R., W. PORTELL, L. FARRAR, S. TENNAKOON, T. B. GRUN, M. KOWALEWSKI, and C. L. TYLER. 2021. An asynchronous Mesozoic marine revolution: The Cenozoic intensification of predation on echinoids. *Proceedings of the Royal Society B*, 288: 20210400.
- SEILACHER, A. 1979. Constructional morphology of sand dollars. *Paleobiology*, 5: 191–221.
- SIEVERS, D. and J. H. NEBELSICK. 2018. Fish predation on a Mediterranean echinoid: Identification and preservation potential. *Palaios*, 33: 1–8.
- \_\_\_\_\_, and J.–P. FRIEDRICH, and J. H. NEBELSICK. 2014. A feast for crows: bird predation on irregular echinoids from Brittany, France. *Palaios*, 29: 87–94.
- TYLER, C. I., T. A., DEXTER, R. W. PORTELL, and M. KOWALEWSKI. 2018. Predation–facilitated

- preservation of echinoids in a tropical marine environment. *Palaios*, 33: 478–486.
- WALKER, S. and C. E. BRETT. 2002. Post–Paleozoic patterns in marine predation: Was there a Mesozoic and Cenozoic Marine Predatory Revolution? *Paleontological Society Papers*, 8: 119–193.
- WILSON, M.A., T., BORSZCZ, and M. ZATOŃ. 2015. Bitten spines reveal unique evidence for fish predation on Middle Jurassic echinoids. *Lethaia*, 48: 4–9.
- YOUNG, M. A. L. and D. R. BELLWOOD. 2012. Fish predation on sea urchins on the Great Barrier Reef. *Coral Reefs*, 31: 731–738.
- ZŁOTNIK, M. and T. CERANKA. 2005. Patterns of drilling predation of cassid gastropods preying on echinoids from the middle Miocene of Poland. *Acta Palaeontologica Polonica*, 50: 409–428.

---

Museum of Paleontology, The University of Michigan  
1105 North University Avenue, Ann Arbor, Michigan 48109-1085  
Matt Friedman, Director

*Contributions from the Museum of Paleontology, University of Michigan* is a medium for publication of reports based chiefly on museum collections and field research sponsored by the museum. Jennifer Bauer and William Ausich, Guest Editors;  
Jeffrey Wilson Mantilla, Editor.

Publications of the Museum of Paleontology are accessible online at: <http://deepblue.lib.umich.edu/handle/2027.42/41251>  
This is an open access article distributed under the terms of the Creative Commons CC-BY-NC-ND 4.0 license, which permits non-commercial distribution and reproduction in any medium, provided the original work is properly cited.

You are not required to obtain permission to reuse this article. To request permission for a type of use not listed, please contact the Museum of Paleontology at [Paleo-Museum@umich.edu](mailto:Paleo-Museum@umich.edu).

Print (ISSN 0097-3556), Online (ISSN 2771-2192)