Comparative taphonomy of Clypeasteroids

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ABSTRACT

The taphonomy and preservation potential of five different shallow water, Red Sea clypeasteroid genera are compared and contrasted. Although these echinoid genera are unified by several constructional morphological as well as ecological aspects, significant differences remain as far as the size, habitat and skeletal details are concerned. Differences in preservation are correlated to to a number of factors including 1) constructional morphological aspects including test size and thickness as well as the presence and nature of the internal support system, 2) the presence of potential predators and 3) the sedimentary environment in which these echinoids are found. The comparison of the taphonomy of these genera can help to shed light upon the preservation potentials not only of fossil Clypeasteroids but also of echinoids in general.

ZUSAMMENFASSUNG

Die Erhaltungsfähigkeit der Schalen von fünf verschiedenen Gattungen der Seeigelordnung Clypeasteroidea (*Clypeaster, Echinodiscus, Laganum, Echinocyamus* und *Fibularia*) aus dem Roten Meer werden bezüglich ihrer Skelettmorphologie, Faziesverteilung und ihrem resultierenden taphonomischen Zustand miteinander verglichen. Wichtige Unterschiede sind die Größe und Dicke der Schale, das Vorhandensein von Räubern und der Aufbau der Internstützpfeiler sowie der Charakter des Substrates, das sie bewohnen. Der taphonomische Vergleich dieser Gattungen kann nicht nur über die fossile Erhaltung von Clypeasteroidea sondern auch über Echiniden im allgemeinen Auskunft geben.

1. Introduction

Clypeasteroids are an extensive group of irregular echinoids which, following adaptive radiation in the early Tertiary, are common elements of many shallow water benthic faunas. They are the most recent group of echinoids to have evolved (see Smith 1984). General test characteristics include a well developed petaloid with numerous respiratory tube feet on the aboral test surface, a centrally position mouth on the oral surface as well as numerous accessory podia and minute spines. The mouth leads to a reduced, internal jaw apparatus which is used to crush sediment and food particles. Many Clypeasteroids also posses internal support systems. Although important exceptions are known *(Clypeaster rosaceus, Dendraster)*, clypeasteroids are generally shallow infaunal burrowers, a fact also applying to those found in the study area.

Five different genera of Clypeasteroids *(Clypeaster, Echinodiscus, Laganum, Echinocyamus* and *Fibularia)* have been investigated as part of an extensive actuopalaeontologi-

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cal study of sea-urchins from the Northern Bay of Safaga, Red Sea, Egypt (Nebelsick, 1992a, 1992b). These studies combined with a large data base concerning sediment and facies distributions allow the impact of various taphonomic processes from different environments to be analyzed and compared. The Northern Bay of Safaga is a shallow water, carbonate environment consisting of a wide variation of facies ranging from coral reefs to muddy sediments (see Piller & Pervesler 1989; Piller & Mansour 1990; Piller 1994). The taphonomic processes leading to the destruction of the test of *Clypeaster* and *Echinodiscus* is discussed in detail by Nebelsick & Kampfer 1994. This study demonstrated the rapidity of spine loss after death, the nature of plate disarticulation as well as the wide variation of preservation present. There are a number of other studies concerning echinoderm taphonomy (Schäfer 1962, Allison 1990, Kidwell & Baumiller 1990, Donovan 1991 and Greenstein 1991, 1992).

The study material is derived from surface collections and bulk sediment samples. This allowed for the collection of not only living animals, but also of dead tests as well as a large number of fragmented skeletal material (for detailed description of methods see Nebelsick (1992b). Material smaller than 2 mm was not recovered and thus not included in this study.

2. Results

The following qualitative results are summarized in Figure 4–7. Extensive photographic documentation of the different taphonomic features described can be found in Nebelsick (1992a, 1992b) and Nebelsick & Kampfer (1994).

Echinodiscus is a typical sand dollar with a large (up to 15 cm), very flat test showing typical paired posterior lunules and complex food grooves on the oral surface. A single species *Echinodiscus auritus* was found restricted to shallow water, nearshore sands (Fig. 1). Its extensive internal support system consists of a dense mesh of supports occupying much of the very thin rim of the test (Fig. 3A). *Echinodiscus* shows a wide range of preservation from recently dead specimens with spines still *in situ;* to denuded spineless test showing very well preserved surface characters (Fig. 3A); slightly abraded test which often show encrustation and signs of bioerosion (Fig. 3B); as well as highly corroded, highly abraded specimens with barely recognizable surface features (Fig. 3C).

A common feature of *Echinodiscus* is the removal of large areas of the test presumably by fish predation (see Nebelsick & Kampfer 1994). This produces wounds consisting of elongate scratch marks which are often paired as well as cuspate marks along the margin of the removed centrally positioned plates (Fig. 3D). In *Echinodiscus* both oral as well as apical surfaces are attacked, obviously leading to the death of the animal as well as the production of echinoid remains showing intra-plate fragmentation. *Echinodiscus* is also characterized by a large number of non-lethal predation events which are largely restricted to the posterior margin (Fig. 3D). Fragments of this genera also show a wide variation of preservation (Fig. 3E). These often consist of "pie slices" of the test broken between the parallel ambulacral plate rows. Single isolated plates also occur, though not as common as those of *Clypeaster* (see below).

Clypeaster is the most common echinoid found in the study area and was the highest contributor to fragmented material taken from bulk sediment samples. This genus is found in a wide range of different facies types which may be due to the presence of at
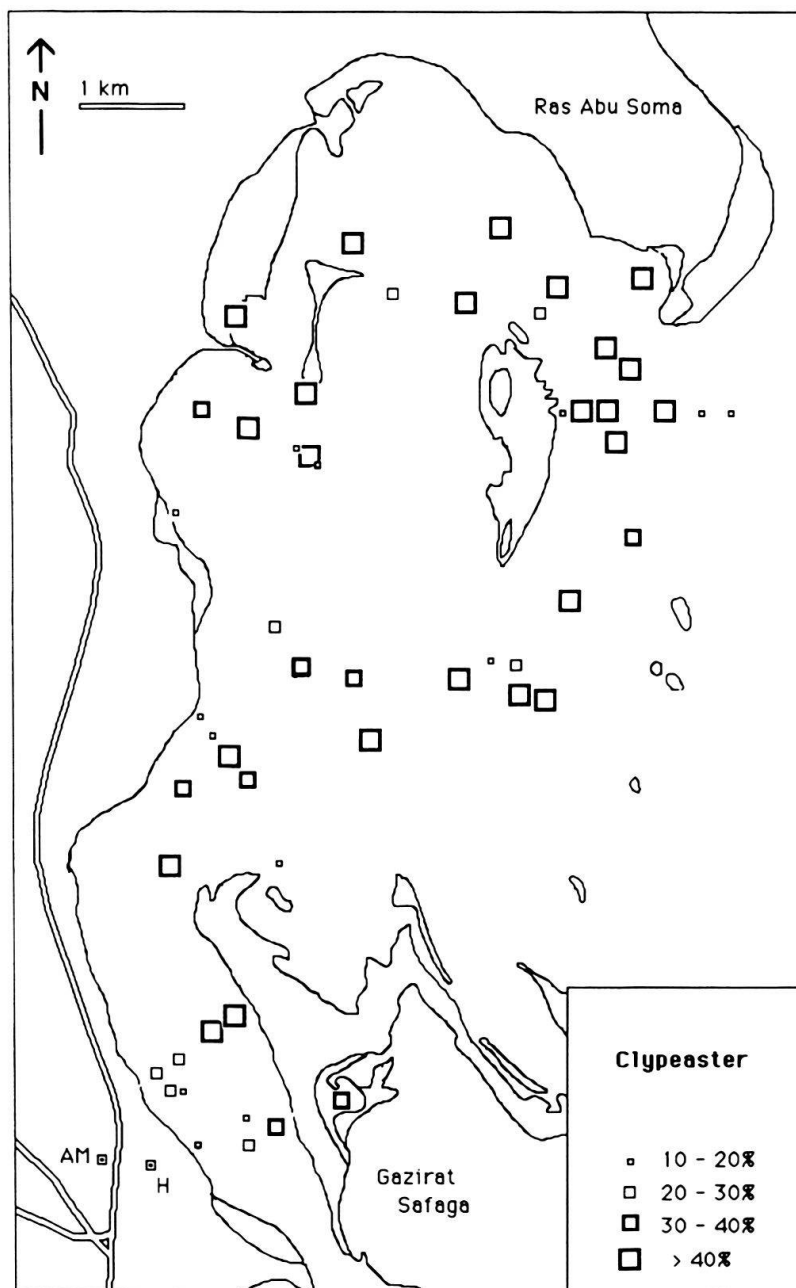
Fig. 1. Distribution of *Clyp-easter* sp. in the Northern Bay of Safaga (after Nebelsick, 1992b). This distribution is based on the frequency of fragment occurrence within bulk sediment samples.

least 4 sympatric species *(Clypeaster humilis, C. fervens, C. reticulatus,* and *C. rarispinus),* (Fig. 1). It is has a relative large size (up to 10 cm), a thick test and is characterized by massiv internal supports along the interambulacra as well as along the rim of the speci-mens (Fig. 4). A very wide range of preservation was also found for articulated test of *Clypeaster.* Lethal predation events are common and are similar to those found for Echi-nodiscus (see above). They are, however, restricted to the oral surface. Evidence for non-lethal predation was not found. Although larger fragments do occur, test destruction usually leads to the production of single plates which themselves show as wide a range of taphonomic features as the complete specimens.
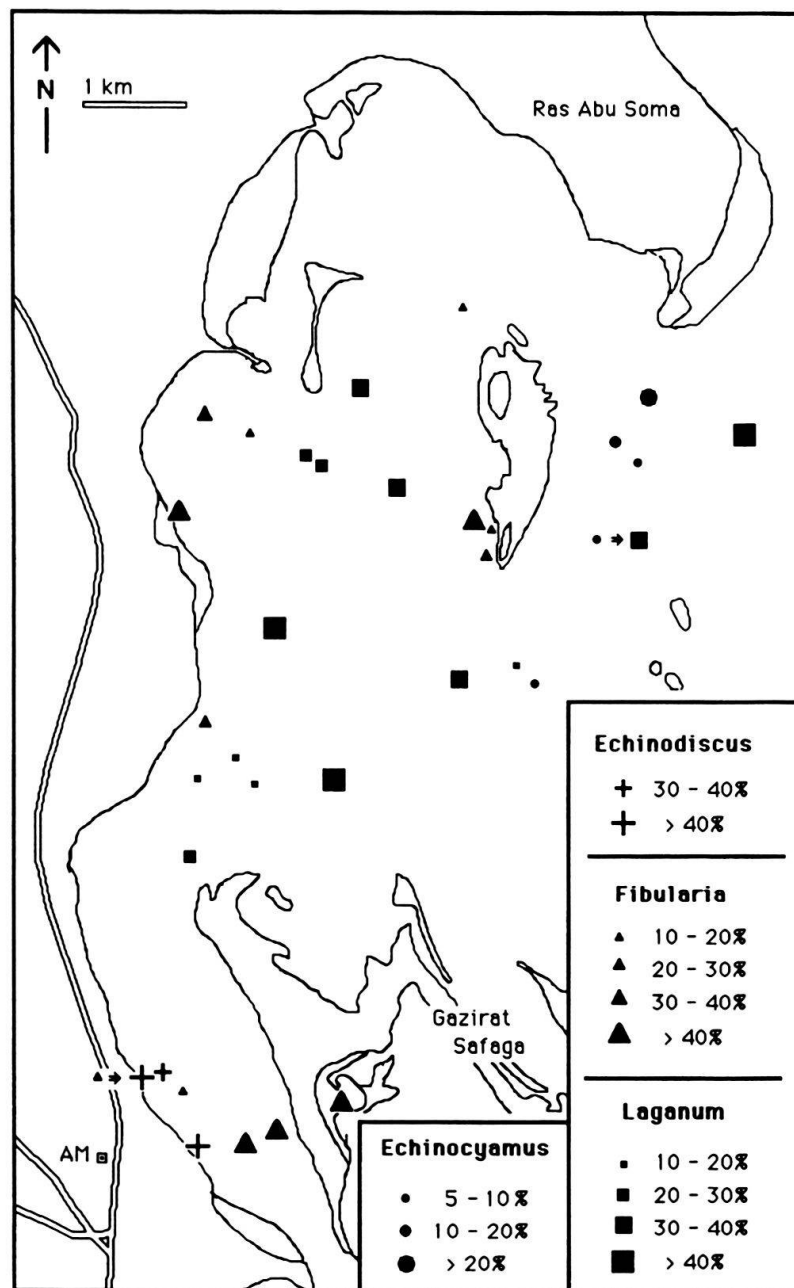
Fig. 2. Distribution of *Echinodiscus*, *Laganum*, *Fibularia* and *Echinocyamus* in the Northern Bay of Safaga (after Nebelsick, 1992b). These distributions are based on the frequency of fragment occurrence within bulk sediment samples.

Echinocyamus is a very small clypeasteroid rarely reaching sizes more than 1 cm in length with a thin, flattened test with internal radiating supports (see Figs. 5A, 5C). The species *Echinocyamus crispus* is found restricted to deeper muddy sands (25–40 m depth) associated with sea grass (Fig. 2). It is often found as complete dead test. A number of specimens show indication of gastropod predation as indicated by single round holes puncturing the test (Fig. 5B). Larger test remains survive although showing heavy damage thus revealing the internal supports. (Fig. 5C). Fragmented material is common consisting mostly of larger fragments originating from the ambitus (rim) of the echinoid (Fig. 5D). Smaller fragments were not recovered.

Fibularia is similar to *Echinocyamus* in being very small (< 1 cm), but differs from all the other clypeasteroid genera of the study area in lacking internal supports and showing a highly globular very thin-shelled test (Fig. 6A). *Fibularia ovulum* is found most commonly in shallow water, fine to coarse sands with seagrass (0–15 m depth) (Fig. 2). This genus is also common in "strandline" deposits and was found to float very easily after having been drained of water. Complete tests were often showing rounded holes (Fig. 6B), again possibly resulting from gastropod predation (as for *Echinocyamus)*. A major difference to *Echinocyamus* is the fact that larger fragments were not common. The few damaged tests found were often filled with sediment (Fig. 6C).

Laganum is found in very large numbers in deeper silty sands (20–30 m) restricted to basins within the study area (Fig. 2). It has a medium-sized test up to 3 cm and is thin-shelled with internal supports developed along the margins. Complete, undamaged, well preserved tests (Fig.7A) were numerous, sometimes littering the sediment surface. Complete tests as well as larger fragments commonly show incrustation (Fig. 7B). The central oral and apical areas of the test are often damaged showing intraplate breakage (Fig. 7C). This may be the result of predation events, though additional indications such as scratch marks (see above) are missing. A peculiar preservation feature of *Laganum* is the presence of "skeletal rings", consisting solely of the strengthened ambitus (rim) of the test after removal of the thin unsupported, centrally positioned oral and apical plates (Fig. 7D). Correspondingly, fragments of this genera consist mostly of segments of the rim (Fig. 7E).

3. Discussion

The taphonomic pathways shown by *Clypeaster* and *Echinodiscus* show the importance of constructional morphological aspects in the preservation of the animal skeletons after death. Both have massive internal support systems which make these clypeasteroids the most robust and taphonomically resistant of all echinoderm taxa throughout earth history. The internal support systems have been interpreted as adaptive innovations to living in high energy environments as well as allowing the construction of an extremely flattened test form (see Seilacher 1979 and Smith 1984 for discussion). The role of internal supports in decreasing the vulnerability of these sea-urchins to fish predation (see Zinsmeister 1980; Nebelsick & Kampfer 1994; Kurz 1995) should, however, not be underestimated. The fact that *Echinodiscus* fragments are often larger than those of *Clypeaster* may be due to differences in the internal support systems of these two genera. That of *Echinodiscus* consists of a more homogeneous mesh, that of *Clypeaster* of more massive though isolated pillars. The robustness of these genera has lead to the fact that both the genus *Clypeaster* as well as the sand dollars in general show an extensive fossil record (Boggild & Rose 1984). The detailed investigations on *Dendraster* evolution can also be taken as a good example in this regard (Dodd et al. 1985; Beadle 1989).

The common occurrence of *Laganum* in the study area can be taken as an example of the fact that additional factors other than test stability play important roles in their preservation. The internal supports of *Laganum* which are restricted to the rim ensure that at least fragments are common. Two other factors should ensure a relatively good fossilization potential. These are their mass occurrence and the fact that they occur in deeper
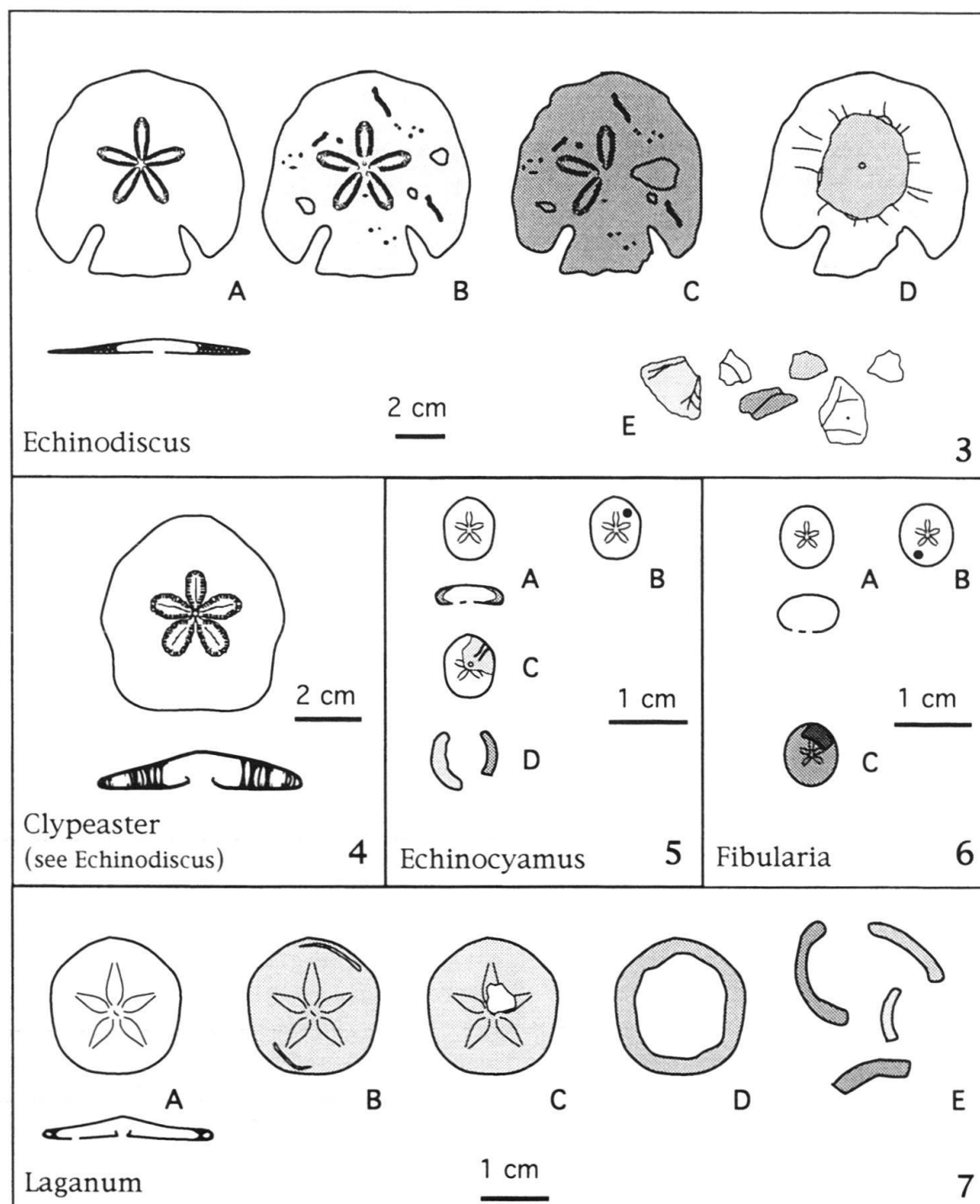
Fig. 3.–7. Schematic diagram showing the observed states of preservation and taphonomic features of five different Clypeasteroid genera from the Red Sea. Note that jaws and spines are not represented (see next page for detailed explanation).

silty sediments. The latter ensures that the specimens are not as exposed to wave movement and sediment agitation as those echinoids found in shallower water settings.

The contrasting taphonomy of the *Echinocyamus* and *Fibularia* demonstrates that, even at this small size, constructional differences (presence or lack of radial partitions) will have a substantial influence on preservation potential. *Echinocyamus* with internal supports has a better preservation potential than *Fibularia* which lacks internal supports. The test of *Echinocyamus* can be broken, but relatively large recognizable fragments still remain. *Fibularia* completely disarticulates into its constituent plates upon fragmentation, thus explaining the lack of larger fragments. This observation is confirmed by the discovery of *Echinocyamus* in a wide variety of different fossil habitats (Boggild & Rose 1984). The lack of internal supports in *Fibularia*, interpreted as a secondary loss due to paedomorphosis (Mooi 1990), has led to its increased susceptibility to fragmentation and transport by flotation.

4. Conclusion

1) This study suggests that the internal support system of Clypeasteroids is a major factor leading to their relatively good preservation in the fossil record. Differences within the order depend on the degree to which these internal supports are developed or reduced. The development of paired radially orientated buttresses as well as circumferentially arranged pillars are important characters in the determination of clypeasteroid ancestries (Mooi 1990). The differences among Clypeasteroids discussed below thus have important implications as far as the amount of taphonomic bias affecting primitive clypeasteroids is concerned.

Fig. 3. *Echinodiscus* (based on *Echinodiscus auritus*): 3A) complete test in apical view and cross section; note the skeletal supports filling in the margins of the test; 3B) slightly abraded test showing encrustation and bioerosion; 3C) highly corroded, highly abraded specimens with barely recognizable surface features; 3C) lethal predation showing removal of a large area of the apical surface as well as elongated scratch marks; nonlethal predation is visible on the posterior margin of the test; 3E) fragments showing a wide variation of preservation.

Fig. 4. *Clypeaster* (based on *Clypeaster humilis*): apical view and cross sectional; note the massive pillars connecting the oral and apical surfaces. For different preservational states see *Echinodiscus* (Fig. 1).

Fig. 5. *Echinocyamus* (based on *Echinocyamus crispus*): 5A) complete test with apical view and cross section; note the internal supports; 5B) complete test showing rounded hole (? gastropod predation); 5C) larger test fragment showing heavy damage revealing the internal supports; 5D) fragmented material consisting mostly of larger fragments originating from the ambitus (rim).

Fig. 6. *Fibularia* (based on *Fibularia ovulum*): 6A) complete test, apical view and cross section; note the lack of internal supports; 6B) complete test showing rounded hole (? gastropod predation); 6C) damaged test filled with sediment.

Fig. 7. *Laganum* (based on *Laganum depressum*): 7A) complete, undamaged, well preserved test; note the internal supports lang the margin; 7B) complete tests showing incrustation; 7C) test showing damaged apical surface; 7D) "skeletal rings" consisting solely of the strengthened ambitus (rim) of the test; 7E) fragments consisting mostly of rim segments.

2) Additional factors affecting the taphonomic pathways of Clypeasteroids include the presence and nature of predatory events. Predation events on *Clypeaster* and *Echinodiscus*, presumably by fish, leads to severe test destruction with the removal of large areas of the skeleton if not total destruction. Recorded predation events on *Echinocyamus* and *Fibularia*, presumably by gastropods, does not severely affect their preservation potentials.

3) The nature of the sedimentary environment in which the echinoids live will also affect the preservation potential of echinoids, living in highly exposed, shallow water environments on the one hand, and sheltered, deeper water settings on the other.

4) The adaptive morphologies of echinoids to higher energy environments can, however, offset disadvantages to test preservation after the death of the animal. Thus, the sand dollar *Echinodiscus* which is more exposed to water and sediment movement has developed a correspondingly stronger skeleton than *Laganum* which is found in lower energy environments. Thus, both taxa have a good chance of eventually becoming included in the fossil record.

Acknowledgements

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