

## 1 General Introduction

Throughout the history of studying fossil echinoids, researchers have had to deal with preserved remnants that are incomplete. Although these fossils may be common, almost all lack many of their original elements, are curiously incomplete or crushed, or even consist of only single elements. The fact that fossil sea urchins do not represent complete individual organisms was already apparent in early descriptions and illustrations of fossilized sea urchins. Agostino Scilla (1670), in his remarkable discourse on the true nature and origin of fossil remains, includes superb illustrations of fragmented and in situ crushed echinoid specimens (see also Romano 2013, Findlen 2018). The Welsh naturalist Edmund Lhuyd, known as Luidius (1699), as remarked in Baier (1708) and Bantz (1969), noted that of the more than 400 specimens of fossil urchins in his collection, not a single one still retained its spines. Comprehensive monographs on important fauna are based solely on disarticulated material, for example, Bather's monograph of Hungarian Triassic echinoids from Bakony (Bather 1909), among others.

Taphonomy plays a key role in the representation of echinoderms in the fossil record, dictating the taxonomic rank that can be identified, allowing evolutionary lineages to be established, and studies pertaining to diversity and disparity to be made. The taphonomy of echinoids has been included in research into the broad context of mass extinctions and recovery (Smith 1990), biogeographic patterns (Carter & McKinney 1992), time averaging (Kowalewski et al. 2018), paleoecological interpretation (e.g., Ernst 1969, 1970, Smith et al. 1995, Kroh & Nebelsick 2003, Smith & Rader 2009, Thompson & Ausich 2016, Thompson et al. 2015, see section 6 below), and quantification of taphonomic variables (Grun & Nebelsick 2016). Echinoids are important for the interpretation of *Lagerstätten* (Seilacher 1970, Seilacher et al. 1985, Brett & Seilacher 1991, Brett et al. 1997) in which the spectacular preservation of echinoids, along with other biota, indicate special environmental sedimentary conditions. These deposits include tempestites and obrution deposits in both shallow and deeper water (Kutscher 1970, Rosenkranz 1971, Hess 1972, Radwański & Wysocka 2001, Wysocka et al. 2001, Radwański & Wysocka 2004, Schneider et al. 2005, Thuy et al. 2011) as well as lithographic limestones (Bantz 1969, Roman & Fabre 1986, Roman et al. 1991, 1994, Roman 1993, Bourseau et al. 1994, Grawe-Baumeister et al. 2000, Chellouche et al. 2012, Peyer et al. 2014). Additionally, taphonomic pathways influence the extent to which echinoids contribute as sedimentary particles to the rock record, especially within mass accumulations (e.g., Nebelsick & Kroh 2002, Belaústegui et al. 2012, Mancosu & Nebelsick 2013, 2015, 2017a). Insights into the taphonomy of echinoderms

are often embedded, if not hidden, within other biological and geological studies, though there have been some reviews regarding this (see Lewis 1980, Donovan 1991, 2003, Brett et al. 1997, Ausich 2001, Nebelsick 2004).

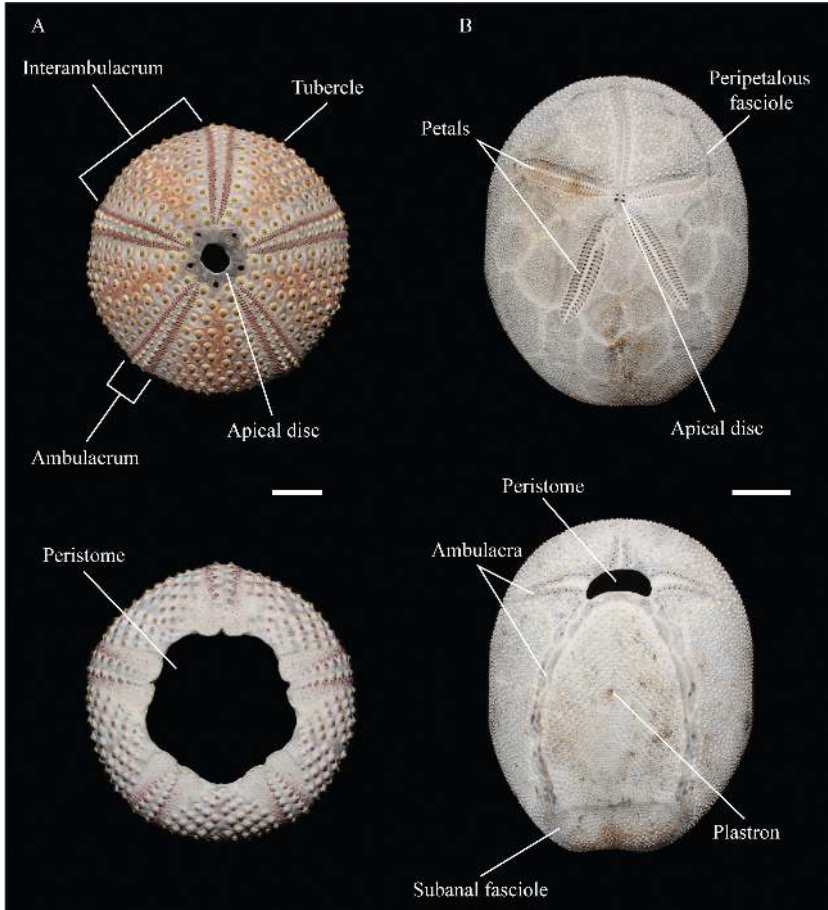
Studying the taphonomy of echinoids is thus of great importance with respect to interpreting their presence for a wide range of applications. Understanding the preservation potential of echinoid remains is paramount for their inclusion within studies with respect to evolution, biodiversity, paleoecology, sedimentation events, and other subjects.

## 2 Multi-plated Skeletons and Regeneration

There are two important caveats concerning the taphonomy of echinoderms that distinguish them from most other benthic marine organisms: 1) the presence of hierarchically organized, multi-plated skeletons consisting of high-magnesium calcite stereom; and 2) the loss of attached appendages, through autotomy and sub-lethal predation leading to the continuous production of skeletal elements during the life span of a single organism.

Echinoids possess multi-plated, hierarchically organized skeletons (e.g., Smith 1984, Nebelsick et al. 2015) containing numerous elements of different shapes and sizes ranging from miniscule spicules to massive spines. These elements include: 1) ambulacral and interambulacral plates; 2) ocular and genital plates including the madreporite; 3) plates within the peristomal and periproctal membranes; 4) elements of the jaw apparatus including hemipyramids, rotulae, epiphyses, compasses, and teeth; 5) spines in a great many variations and sizes; 6) supporting elements in the pedicellaria within valves and rods in their stalks; 7) rosettes of adhesive tube feet; and, finally, 8) various calcareous spicules within the body wall. In exceptional cases, articulated echinoids complete with spines, jaw elements, and pedicellaria can be preserved, and separated elements can also be recognized in the fossil record though to different taxonomic levels. The presence of plates and spines can be used to distinguish echinoid presence and distribution (e.g., Donovan 1991, 2003, Gordon & Donovan 1992, Nebelsick 1992a, 1992b, Dynowski 2012, Thompson & Denayer 2017). Other remnants recovered from the fossil record include isolated pedicellaria valves, typically within the context of micropaleontological studies (e.g., Mortensen 1934, 1937, Geis 1936, Blake 1968, Krainer et al. 1994, Mostler 2009), and even partially preserved tube feet rosettes (Mortensen 1937).

Similarly to ecdysis by crustaceans and leaf abscission by plants, a single echinoid will produce more hard parts than its constituent skeletal elements at a single point in time. Loss of skeletal elements during life can be caused by



**Figure 1** Morphological features of A) a regular camardont echinoid *Arbaxia lixula* and B) an irregular spatangoid echinoid *Brissus unicolor*, both from the Mediterranean Sea. The top row shows aboral (top) views of the test; the lower row shows oral (lower) views of the test. Scale bars = 1 cm.

mechanical breakage, disease, parasitism, sub-lethal predation (Lawrence & Vasquez 1996), and autotomy (Prouho 1887, Märkel & Röser 1983). Many elements such as spines, pedicellaria, and tube feet can be regenerated (Cutress 1965, Ebert 1967, 1988, Heatfield 1971, Dubois & Ameye 2001) and, thus, produce further calcitic elements. Sub-lethal predation on the tests of echinoids, especially clypeasteroids, can heal, leaving characteristic wounds in the test that can be recognized in the fossil record (see section 4). Furthermore, echinoid teeth are continuously renewed in order to compensate for abrasion at the biting surface (see Ellers & Telford 1996).

In summary, there are two characteristic features of echinoderms that have a large influence on their presence in the fossil record. The first is the presence of a multi-plated skeleton that can disarticulate to various degrees during taphonomic processes. The second is the fact that regeneration can lead to increased production of skeletal elements during the life span of an individual organism.

### 3 Influence of Test Architecture and Environment

Taphonomic processes determine preservation patterns of once living animals and their final representation in the rock record. There are numerous factors leading to differential preservation of echinoids, some characteristic of echinoderms as a whole, others limited to sea urchins generally, or even to specific taxa.

The general distribution of regular echinoids on hard substrates in high-energy environments and the presence of irregular echinoids within soft sediments leads to a better preservation potential for irregular echinoids (Ernst & Seibertz 1977, Kier 1977). This depends to a large extent on what type of remains are being considered: complete fossils with spines attached, preserved tests, or single fragments (see Nebelsick 1996). This, in turn, not only depends on the ambient environment, but also on the durability of both soft and hard parts. Soft parts, including connective ligaments, muscle tissues, and epithelium will decay (see Smith 1984, Allison 1990, Kidwell & Baumiller 1990). In high-energy environments, echinoid remains can be restricted to fragmented portions of the test, often showing interplate breakage and abraded fragment boundaries. In addition, spines are mostly broken, with few complete examples (Mancosu & Nebelsick 2020) preserved.

Skeletal integrity depends on the presence or lack of stereomic strengthening between plates, as discussed by Smith (1990, 2005) within an evolutionary context. Test architectures range from loose plate connections in Paleozoic echinoids, echinothuroids, and diadematooids to skeletal projections between plates in more derived regular echinoids, to robust connections including internal supports, which are found in clypeasteroids. The architecture of the echinoid skeleton has been the subject of detailed studies with respect to growth trajectories, plate proliferation, biomimetic, and taphonomic applications (e.g., Seilacher 1979, Telford 1985a, 1985b, Philippi & Nachtigall 1996, Zachos 2009, Grun et al. 2016, 2018, Grun & Nebelsick 2018a, 2018b, 2018c, Perricone et al. 2021).

There are thus numerous factors leading to the differential preservation potential of echinoids through time. These include intrinsic factors of skeletal architectures and plate connections as well as extrinsic environmental factors such as water energy and substrate conditions.

## 4 Predation and Parasitism as Taphonomic Agents

Both predation and parasitism can alter the skeletons of echinoids and, thus, represent important taphonomic processes. Their identification in the fossil record can be used to record predator/prey relationships through time (see Kowalewski & Nebelsick 2003, Petsios et al. 2021). Both regular and irregular echinoids serve as prey to a variety of predators, including numerous marine invertebrates, but also vertebrates including, among others, birds, sea otters, and humans. There is a large body of biological literature pertaining to echinoid predation (see chapters on specific taxa in Lawrence 2020) because echinoid predation plays a key role in structuring communities (e.g., Hendler 1977, Estes et al. 1978, McClanahan 1988, 1995, 1998, Sala & Zabala 1996, Guidetti & Mori 2005, Young & Bellwood 2011, Johansson et al. 2013). Predation on echinoids can lead to a range of different preservation styles (Nebelsick 1999b), some of them potentially recognizable in the fossil record including: 1) no signs at all (for example, predation by starfish or predators that enter the peristomal or periproctal membrane) (see also Kidwell & Baumiller 1990); 2) non-distinct wounds on the test that cannot be assigned to any specific predator, as for predation by many fish, decapod, and bird species; 3) distinct characteristic wounds that can be attributed to specific predators including gastropods and some fish; and 4) the total destruction of the test into non-distinct fragmentary skeletal elements (most durophagous predators).

### 4.1 Holes and Pits

There are a host of parasites that also affect echinoids (Jangoux 1984), some of them leaving distinct traces on the skeleton. Various traces attributed to parasites include galls in tests and spines (see the compilations in Donovan 2015, Belaústegui et al. 2017). Malformations include pinching of ambulacral pore rows present in fossils (e.g., Tavani 1935, Roman 1952, 1953, Marcopoulos-Diacantoni 1970, Abdelhamid 1999, Zamora et al. 2008) as well as pits and holes in the tests (Grun et al. 2020). Pinnotherid crabs infest echinoids, in sand dollars shaving off patches of the minute spines (see Martinelli Filho et al. 2014, Nebelsick 2020). Parasitic gastropods enter through ambulacral pores or produce holes in the test. Detailed description and ichnotaxa are especially well represented for Cretaceous echinoid tests (Jagt et al. 2007, Donovan et al. 2008, 2014, 2017, Donovan & Jagt 2013, Neumann & Wisshak 2006, 2009, Neumann et al. 2008) and include a wealth of holes and pits caused by, among others, foraminifera, gastropods, and brachiopods. For a summary of the protracted discussions with respect to the naming and interpretation of these ichnotaxa, see Belaústegui et al. (2017).