

Chapter 8

Echinoderms: Hierarchically Organized Light Weight Skeletons

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8.1 Introduction

This overview of echinoderm skeletal structures is presented from a hierarchical point of view ranging from: (1) the complete organisms including all skeletal elements and soft part morphologies, to (2) coherent plate combinations including echinoid coronas and crinoid stems and arms, (3) single skeletal elements, (4) the micro-architecture of stereom types, and (5) ultrastructural aspects of biomineralization. This review mostly pertains to the echinoids and in part to the crinoids to which most attention has been directed in the literature. The consideration of skeletal hierarchies is accompanied by examining a suite of symmetries represented by the echinoderms as a whole or within the isolated elements. Usually beginning as free-swimming bilateral larvae, they undergo metamorphism to an organism based on a pentamerous arrangement, which as in the irregular echinoids and holothurians, can be overprinted by a return to

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bilateral symmetry. Isolated elements can show radial symmetry in echinoids spines, pentamerous symmetry in the case of crinoid stalk elements, bilateral symmetry in the case of ophiuroid arm elements or can lack symmetry completely.

Echinoderms are marine organisms which belong as adults to the benthic realm on or within the substrate. They are important, and in some cases dominant, members of diverse benthic habitats in all depths of the seas. All echinoderms are light weight in that their skeletal elements are constructed of stereom, a variously arranged mesh-work-like lattice made up of struts termed trabeculae. This stereom is highly variable as far as density and structure is concerned ranging from chaotic to strictly directionally oriented to highly dense. The possession of stereom in the skeleton is one of the main diagnostic characters of echinoderms and allows even highly fragmented, single ossicles to be identified in the sedimentary rock record. The skeleton has long been an object of interest from a constructional design perspective and has been approached from various angles including the manner in which single elements are added to the skeleton and to how these elements, together with the whole skeleton, increase in size while retaining their general shape and structural integrity.

Echinoderm skeletons are mesodermal, similar to that of the bones of vertebrates. This means that the skeleton, with very few exceptions, is enveloped by soft tissue at all size scales: (1) the corona of echinoids and the calyx of crinoids surround and protect the major organs of the body, (2) muscle fibers and ligaments connect single plates to one another, (3) organic material (stroma) is present between the struts of the stereom and, at the lowest hierarchical level, (4) organic material is present within the skeletal struts themselves. The skeleton itself is constructed of high magnesium calcium carbonate which contains variable amounts of magnesium within the crystal lattice. Finally, the possession of a more or less durable skeleton has led to an impressive fossil record allowing the evolution of the echinoderms to be followed. There are a number of extinct taxa with, in part, even more bewildering and complex skeletal arrangements than among the five classes still present today.

8.2 Complete Skeletons and Basic Symmetry

The skeletons of echinoderms are highly variable and range from (1) loose ossicles in the body wall as found in the holothurians, to (2) serial rows of highly articulated skeletal elements connected by ligaments and muscle tissues as found in ophiuroids and many asteroids, to (3) rigid rows of plates locked together as in the corona of some, but not all, echinoids and the calyx of crinoids. There are many variations of these skeleton types and in most cases a combination can be present. In echinoids, the test consists of numerous plates that serve as an outer case of plates protecting the internal organs while serving as a platform for various appendages such as spines (Fig. 8.1) and pincher-like pedicellariae. Even the most compact and stable tests are penetrated by various holes including, among others, the mouth, anus and pore pairs of the ambulacral system. In crinoids, a clear tripartite organization can be present with the stems (if present) and arms of crinoids consisting of articulated elements attached to a rigid calyx.

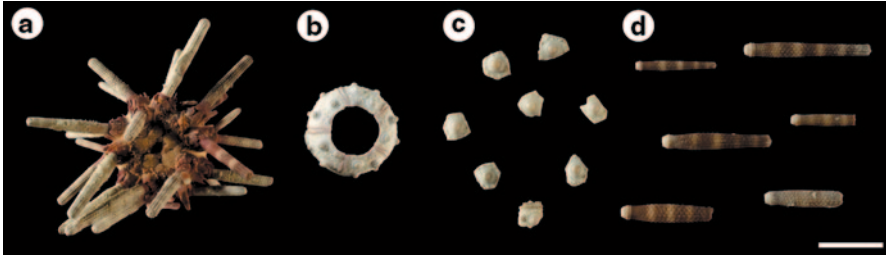


Fig. 8.1 *Eucidaris metularia* from the northern Bay of Safaga, Red Sea (see Nebelsick 1992). **a** Complete individual with spines and apical disc. **b** Denuded test lacking spines, note large primary tubercles which support the spines and sinuous ambulacral plate rows which harbor the tube feet. **c** Disarticulated plates, mostly single large interambulacral plates with primary tubercles. Lowermost element is fragmented and includes attached minute ambulacral plates. **d** Single primary spines showing banding patterning and surface protuberances. Scale bar = 1 cm.

Echinoderms are well known in showing a general five-fold pattern of body parts or plating pattern (Hotchkiss 1998; Smith et al. 2004; Morris 2007). Although most recent echinoderms generally follow this, there are notable exceptions. Recent sea stars often deviate from a fivefold pattern of arms and irregular echinoids show a clear bilateral symmetrical overprint. All echinoderm larvae show bilateral symmetry and undergo a complex metamorphosis into adults (e.g. Smith 1997). Even those animals such as regular sea urchins in which clear pentamery can be readily recognized in adults, distinct asymmetry occurs in the position of specific single plates, such as the madreporite. Pentamery is not an apomorphic character for the echinoderms as basal echinoderms such as carroids found only in the fossil record lack symmetry. The bilateral symmetry of crown group echinoderms was followed by asymmetrical skeletons and then by the familiar pentamerous extant echinoderms (see discussion in Smith 2005a; Zamora et al. 2012). The exact symmetry of irregular echinoids has also been subject to analysis with deviations being attributed to internal morphology or as a possible indicator of stress (Lawrence et al. 1988). Symmetry relationships can also be found between rows of plates as in echinoids or in the arms of ophiuroids and asteroids as well as in individual plates (see below). There have also been attempts to correlate phenotypic size variations of echinoderms to environmental parameters (Laurin et al. 1979; Laurin and David 1990; Dynowski and Nebelsick 2011).

8.3 Structural Analysis and Modeling of Echinoids and Crinoids

Echinoderm body shape can be highly mutable as in the holothurians with their leathery body walls containing minute calcite inclusions or more or less rigid skeletons as found in the corona of many echinoids and the calyx of crinoids. The echinoids have attracted the most attention as far as skeletal architectures and functional morphology is concerned. During their evolution, echinoids show a general

trend from having a uniform test shape, but variable test structure within Paleozoic stem groups to having a variable test shape and uniform test structure in the still extent crown group echinoids (Smith 2005b; Kroh and Smith 2010).

The echinoids shown in Fig. 8.2 thus show a variety of shapes and sizes among the regular and irregular echinoids. The regular echinoids differ in the size of plates,

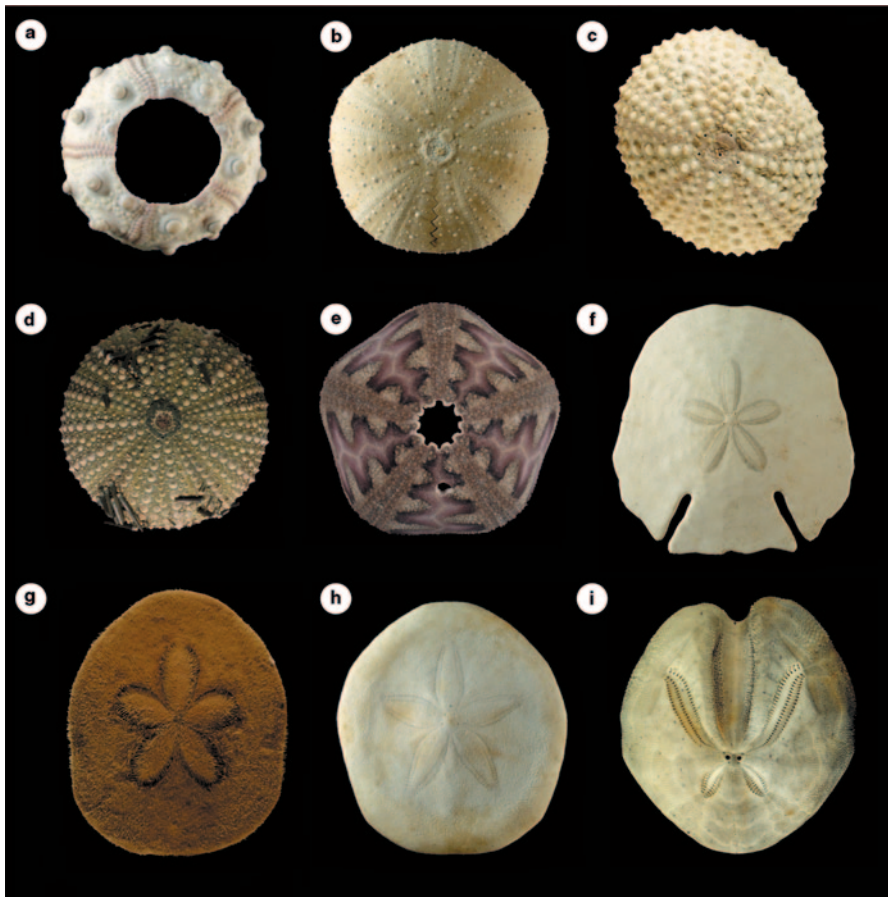


Fig. 8.2 Morphological comparison of tests of regular (*a–e*) and irregular (*f–i*) echinoids. *a–c*, *e–h*: Northern Bay of Safaga red sea, Egypt (see Nebelsick 1992), *d* and *i*: Northern Adriatic Sea. **a** The cidaroid *Eucidaris metularia* with large interambulacral tubercles and sinuous ambulacra. Test width=1.4 cm. **b** *Tripneustes gratilla* with intact apical system and compound ambulacral plates. Test width=4.5 cm. **c** Oblong *Echinometra mathaei* with dense tubercles. Test length=4.3 cm. **d** *Paracentrotus lividus* with a few attached primary spines. Test width=4.7 cm. **e** *Microcyphus roussouii* with distinct naked area in the interambulacra. Apical disc is missing, predatory borehole also present. Test width=5.3 cm. **f** Sand dollar *Echinodiscus auritus* showing petalodium and open posterior lunules. Test length=9.2 cm. **g** *Clypeaster humilis* still covered by minute spines. Test length=7.6 cm. **h** *Jacksonaster depressum* with distinct petalodium. Test length=2.6 cm. **i** Spatangoid *Schizaster canaliferous* with deeply sunken anterior ambulacra and differentially curved paired ambulacra. Test length=4.7 cm.

ambulacral plate compounding, the number of ambulacral pore pairs per ambulacral plate, the size and number of primary tubercle per plate and so on. The bilateral irregular echinoids show highly divergent morphologies among the flattened clypeasteroid and the more globose spatangoids with respect to, among others, their basic outline, the morphology of the ambulacralia and the size variations of plates. Clypeasteroids show a special constructional principle (see Seilacher 1979) showing not only interlocking plates but also internal supports connecting the upper and lower surface of the test (Fig. 8.3). Despite all these variations, the body form of echinoids is clearly recognizable and almost all extant taxa show double rows of ambulacralia (bearing the tube feet) and interambulacralia.

Echinoids have been the subject of a number of studies analyzing growth and test architectures (e.g. Moss and Mehan 1968; Raup 1968; Seilacher 1979; Johnson

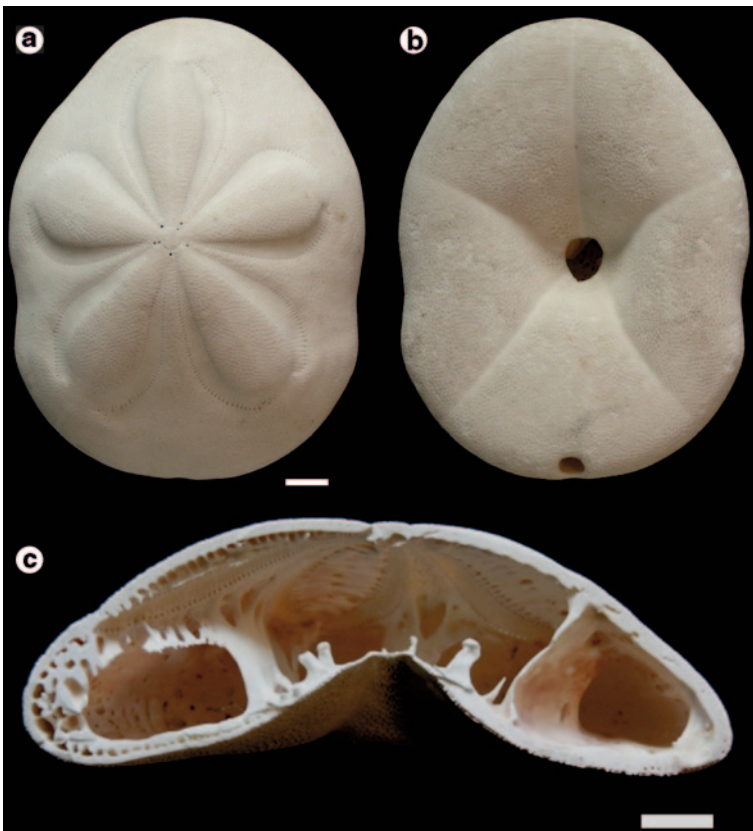


Fig. 8.3 Different views of the irregular clypeasteroid echinoid *Clypeaster rosaceus*. **a** Apical view showing petalodium with ambulacral pores. Apical disc at centre of test with 5 genital pores. **b** Oral view showing central peristome (*mouth*) and periproct near the posterior edge. Test covered by minute tubercles. **c** Cross section showing internal supports connecting the oral and apical side of the test. Double wall structure visible at the test anterior (*left*). Scale bars = 1 cm.

et al. 2002; Telford 1985; Phillipi and Nachtigall 1996; Zachos 2009; Chakra and Stone 2011; Mihaljević et al. 2011). A combination of simple membrane theory and static analysis was used by Telford (1985) to determine how stresses are carried in the skeleton. Ellers et al. (1998) demonstrated the importance of structural strengthening of these urchin skeletons by collagenous sutural ligaments which connect the plates. The interpretation of the echinoid skeleton as representing pressurized pneus (Moss and Mehan 1968; Seilacher 1979; Dafni 1986; 1988) at least during growth was convincingly challenged by Ellers and Telford (1992) who, upon measuring actual coelomic pressures within sea urchins, did not find increased pressure patterns or differences between growing (fed) and non-growing (starved) individuals. Measured pressure differences are caused by extruding and retracting the lantern during feeding which affected the displacement of internal fluids and the peristomal membrane, an area of soft tissue which surrounds the mouth.

The functional morphology of the regular echinoid *Echinus esculentus* performed by Phillipi and Nachtigall (1996) using Finite Element Analysis (FEA) analyzed the reaction of the test to different types of loading and argue that test growth and shape cannot be due to internal pressure. Furthermore, the general test shape of regular echinoids is shown to be well adapted to the activity of tube feet. A three-dimensional model of growth is presented by Zachos (2009) which includes both plate addition and plate growth. Individual plate growth is considered along with the insertion of new plates which is continuous until a distance threshold is reached upon which a new plate is added.

Biomechanical considerations concerning crinoids have concentrated on the stalks and the arms using both recent as well as fossil examples. The arm arrangement of fossil crinoids is compared by Cowen (1981) to the distribution patterns found in banana plantations. The dependency of both systems on optimal transport efficiencies are shown in a cost-benefit analysis. A review of the morphology of crinoids and how this pertains to ecology is given by Baumiller (2008). Functional analyses of stalk morphologies comparing skeletal characteristics and the role of mutable collagenous tissue have been used to reconstruct postures of fossil crinoids by Baumiller and Ausich (1996). Baumiller and LaBarbera (1993) studied the structural characteristics of the stalk and the cirri of the crinoid *Cenocrinus asterius*. The mechanics associated with the surprising discovery that stalked crinoids can actually move over the substrate surface are presented in Baumiller and Messing (2007). Further studies on the skeleton and collagenous arm ligaments on crinoids have been made on the arms and their movement (Birenheide and Motokowa 1994, 1996, 1997; Motokawa et al. 2004).

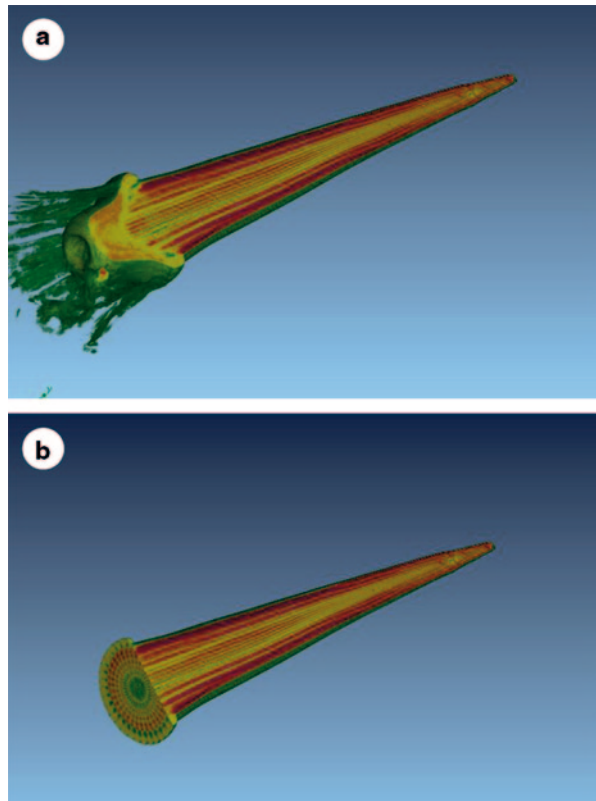
8.4 Single Skeletal Elements

Single plates range in size from minute sclerites (such as in the body wall of holothurians; pedicellariae and tube feet supports in echinoids) to the massive spines of regular echinoids which can reach lengths of 10 cm or more. Individual plates are

present distributed loosely within the body wall, connected to one another by muscles and ligaments, or structurally locked by interconnecting trabecular extensions (see Seilacher 1979; Hidaka and Takahashi 1983; Smith et al. 1990). The single skeletal elements are highly variable in morphology and their detailed form can be closely related to functional aspects (Smith 1978; 1980a, b). Growth of echinoderm plates can occur in discrete increments leading to clear concentric banding which may or may not represent annual events (Raup 1968; Ebert 1975, 1985; Pearse and Pearse 1975). Resorption of skeletal material, though rare, has also been observed (Märkel and Röser 1983) becoming necessary in order to preserve the geometric integrity of the growing animals.

Echinoderm elements themselves also show a wide range of symmetries (Figs. 8.4, 8.5, 8.6, 8.7). Radial symmetry is present in the spines of echinoids. Pentamerous symmetry can be found in the stalk elements of crinoids, but is generally rare. Bilateral symmetric elements are present in ophiuroids and crinoid arms. Coronal plates of echinoids are flattened and show parallel surfaces while other elements show no symmetry at all. Two single echinoderm elements which have attracted special attention with respect to morphology and biomimetic potential are echinoid spines and teeth. Echinoid spines as single elements have been studied due to their relatively large size, growth characteristics and mechanical properties (e.g.

Fig. 8.4 CT-Scans of primary spine of *Echinometra mathaei* showing radial symmetry. **a** Longitudinal section showing consecutive growth stages of the spine. The base of the spine shows attached muscle fibers which attach the spines to the tubercles of the test plates. **b** As above with additional cross section at the level of the milled ring showing concentric layers. Length of spine = 2.5 cm.



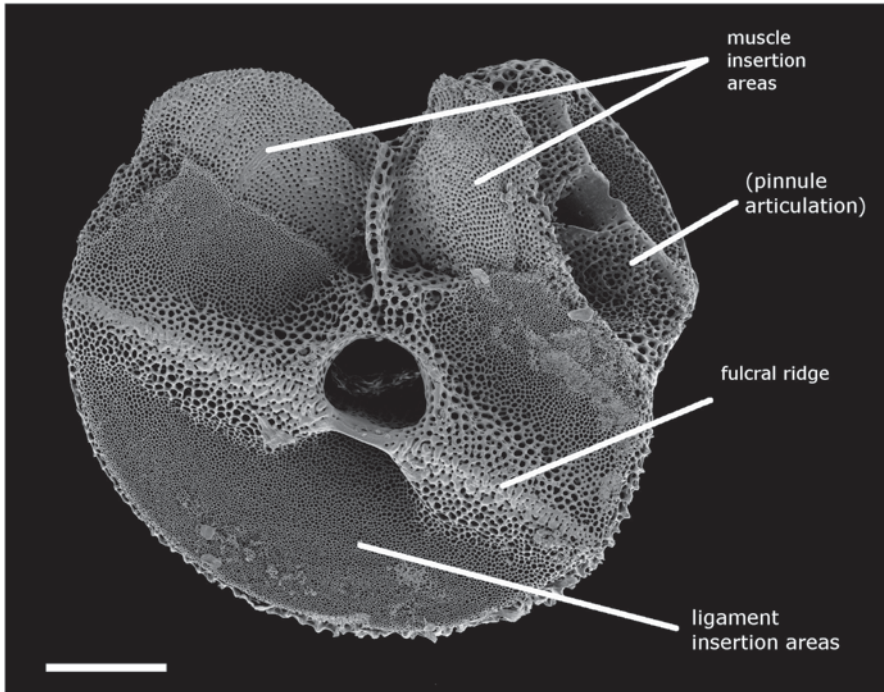


Fig. 8.5 Single arm plate of the stalkless crinoid *Antedon mediterranea* from the Tyrrhenian Sea, Giglio, Italy. Oblique muscular articulation is present with a central canal. Stereom differentiation is clearly developed (see text). Pinnular articulation to the *upper right*. Scale bar = 200 μ m.

Strathmann 1981; Currey 1975; Burkhardt et al. 1983; Ebert 1986; Coppard and Campbell 2004; Davide et al. 2009; Presser et al. 2009; Moureaux 2010; Tsafnat et al. 2012; Grossmann and Nebelsick 2013a, b), Echinoid teeth are characterized by their complex morphology, continuous growth and hardness (e.g. Märkel and Gorny 1973; Stock et al. 2003; Wang et al. 1997; Gilbert and Weiner 2009; Robach et al. 2009; Killian et al. 2011; Veis et al. 2011; Ziegler et al. 2012).

8.5 Stereom Architecture

The presence of stereom within the skeletons is one of the features which characterize the echinoderms as a whole (Smith 2005a) and can be readily differentiated if under the scanning electron microscope (Figs. 8.5, 8.6, 8.7). Defined types of stereom include, for example, solid imperforate stereom, microperforate stereom containing few small pores, galleried stereom consisting of galleries of parallel arrangement of connected trabecular struts and chaotically arranged loose labyrinthic stereom (Smith 1980c, 1990). Stereom differentiation has been shown to be specifically

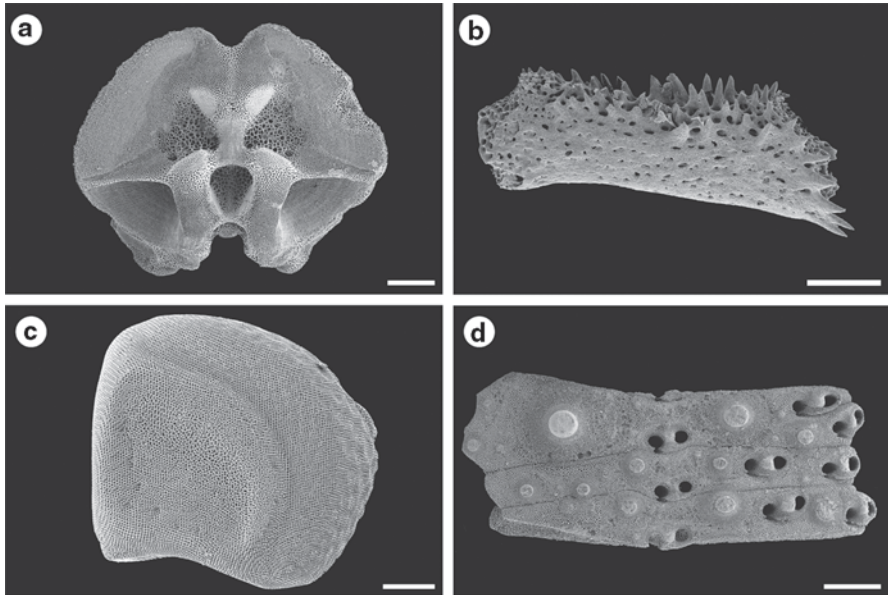


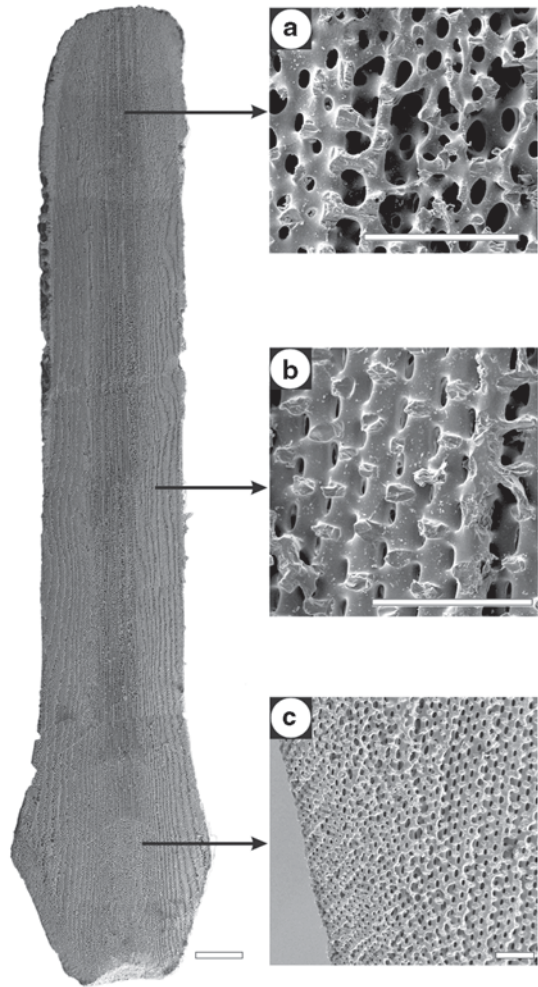
Fig. 8.6 Morphological and stereom variations among single ossicles (*a–e*) and conjoined plates of various echinoderms (*f*); *a*, *c* and *d* from sediment samples from San Salvador, Bahamas (see Dynowski 2012); *b* from the Tyrrhenian Sea, Giglio, Italy. **a** Bilateral symmetrical proximal face of an arm vertebra of the ophiuroid *Ophiocoma echinata*. Scale bar=100 μm . **b** Single asymmetrical pinnular plate of *Antedon mediterranea* showing dense stereom and delicate spikes. Scale bar=200 μm . **c** Marginal plate of the sea star *Astropecten duplicatus*. Scale bar=400 μm . **d** Three conjoined compound ambulacral plates of the regular sea urchin *Tripneustes ventricosus*. Each compound plate is made of three elements resulting in 9 elements in all. Each compound plate bears three pore pairs and several tubercles. Tubercles show very dense stereom which serve as articulation surfaces. Scale bar=400 μm .

correlated to the function of the skeletal elements or areas of the elements involved. Stereom can thus differ highly within single plates. In general, denser stereom is present where mechanical demands are high such as in the tubercles of echinoid plates on which the spine articulate. Highly structured stereom is needed where muscle fibers attach to the plates; loose stereom is found as a volume filler preserving the integrity plate shapes intact during growth (Smith 1980c, 1990).

A specific example for stereom differentiation and functionality is shown in Fig. 8.5 which shows a crinoid brachial with muscular articulation surfaces. Ligament insertion areas show stereom with an open mesh for the ligaments to attach deeply into the ossicles or even penetrate it. Muscle insertion areas have fine pores where the muscles attach but do not need to penetrate deep into the ossicles. The fulcral ridge consists of a robust dense calcite where adjoining ossicles form a kind of hinge for movement and have to withstand friction pressure. Further examples of stereom differentiation can be seen in Figs. 8.6 and 8.7.

The detailed structure of spines and their potential biomimetic applications has recently gathered more attention (Presser et al. 2009; Moureaux et al. 2010; Tsafnat

Fig. 8.7 Compiled SEM image of sectioned longitudinal oral primary spine of *Phyllacanthus imperialis* (to the left) and details of the stereom structure (to the right). **a** Medulla near the spine tip. **b** Radiating layer. **c** Spine base. Spine scale bar=1 mm, detailed scale bars=100 μ m.



et al. 2012). Studies applied to the stereom of spines of cidaroid and camaradont echinoids by Grossmann and Nebelsick (2013a, b) have shown that a number of stereom types are present in the spines depending not only on the species involved, but also on the location of stereom with respect to position along the spines. Stereom types thus differ not only from the base to the tip (Figs. 8.4 and 8.7) but also radially from the centre of the spine to the outside. These stereom differentiations have structural implications as measured by three point bending tests (Grossmann and Nebelsick 2013b).

8.6 Calcification and Biomineralization

The mineralogy of the echinoderm skeleton as a high magnesium calcium carbonate material has attracted much attention (e.g. Raup 1966; Towe 1967; Weber 1969; Märkel et al. 1971; Blake et al. 1984; Emler 1982; Tsipursky and Buseck 1993; Gilbert and Weiner 2009; see compilation in Kroh and Nebelsick 2010). Calcite forms in echinoderms after the transformation from amorphous calcite (Politi et al. 2004, 2008; Killian et al. 2011). Although echinoderm skeletal elements behave as single crystals of calcite in polarized light especially after diagenesis in the rock record, they are constructed of a mosaic structure with slight alterations in the orientation of sub- μm sized crystallite. This polycrystalline aggregate along with differential inclusion of magnesium even within single elements may be a factor in hindering crack propagation in the struts of the stereom, while also imparting the typical conchoidal fracturing found at the trabecular scale (Berman et al. 1988).

Ultrastructural research has been conducted on early calcification sites and on the mineralizing organic matrix (e.g. Märkel et al. 1986; Ameye et al. 1998, 2000 see reviews in Killian and Wilt 2008; Gilbert and Wilt 2011). Biomineralization in echinoderms has been studied in larval skeletons (Wilt 1999, 2002; Wilt et al. 2008), teeth (Kniprath 1974; Mann et al. 2010a, b; Veis 2011) and in spine regeneration. Although present in low levels, numerous proteins of the intracrystalline organic matrix of the echinoderm skeleton and have been identified at the molecular level (e.g. Albeck et al. 1996; MacKenzie et al. 2001; Peled-Kamar et al. 2002; Gilbert and Wilt 2011; Matraga et al. 2011). The skeletons of echinoderms thus represent composites of mineralized and organic materials.

8.7 Conclusions

The echinoderm skeleton has long attracted attention due to its highly unique morphological, structural and chemical characteristics. The skeleton and its many discrete elements can be observed at a number of hierarchical levels including: (1) complete organisms, (2) plate aggregates, (3) isolated single plate elements, (4) stereom architectures, and (5) the molecular level of biomineralization. These hierarchical levels can be seen in all five extant classes and in extinct taxa. Various types of symmetry are present within the different hierarchical levels ranging from bilateral to pentamerous to asymmetrical. Constructional principles have been studied in detail in echinoid coronas and in the stalk and arms or crinoids. Light weight architectures also become obvious at the level of single elements and in the different types of stereom present in all echinoderms.

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