Bioinspiration & Biomimetics

TOPICAL REVIEW • OPEN ACCESS

Constructional design of echinoid endoskeleton: main structural components and their potential for biomimetic applications

To cite this article: Valentina Perricone *et al* 2020 *Bioinspir. Biomim.* **16** 011001

View the article online for updates and enhancements.

IOP ebooks™

Bringing together innovative digital publishing with leading authors from the global scientific community.

Start exploring the collection–download the first chapter of every title for free.

This content was downloaded from IP address 82.49.89.177 on 09/12/2020 at 10:52

Bioinspiration & Biomimetics

OPEN ACCESS

TOPICAL REVIEW

Constructional design of echinoid endoskeleton: main structural components and their potential for biomimetic applications

Valentina Perricone[1,*], Tobias B Grun[2], Francesco Marmo[3], Carla Langella[4] and Maria Daniela Candia Carnevali[5]

[1] Dept. of Engineering, University of Campania Luigi Vanvitelli, Aversa, Italy
[2] Dept. of Invertebrate Paleontology, University of Florida, Florida Museum, Gainesville, Florida, United States of America
[3] Dept. of Structures for Engineering and Architecture, University of Naples Federico II, Napoli, Italy
[4] Dept. of Architecture and Industrial Design, University of Campania Luigi Vanvitelli, Aversa, Italy
[5] Dept. of Environmental Science and Policy, University of Milano, Milan, Italy
[*] Author to whom any correspondence should be addressed.

E-mail: valentina.perricone@unicampania.it

Keywords: echinoids, mechanical design, constructional morphology, biomimetics

RECEIVED
28 May 2020

REVISED
15 August 2020

ACCEPTED FOR PUBLICATION
14 September 2020

PUBLISHED
30 November 2020

Original content from this work may be used under the terms of the Creative Commons Attribution 4.0 licence.

Any further distribution of this work must maintain attribution to the author(s) and the title of the work, journal citation and DOI.

Abstract

The endoskeleton of echinoderms (*Deuterostomia: Echinodermata*) is of mesodermal origin and consists of cells, organic components, as well as an inorganic mineral matrix. The echinoderm skeleton forms a complex lattice-system, which represents a model structure for naturally inspired engineering in terms of construction, mechanical behaviour and functional design. The sea urchin (*Echinodermata: Echinoidea*) endoskeleton consists of three main structural components: test, dental apparatus and accessory appendages. Although, all parts of the echinoid skeleton consist of the same basic material, their microstructure displays a great potential in meeting several mechanical needs according to a direct and clear structure–function relationship. This versatility has allowed the echinoid skeleton to adapt to different activities such as structural support, defence, feeding, burrowing and cleaning. Although, constrained by energy and resource efficiency, many of the structures found in the echinoid skeleton are optimized in terms of functional performances. Therefore, these structures can be used as role models for bio-inspired solutions in various industrial sectors such as building constructions, robotics, biomedical and material engineering. The present review provides an overview of previous mechanical and biomimetic research on the echinoid endoskeleton, describing the current state of knowledge and providing a reference for future studies.

Introduction

Sea urchins (*Echinodermata: Echinoidea*) are known to have been in existence since the Middle Ordovician, about 460 million years ago [1]. During the Early Jurassic, they underwent an intensive adaptive radiation leading to a variety of specialized forms and lifestyles adapted to different marine habitats [2–13]. Echinoids are traditionally subdivided into two groups: regularia and irregularia, mainly identifiable based on test morphology and lifestyle [14, 15]. Regular echinoids are typically spherical in shape with the peristome (mouth region) on the central oral side and the periproct (anal region) aborally located. The area spanning from the apical system throughout the peristome is divided in five ambulacral and five interambulacral fields, each one characterized by ten double columns of different skeletal plates with species-specific fine-relief ornaments [16]. Regular echinoids possess a prominent pentaradial symmetry superimposed on the ancestral echinoderm bilateral symmetry. In contrast, irregular echinoids are typically aboral-orally flattened and elongated or heart-shaped. The peristome is orally located, but not necessarily in the centre of the oral surface. The periproct migrated from the central aboral side towards the oral side assuming variable positions in the test [12, 17]. The ambulacral fields are often restricted to the aboral side forming the *petalodium* [18]. Thus, irregular echinoids

© 2020 The Author(s). Published by IOP Publishing Ltd

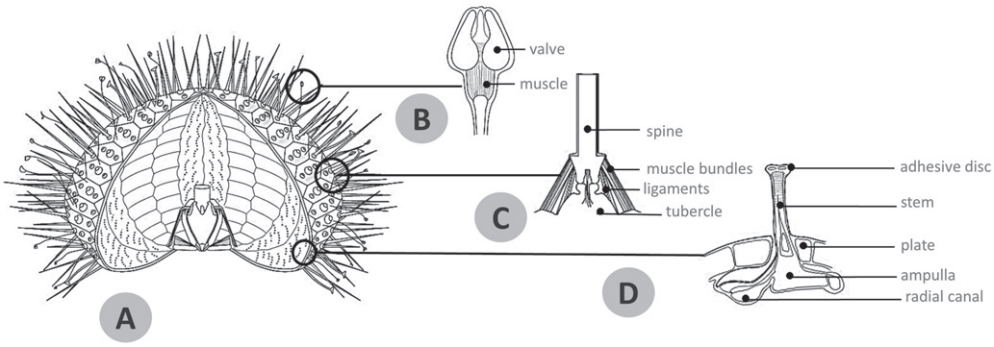

Figure 1. *Overview of the echinoid test and appendages.* (A) Schematic reconstruction of regular echinoid test showing its overall external and internal anatomy including the lantern system. (B) Detail of pedicellaria tip illustrating the three valves and muscles. (C) Detail of the spine-test articulation showing the typical ball-and-socket joint in a vertical section: the spine is articulated to the plate tubercle through the muscle bundles and ligaments of the 'catch apparatus'. (D) Detail of a tube foot displaying the main components of its microanatomy: basal ampulla, stem and apical adhesive disc including tiny skeletal ossicles.

typically possess a strong bilateral symmetry superimposed on the radial symmetry acquired [4–8, 19–25]. The evolutionary success of echinoids is undoubtedly due to the strategic employment of their endoskeleton, macroscopically consisting of three main functional components: test, dental apparatus (Aristotle's lantern) and accessory appendages (such as spines and pedicellariae) [26, 27] (figure 1).

In the course of evolution, the echinoid skeletal parts transformed in morphology and physiology adapting to novel functions [28]. For example, in some species the main function of the spines shifted from protection to burrowing [29–33]. Also, pedicellariae, the small pincer-like appendages, developed different forms, including venomous types [34]. In addition, the morphology of the dental apparatus differed due to feeding strategies, such as scraping and crushing, or it has been entirely eliminated [35–38]. Complementarily, the modifications during evolution have specialized and adapted these skeletal parts to efficiently absolve specific mechanical roles. In particular, spines and test protect the animal by withstanding biotic (e.g. predatory attacks) and abiotic (e.g. strong wave motion or substrate impact during burrowing or locomotion) mechanical stresses [39–46]; pedicellariae, provide further defence and are used for cleaning the echinoid's epidermis [34, 47]. Aristotle's lantern plays a direct role in multiple activities such as gripping, scraping, digging, and even locomotion [48]. In particular, the lantern, which consists of an integrated system of 40 skeletal elements, joined and moved by specific muscles and ligaments, represents one of the most complex and optimized biomechanical models in the animal kingdom [49–53].

Due to its unique features, it does not surprize that the constructional design of the echinoid skeleton has attracted the interest of both biologists and engineers. Accordingly, mechanical engineering and material science principles, methods and tools have been applied in exploring the mechanical performances of sea urchins as an integrated system or single component [23, 45, 46, 54–63]. This biomechanical approach provided important biological insights on form-function skeletal features, taxa comparisons, ecological and evolutionary trends and adaptive meanings, as well as, new functional principles used to design innovative bioinspired technical solutions [27, 46, 54, 64–68]. Echinoid skeletal components are structurally and functionally organized regarding, among others, lightness, stability, strength, flexibility and stress resistance. Presently, due to the availability of novel analytical methods, the underlying principles can be better understood and transferred into building constructions and industrial products; a process known as 'biomimetics' and 'bionics' [69]. Otto Herbert Schmitt an engineer and physicist coined the term biomimetics in 1957 and its approach was regulated and certified in 2015 by the International Organization for Standardization (ISO 18458) [70]; whereas, the term bionics, a combination of the words 'biology' and 'technics', was coined by the US Air Force Major J E Steele in 1960 [71–75]. Often used as an equivalent, both terms identify a design process inspired by nature that generated innovative technological solutions. Over the past decade, other terms have occurred in conjunction with this process, such as *biomimicry*, *biomimesis*, *bio-inspiration*, *nature-based solutions*, *biologically inspired designs* and numerous others; although often used as synonyms, each one differs in objectives, principles and approaches [69, 74–76].

The present review provides an overview of recent knowledge on echinoid skeletal structures. Its intention is to identify the main morphological features and mechanical aspects, in order to provide a reference for future research on biomimetic applications. Accordingly, the following issues will be discussed in detail: (1) current knowledge of biomineralization and material properties of the echinoid endoskeleton; (2) skeletal microstructure (stereom); (3) the

three main skeletal components: i.e. test, Aristotle's lantern and accessory appendages; (4) biomimetic process and echinoid-inspired applications in building constructions, robotics, biomedical and material engineering.

1. Biomineralization

The biomineralization process in echinoid skeletons has been extensively investigated throughout different developmental stages from larvae to adults [77–85]. Detailed mineralogical analyses revealed that its mineral matrix consists of calcite, containing up to 15% magnesium [86, 87]. Hence, the echinoid skeleton is generally considered a high-magnesium calcitic structure, although its magnesium content can vary significantly according to species and specific skeletal parts, as well as, environmental factors such as temperature or pH [88–92]. These variations determine different mechanical properties of the skeletal parts [88, 93]. The calcite in echinoid skeletons displays the optical behaviour of a monocrystalline structure with definite orientation of the optical axes [87, 94]. In terms of mechanical behaviour, the rupture response of the echinoid biocalcite results in conchoidal fractured surfaces, which differ from the well-defined cleavage of pure calcite crystals [95–98]. For many years, this fracturing behaviour was attributed to the presence of organic components (proteins) within the stereom structure [95]. Seto *et al* (2012) later found evidence that this behaviour is mostly due to the particular echinoid calcite structure [99]. Indeed, this calcite is a mesocrystal composed by numerous aligned calcite nanocrystals (∼100 nm) embedded in a matrix of amorphous calcium carbonate (ACC) and macromolecules [95–102]. These last two components cause the conchoidal fracture properties. Echinoid biocalcite has often been discussed as representing a composite material because it contains up to 0.2% proteins by weight [84, 103, 104]. From a material engineering perspective, materials composed of two or more constituents with different physical, chemical and mechanical properties are defined composites. The combination of different constituents produces a material with advantageous emerging properties, strongly different from the properties of the same constituents [45]. This is usually the case when the fraction of each composite reaches a relevant amount of the total volume [105]. When the amount of one of the components is too low, the material is not considered a composite; in fact, the second constituent affects the material properties by interacting with the main component rather than contributing its own advantageous properties to the material composition [105].

Vertebrate bone for example, represents a high-performance composite material consisting primarily of collagen and hydroxyapatite. The mineral component provides bone with mechanical rigidity and load-bearing strength, whereas the organic fibrous component provides elasticity and flexibility [106]. In quantitative terms, the hydroxyapatite fraction should account for 35% of the volume in order to reinforce the skeletal material effectively. Nevertheless, the amount of hydroxyapatite in vertebrate bone reaches roughly 50% and the collagen represents the other 50% providing advantageous tensile properties; for this reason, vertebrate bone represents a true composite material, of which anisotropy provides considerable strength and stiffness in at least one direction [45, 106, 107].

Herman *et al* (1988) demonstrated that the amount of organic matrix in echinoid calcite is not sufficient to form a continuous layer within the stereom and does not represent a considerable amount of the total volume; thus, it cannot be considered as an effective constituent in making the echinoid calcite a composite material [96, 108]. However, Seto *et al* (2012) demonstrated that the mesocrystal structure of the echinoid calcite contains between 8 and 10 wt % ACC in mature spines, consequently revealing that ACC calcite could itself serve as a second component of this composite material [99].

Composite systems, usually feature the advantage that cleavage propagation is prevented by a suitable alternating arrangement of stiff, strong materials with less stiff materials creating a functional interface where the latter, having a reduced elastic modulus, assumes a stress-breaking role absorbing stresses [105, 107, 109]. This is the case of nacre that is composed of 95% aragonite and 5% proteins and polysaccharides, as well as, vertebrate bone [45, 107]. The employment of calcified collagenous fibres consequently results in an anisotropic material, which is stiff and tough in one direction, but brittle in at least another [45, 107].

Recently, Lauer *et al* (2020) demonstrated that unlike mechanical properties of other biogenic ceramic composite materials, such as nacre, the combination of high Mg-calcite with ACC and organic phases have little effect on macromechanical properties of the *Heterocentrotus mamillatus* spines [110]. Thus, although the micromechanical properties of the echinoid skeleton are governed by the interplay of ACC, organic phase and Mg calcite [96, 99, 111], the macromechanical properties seem mainly governed by the porous stereom structure and architecture resulting in a remarkable damage tolerance [110].

Interestingly, the crystallographic design and macromolecule distribution makes the echinoid biocalcite a more isotropic material [112]. In this regard, it has been demonstrated that the anisotropy is larger in synthetic crystals than in young sea urchin spines; whereas, mature spines have an extended anisotropy, ranging between those of synthetic crystals and young spines, suggesting the existence of

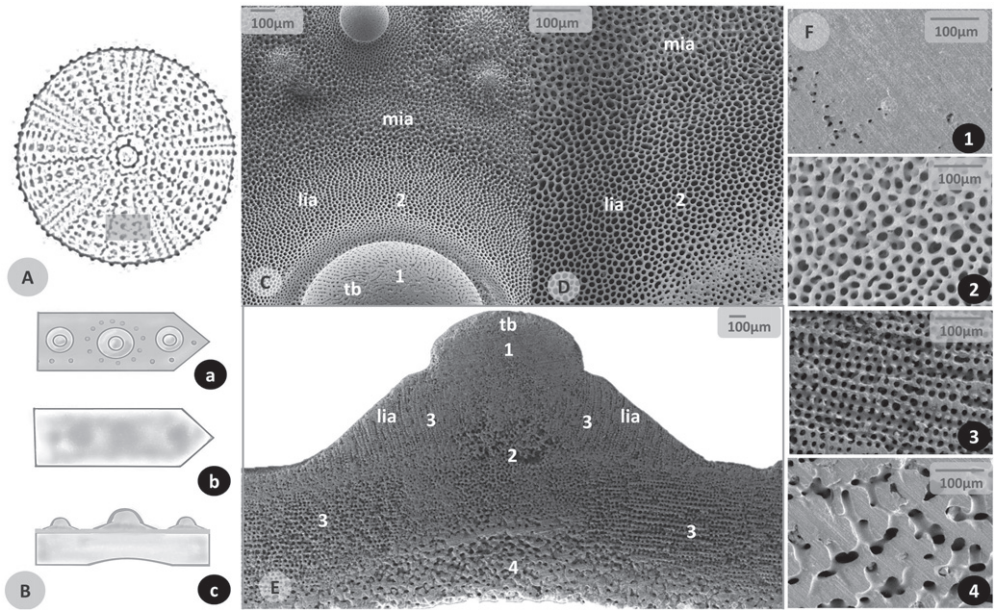

Figure 2. *SEM micrographs showing microstructure and stereom variability of the test plates.* (A) Topographic reference of the interambulacral region inspected. (B) Schematic reconstruction of an interambulacral plate: (a) top view, (b) internal view, (c) lateral view. (C) Top view of *Paracentrotus lividus* interambulacral plate; (D) enlargement of figure (C). Labyrinthic stereom with variable porous texture is the dominant microstructural pattern. In the wide circular insertion area of the overall catch apparatus it is possible to distinguish specific stereom patterns related to muscle and ligament insertions, density and sizes of porosity, closer and more regular in the ligament area. Adjacent to the tubercle where the stereom structure tends to become imperforate, pore size decreases. (E) Vertical section of the plate showing a high diversity of the stereom microarchitecture according to zones and related specific mechanical needs. (F) Details of stereom types detected: (1) imperforate stereom; (2) labyrinthic stereom; (3) galleried stereom; (4) microperforate stereom. Bar = 100 μm. lia = ligaments insertion area, mia = muscles insertion area, tb = tubercle.

remarkable differences in the biological crystal composition during spine formation and growth [113]. In contrast, vertebrate bones (such as femurs) display a clear and defined preferential orientation of collagen and apatite inside trabeculae, as well as, a highly anisotropic trabecular architecture; thus, it is capable of transferring loads more effectively in only one direction [45, 107]. However, apart from the mineral composition, echinoid stereom is similarly characterized by a variable oriented trabecular architecture ensuring a more directional resilience [57, 114]. Moreover, due to its trabecular meshwork, the echinoid stereom is a lightweight construction and possesses a high level of robustness, e.g. allowing the applied forces to bypass malfunctional trabeculae and to be transferred to the functional surrounding ones. [57, 94, 114].

2. Stereom

Stereom [115] is a 3D mesh of trabeculae, i.e. struts, made of biocalcite [114]. It represents a key element responding to the principles of robustness, lightness and stability, due to three primary factors: (1) material composition and related mechanical properties based on material variations through strategic substitution of calcium (Ca) with magnesium (Mg) in the calcite crystal, and alterations of fracture behaviour [94–98, 102, 116–121]; (2) high structural porosity of about 50%–75% [45, 59, 122]; (3) large structural variability (related to e.g. phylogeny, functional adaptations, growth rate and soft tissue types) allowing specific mechanical demands to be met [46, 54–59, 84, 114, 123, 124]. Consequently, this lightweight structure denotes an important adaptive achievement within the entire phylum Echinodermata contributing to its evolutionary success [125–127]. The complex constructional design of the stereom varies from species to species and within both individuals and skeletal elements. Nevertheless, known far away in time [128], this structural variability was described in detail by Smith (1980) identifying ten different stereom types in the test: imperforate, microperforate, simple perforate, galleried, rectilinear, retiform, laminar, fascicular, labyrinthic and irregular perforate [114]. All of which can be employed in a number of combinations, creating species-specific 3D structural patterns easily recognizable in scanning electron microscope (SEM) images. Architectural variability and possible modulations based on specific mechanical needs have been described in several studies regarding: (1) the test and its individual plates [46, 55–57, 87, 97, 116, 124, 129, 130]; (2) Aristotle's lantern ossicles [52, 131]; and (3), more frequently, spines [27, 30, 52, 54, 58, 61, 65, 123, 132–135]. As a rule, stereom density tends to increase in regions subjected to high mechanical stresses resulting in imperforate or microperforate types; in particular, this occurs in those areas exposed

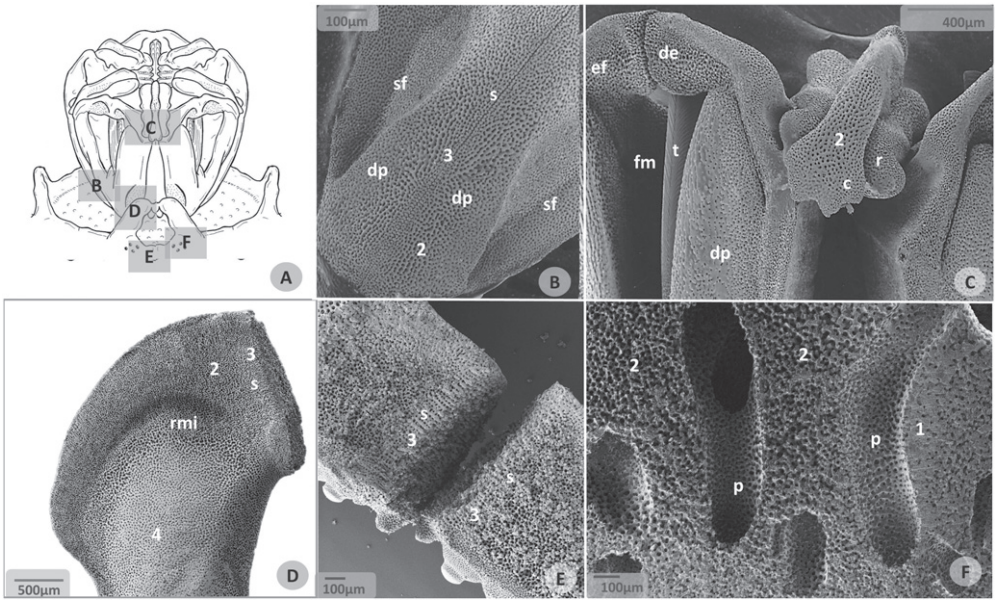

Figure 3. *SEM micrographs showing structure and stereom variability in the Aristotle's lantern components.* (A) Topographic reference of the skeletal parts inspected. (B) Detail of the intrapyramidal suture: galleried stereom is dominant in those areas near the suture running perpendicularly in correspondence to its borders; dense labyrinthic stereom prevails in the unspecialized superficial areas. Bar = 100 μm. (C) Frontal view detail of a jaw showing the epiphyseal arch and the compass-rotula complex. Labyrinthic stereom is the dominant microstructural pattern. At the epiphyseal fossa level, an increased open pattern provides suitable anchorage for the protractor muscles. Bar = 400 μm. (D) Internal view of a demi-auricle showing the attachment area of the retractor muscle. Fascicular-labyrinthic stereom prevails in the upper part of the auricle, whereas microperforate stereom is the dominant pattern in the central region. Bar = 500 μm. (E) In detail the suture of the auricle basal plate (opened complementary parts): galleried stereom runs perpendicular to the sutural surfaces. (F) Vertical section of the auricle basal plate showing the variability and complexity of its internal microarchitecture in relation to the ambulacral pore arrangement: labyrinthic and microperforate stereom prevailing. Bar = 100 μm. irm = retractor muscle insertion area, c = compass, de = demi-epiphysis, dp = demi-pyramid, ef = epiphyseal fossa, p = ambulacral pore, r = rotula, s = suture, subapical fossa, t = tooth.

to high frictional and compressive stresses, such as tubercles (figures 2(C) and (E)), lantern (figure 3(B)), rotulae (figure 3(C)) and spine bases [27, 52]. Also, the microstructure tends to be specialized in regions subjected to directional tensile stresses, i.e. the sutural areas characterized by galleried stereom, which offers a suitable insertion pattern for the attached ligament bundles (figures 2(C)–(E), 3(D) and (E)) [27, 52, 54–57, 114, 123]. On the contrary, labyrinthic stereom is found in zones subjected to multi-directional mechanical stresses, such as in the centre of the plates (figures 2(C)–(E)), lantern demi-pyramid (figures 3(B) and (C)) and in the radiating layer of camarodont spines [52, 54, 114]: according to Grun and Nebelsick (2018) labyrinthic stereom could equally distribute stresses in multiple directions, thus reducing local stresses [46].

In the past decades, the mechanical design of the stereom has been extensively studied in a two-dimensional view [16, 33, 84, 114, 129, 130, 134, 136, 137]; however, with the advent of affordable high-resolution computed tomography (CT) scanning, recent studies explored the stereom using 3D modelling reconstruction, 3D topological and structural analysis (e.g. finite element analysis, FEA). These modern methods allow detailed analyses of mechanical properties, lightweight constructions and load-bearing systems [55–57, 59, 124, 135, 138]. Accordingly, different mechanical tests on the skeletal layout demonstrated how these stereom variabilities have diverse structural implications [54, 61, 67, 90, 122, 132, 133, 139].

Hitherto, it is also important to remark that the echinoderm skeleton is a proper mesodermal tissue, and that the living stereom contains an organic stroma, consisting of cells and extracellular matrix including collagen fibres [45, 114]. The stroma significantly contributes to the integrity of the skeleton providing indispensable resistance and flexibility qualities. In general, this organic component: (1) reinforces the endoskeleton, providing greater mechanical resistance to the overall structure and continuity to the related ligaments, thus avoiding the risk of fracture at low applied forces [140]; (2) transforms the test into a flexible jointed integumental layer meaningfully reducing the impact of bending stresses [140, 141]; (3), acting as an energy absorbance system and stress-breaker interrupting the propagation of fractures due to material component discontinuity (stereom + stroma = rigid + elastic components) [52, 142–144]; (4) confers reinforcement, support and potential repair to the mineral structure [95, 103, 108, 145, 146].

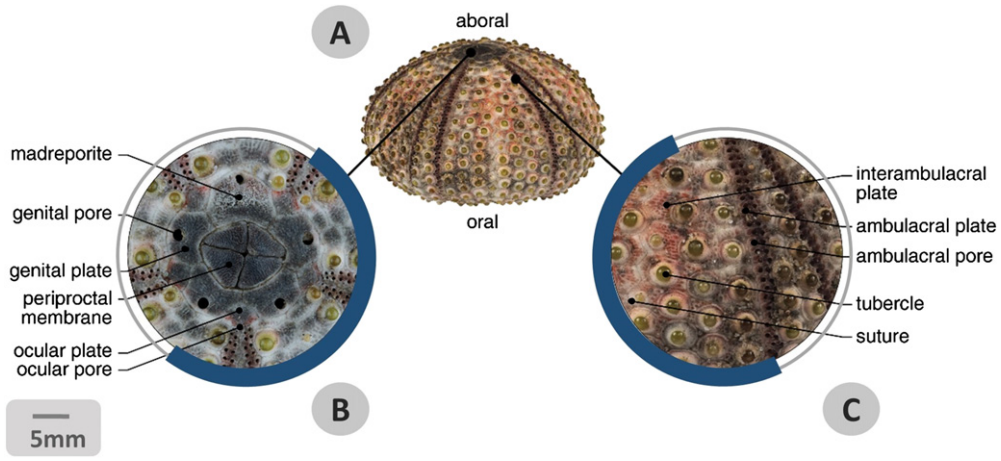

Figure 4. *Stereo-micrographs of regular echinoid test.* (A) Lateral view of *Arbacia lixula* test deprived of its soft tissue component and accessory appendages. It is possible to distinguish an 'oral' side where the mouth opens and an 'aboral' side with the anal opening. (B) Pattern of the apical pole: the detail shows the madreporite, the five genital plates with respective genital pores; five ocular plates with pores; the periproctal membrane with the centrally positioned anus. (C) Details of the lateral side of the test showing the arrangement of double columns of interambulacral and ambulacral plates, the latter ones recognizable by the tube-feet pores. All plates display articular tubercles for spines. Central sutures between two adjacent plate columns are visible. Bar = 5 mm.

3. Test

The echinoid test (figure 4) is a multi-element system consisting of a number of skeletal plates joined by sutures. These sutures can be characterized by the presence of interdigitating articular surfaces (comb-joints) often bound together by short collagenous ligaments [23, 27, 33, 46, 57, 63, 140, 147–149]. This constructional design fulfils several mechanical principles acting as a resistant, lightweight, load-bearing and load-transferring system, as well as being an attachment point for appendages. Structural strength is achieved by hierarchical constructional adaptations, such as: overall shape, plate layout and arrangement (trivalent vertex arrangement, in which three plates meet in one point), skeletal interlocking and reinforcements (e.g. internal buttressing), material distribution and stereom diversity [27, 46, 55–58, 63, 140, 149–151]. These skeletal features have been described as functional strategies which, suitably combined with adaptations of the connective tissue components, allows the echinoid test to withstand compressive, tensile and bending stresses [46, 55, 63, 109, 140, 141, 149]. In particular, collagenous sutural ligaments play a central role in increasing the structural strengthening of the test by binding rigid calcite plates at sutures [140, 141]. By measuring the breaking forces of the *Strongylocentrotus purpuratus* skeleton with intact or removed soft tissues, Ellers *et al* (1998) demonstrated that skeletons without ligaments broke at lower apically applied forces in respect to those with ligaments [140]. Different is the case of the minute clypeasteroid *Echinocyamus pusillus*, of which Grun and Nebelsick (2018) showed that soft tissues do not possess a significant structural function. However, the overall layout and plate connections between *Strongylocentrotus* and *Echinocyamus* are fundamentally different due to the extensive skeletal plate connections in the *Echinocyamus* responsible for its overall stability [46, 55–58, 149]. Some echinoid morphologies are also optimized with respect to hydrodynamic property adaptations such as the *lunulae* of sand dollars, which are considered to reduce lift when sand dollars are on the sea-floor surface and subjected to strong currents [62].

Due to the structural form and architecture of the test, echinoids have been extensively investigated in order to understand their constructional design and mechanical behaviour in detail [23, 45, 46, 55, 60, 63, 68, 107, 148, 150, 152–154]. Detailed morphospace analyses were carried out to explain and predict extinct and extant echinoid test shapes by considering possible phylogenetic, physical and mechanical factors [154–158]. Thompson (1917) in particular, carried out a pioneer study on test shape using a liquid drop analogy to describe the shape and growth of regular echinoids [158]. Ellers (1993) supported this hypothesis using the thin shell theory to explain test curvature defining the echinoid morphospace in two parameters: (1) the apical curvature; (2) a proportion of the vertical gradient of pressure to the internal coelomic pressure [156]. Seilacher (1979) proposed that the echinoid test should be analysed as a mineralized pneu-structure that grows when internal pressure exceeds external tension, varying its morphology through plate growth [23, 28]. However, Ellers and Telford (1992) measured the internal coelomic pressure in the regular sea urchin *S. purpuratus* and *Lytechinus variegatus* [159]. They found that internal pressure fluctuates rhythmically about −8 Pa and was negative for 70%

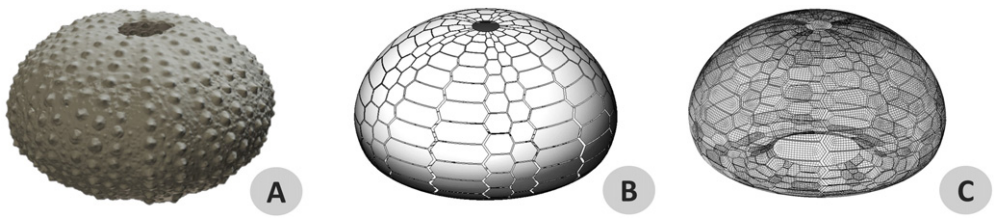

Figure 5. *Virtual models of* Paracentrotus lividus's test. (A) 3D model obtained with a photogrammetric reconstruction. (B) Parametrized geometry model with visible plates and sutures. (C) 3D mesh used for finite element analyses.

of the time, disempowering the pneu-hypothesis that requires an internal positive pressure [23, 28, 160]. These rhythmical fluctuations in pressure could be mainly caused by the lantern movements that change the curvature and tension of the peristomial membrane [159]. Telford (1985) analysed the test as a dome structure utilizing both the membrane theory and static analysis to determine its behaviour under different loads; thereby assessing the hypothesis that the test form was constructed to resist external forces [63]. On the whole, taking into account these and other studies, test form and growth were described and explained using different theoretic models, based on a total of nine hypotheses, in addition to different computational models [for review see 152]. The echinoid test growth is mainly based on two combined processes, namely: plate addition, i.e. the insertion of new plates in the apical system [21], and plate growth, based on a peripherally accretion or reabsorption of skeletal material [161]. However, the main distinctive feature of the growth process lies in the mutable collagenous tissue (MCT) present at plate sutures that can undergo rapid changes in mechanical properties (switching reversibly between stiff and compliant states) accommodating little movement and growth [for review see 162]. In particular, sutures allow growth maintaining a space between plate margins ('plate gapping') [152, 155, 163] in a manner that they do not unite and continuously expand interacting with the adjacent plates. Usually in regular echinoids, sutures remain open up to the adult stage providing the test some degree of flexibility and mechanical advantages in sustaining loads [140, 141].

Modern methods such as 3D acquisition (e.g. μCT and photogrammetry), digital modelling and simulation, e.g. FEA are recently being adopted, providing novel answers to questions about test morphology, functional performance and mechanical behaviour (figure 5) [46, 55, 57, 60, 138, 141, 164, 165]. As pioneers in this field, Philippi and Nachtigall (1996) conducted FEA-analysis describing the behaviour of the regular echinoid test (*Echinus esculentus*) under diverse loads [60]. Their studies highlighted the structural load-bearing efficiency of the test and interpreted its peculiar spherical shape as the most adapted form to sustain the tensile stresses resulting from the tube feet activity [60]. Recently, Grun and co-workers focussed on the clypeasteroid skeleton using x-ray μCT, SEM observations and physical and virtual tests in order to analyse the hierarchical structural design of the *E. pusillus* test [46, 55, 57]. They displayed in detail the mechanical properties of the test at different hierarchical levels, i.e. from the overall shape—although consisting in a discontinuous structure divided into several polygonal plates, it behaves as a monolithic structure—to the plate micro-architecture, internal supports and stereom variability, all described as specific functional devices for bearing and transferring loads.

4. Aristotle's lantern

Most regular echinoids, extant or extinct, possess a complex dental apparatus, traditionally called Aristotle's lantern. The apparatus is a biomechanical and dynamic system arranged according to perfectly pentameral symmetry and consisting of an intrinsic part, the lantern itself, and an extrinsic part, the perignathic girdle, i.e. the inner edge of the test [49–53]. These two parts are connected by muscle bundles (five pairs of retractor muscles and five pairs of protractor muscles), and ligamentous structures (peristomial membrane and five pairs of compass depressor bundles) [51] (figure 6). The lantern consists of forty anatomically distinct skeletal ossicles: ten demi-pyramids, ten epiphyses, five rotulae, ten compasses and five teeth (figure 7) [52]. They are all reciprocally joined by specific articulations (movable joints, semi-movable or rigid sutures), interconnected by articular ligaments and moved by anatomically and functionally well-defined muscles consisting in five pairs of retractor and protractor bundles, five massive inter-pyramidal muscles and five compass elevator muscles. The lantern muscular component is also represented by other muscular elements, namely myocytes of the lantern coelomic epithelium, which are involved to a minor extent (such as the thin muscle layer included in the compass depressor ligaments) [49, 53, 166–169].

Conversely, irregular echinoids do not generally possess a lantern, although in juveniles of Cassiduloida and Spatangoida this can appear as a

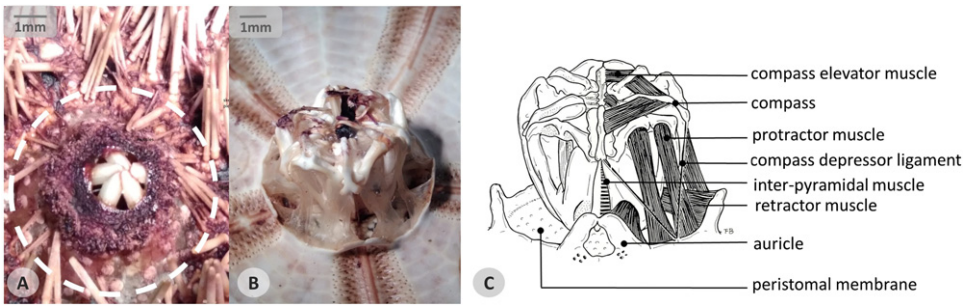

Figure 6. *Aristotle's lantern*. (A) Stereo-micrograph representing an oral view of a *Sphaerechinus granularis* sample showing in detail the peristomial membrane (dotted circle), the mouth opening and five teeth tips. (B) Stereo-micrograph of the lantern in a dissected specimen. (C) Schematic illustration of the lantern anatomy showing: five compasses, respective compass elevator muscles and depressor ligaments; protractor and retractor muscles; inter-pyramidal muscles; auricles; peristomal membrane.

Figure 7. *SEM micrographs of a real Aristotle's lantern (A–C) compared with a three-dimensional reconstruction (D–F).* (A) Front/lateral view of the lantern. The preparation method (semi-digestion of soft tissues) emphasizes the skeletal structure and permits observation of the five jaws comprising their different components. (B) Internal view of two isolated pyramids, compass and teeth. The lateral sides of the pyramid possess comb-like indented inner borders and transversely striated surfaces with regular ridges for the inter-pyramidal muscle attachment. (C) Front/lateral view of a tooth *in toto* showing a T-shaped structure (apical plumula partly removed). Bar = 1 mm. (D) A prospective view of the segmented 3D model of *Paracentrotus lividus* lantern based on micro-CT imageries. (E) A virtual section of pyramids showing teeth position. (F) Isolated teeth. Blue = pyramids and compass, yellow = teeth. Bar = 1 mm. c = compass, de = demi-epiphysis, dp = demi-pyramid, k = keel, m = midshaft, py = pyramid, pl = plumula, r = rotula, t = tooth, tp = tip.

vestigial trait, with the exceptions of adult Holectypoida and Clypeasteroida, [37, 38]. However, these persistent lanterns differ remarkably from regular lantern models: they are flattened and relatively larger, non-protrusible [38] and provided with teeth that move horizontally with respect to the substrate and designed to crush sediment rather than to grasp [170, 171]. Furthermore, in contrast to the lantern of regular echinoids, these flattened types appear to be used only for feeding: the Aristotle's lantern of regular sea urchins is employed in other important activities [33, 53, 166] such as digging, locomotion, respiration and circulation of coelomic fluid [170, 172, 173].

From Aristotle's studies [174], the unique structure of the echinoid dental apparatus has attracted the attention of many scientists [128, 175–178], but only in the last century the interest of biologists and engineers in the lantern has increased, resulting in a wide range of studies aimed to address its morphology [51–53, 179], physiology [180–182] and biomechanics [49, 49–53, 171, 173, 183–194].

Static and dynamic mechanical studies were carried out on the echinoid lantern, specifically on

its skeletal ossicles, muscular system and ligaments [50–53, 194–198], as well as, on the peristomial membrane (figure 6(A)), a flexible area consisting mainly of fibrous connective tissue surrounding the mouth and connecting the lantern to the test; with its dynamic mechanical behaviour it contributes to the lantern's stability and motility [168, 169, 199, 200]. Biomechanical models, experimental mechanical tests and computer simulations were elaborated and integrated to determine lantern movements, muscular forces and constraints during different activities in regular echinoid lanterns [49, 184, 192, 193], whereas other mechanical studies were addressed to define the biting forces developed by the dental apparatus in sand dollars [170]. It was assessed that the overall lantern can show resistance to different mechanical stresses directly or indirectly related to motor activities by means of a number of specific macro- and micro-structural adaptations. From a macrostructural perspective, the first mechanical advantage of the lantern lies in its strategic subdivision into complementary parts and correlated pieces, starting with the five multipiece jaws (figure 7), each consisting of distinct elements sutured together (two symmetrical demi-pyramids and two symmetrical demi-epiphyses) providing a perfect alveolus that contains and protects the long internal tooth ensuring its continuous growth (see below) [52] (figures 7(B) and (C)). The second advantage regards the jaws that are joined to each other by means of complex multivalent articulations endowed with specialized articular ossicles, known as rotulae [52] (figure 3(C)). They play a role in the basic opening and closing of the jaw, modulating its reciprocal tilting and swinging, and in the independent movements of the compasses (raising/lowering) on the aboral side of the lantern. These are sophisticated devices enabling the structure to be mechanically versatile, resistant and deformable [51–53, 143]. Nonetheless, the major complex adaptations were found in both skeletal microstructural variations/differentiations (figure 3) and material composition. The micromechanical design of the skeletal parts of the lantern was extensively investigated and described using SEM by Candia Carnevali and co-workers in comparative studies of the cidarid [51] and camarodont [52] lanterns. Detailed SEM studies also focussed on the micro-structure of sea urchin teeth [171, 183, 187–191, 200]. Subsequently, pyramids and teeth were further analysed employing Micro-CT imaging, which permitted the acquisition of 3D images leading to detailed insights into different species-specific geometries and microstructures [120, 131, 201–205] (figures 7(D)–(F)). These studies demonstrated that the lantern ossicles tend to have a similar basic organization in terms of adaptive stereom variability in relation to interactions with skeletal elements, ligaments or muscles, as well as, in relation to specific functional/mechanical requirements. The only exception appears to be the teeth, which display a unique microstructural architecture composed of a magnesium-bearing calcite crystal combination, such as monocrystalline plate-elements, monocrystalline fibrous-elements and polycrystalline matrix, with a variable amount of organic macromolecules (about 0.2–0.25 wt %) [103, 118, 119, 204, 206–209]. Echinoid teeth are elongated, moderately curved and highly variable in shape, and can be classified in four types (U, T, prism and wedge-shaped teeth) on the basis of their different cross-sectional profile (figure 7(C)) [21, 173, 191, 205, 210]. Along the longitudinal axis, each tooth displays three main well-differentiated parts: an aboral growing portion (plumula), a midshaft and a mature portion characterized by a sharp oral tip [191]. In order to cope with the constant tip abrasion due to the interaction with the substratum, the tooth grows continuously at the plumula level and then slowly descends along the jaw following an inner pyramidal furrow [191, 211, 212]. The mature part consists of three main zones characterized by well differentiated structures and functions: (1) the primary plate zone, organized in lamellar plates and prisms obliquely oriented with respect to the longitudinal tooth axis; (2) the stone part, formed by calcareous needles surrounded by a polycrystalline matrix and connected to the primary plates by lamellae; (3) the keel, consisting mainly of inner prisms and of outer secondary plates with peculiar carinar prolongations [118–120, 131, 202–205, 213]. Echinoid teeth were analysed in detail using various techniques, such as SEM, energy-dispersive x-ray spectroscopy analysis, x-ray micro-tomography and spectromicroscopy, as well as micro- and nanoindentation, in order to identify their microstructure, material distribution, mechanical behaviour, and chemical composition. These analyses allow an interpretation of the tooth's structural architecture and integration in relation to its complex mechanical performance [118–120, 214]. In terms of structure–function correlation, the lamellar plate components appear to be a structural solution adapted to reinforce the zones subjected to maximum compressive stress (abaxial part), whereas the fibrous elements are employed in the zones of maximum tensile stress (adaxial part: the keel) [52, 120, 202, 215]. At the tooth tip, plates and fibrous elements split off due to shearing forces consequently creating a fracture at the surrounding organic layer, generating a mechanism for self-sharpening [119, 215]. Recently, this mechanism has been further investigated using 3D techniques in-situ SEM experiments and mechanical measurements combined with a nonlinear finite-element analysis [216].

In conclusion, the tooth is adapted to minimize and respond to multiple and combined mechanical stresses such as shear, bending, torsion and buckling produced by gripping, scraping, digging and locomotion [52, 119, 120, 204, 210, 215]. The strategic employment of magnesium-calcitic material together

with its mechanical properties, in combination with the orientation of a plate-and-prism arrangement (according to the lines of force of the applied loads), result in a remarkable increase in tooth hardness (twice that of inorganic calcite itself) allowing echinoids to dig efficiently and deeply into calcareous rocks [93, 120, 201, 214, 215, 217–222].

5. Accessory appendages

Echinoids possess a variety of articulated accessory appendages [18, 32, 77] including spines, pedicellariae and sphaeridia. Spines and pedicellariae are primarily involved in defence and cleaning and can often show signs of damage and repair or can even be autotomised [223–225]. Sphaeridia are minute skeletal spheres attached to the test around the peristomial ambulacral regions (lacking in cidaroids) and are considered to be statoreceptor and proprioceptor organs. However, little is known about their morphology and physiology [39, 226, 227].

Pedicellariae are minute pincer-like structures distributed on the test surface, particularly around the peristome (figure 8) and periproct [34, 228] and are employed in different activities such as gripping, defence, covering and cleaning [34, 39, 47, 77, 229–236]. As most musculo-skeletal organs, each pedicellaria consists of a stalk, neck and two to five valves. Pedicellariae are highly variable in shape, often denticulated and sometimes armed with venom glands [77, 233, 237, 238]. Due to their variable shape, pedicellariae have been extensively used in taxonomy [5–11, 34, 239–241]. The valves show specific stereom structures and are equipped with functionally distinct muscles (abductors, adductors and flexors) and collagenous ligaments [242], which contribute to its gripping force [231, 233]. They generally react to chemical and tactile stimuli, in fact most valves are equipped with fields of chemosensitive cells [243–245]. As reported by Cavey and Markel [39], and further investigated by Coppard and co-workers [34], there are four main types of pedicellariae: (1) globiferous pedicellariae, which possess venom glands and denticulated valves with large and strong adductor muscles: they are employed as a deterrent against medium and larger predators; (2) ophicephalous pedicellariae, which possess three denticulated valves, provided with a glandular portion involved in releasing anti-fouling substances onto the test surface, and larger processes for muscle attachments enabling them to exert more strength and reduce muscle fatigue during object holding (figure 8(B)); (3) triphyllous pedicellariae, which are the smallest type of pedicellariae, are characterized by three small valves, long muscular neck and stalk: they are not sensitive to touch, have limited holding time and are employed to free test surface of minute particles (figure 8(C)); (4) tridentate pedicellariae, which are the largest and most common type, consist of three denticulated valves: they are activated by tactile stimulation and employed in removing larger particles or preventing test contamination by invertebrate pests. Past studies on pedicellariae generally consisted in descriptions of their morphology, activities and functions [228, 236, 246, 247]. Noteworthy are Campbell's studies that analyse in detail the forms and activities of the pedicellariae, identifying jaw movements, closing and opening responses (occurring after direct reflex-arc stimulation or indirect nerve stimulation), as well as, their latency, speed and duration, receptor distribution and reaction [229–233, 244].

Spines are elongated structures consisting of shaft (neck and tip), milled ring and base [80]. Each spine is joined to a respective tubercle at a ball-and-socket joint [80, 114, 248] and can be moved or firmly maintained in position due to the combined synergic action of a muscle and a ligament, known as the 'catch apparatus' [249]. The spine base enclosed by an articular envelope including a continuous outer layer of parallel muscle fibres runs from the spine to the test, and an inner layer of parallel ligament fibres with spine-test attachments. The ligaments consist of MCT [for review see 162, 250] enabled to drastically and quickly change its mechanical properties under nervous control. The presence of MCT allows the tensile state of the ligament to change rapidly from a soft and flexible condition, favouring muscle action during movement, to a rigid condition, locking the spine in position without muscle involvement, providing a fatigue/ energy-free holding mechanism [251]. Spine shape and size differ greatly from species to species: like a needle they can be long, hollow, thin and pointed as those in camarodonts; or look cylindrical or flattened, long or short, streaked or variously decorated, as in cidaroids; or moreover, appear modified and miniaturized as in irregular echinoids (figure 9) [29–33]. Spines perform different functions, such as locomotion, feeding and burrowing [29, 39, 42, 252]. They also act as a protection from physical trauma and predators [40, 253, 254] and as a stress impact reducer [43, 255–258], which is one of their main roles in the prevention of structural test damage. As reported by Tsafnat and co-workers [135] this is achieved by the spine microstructure, which improves resistance to compression. Thus, spines are structurally highly adapted to withstand different mechanical stresses, combining high impact resistance with high-energy absorption [43, 54, 59, 61, 65, 123, 132, 133, 135, 239, 258–261]. As for other skeletal components, the mechanical performance of the spines is the result of three hierarchical features, i.e. material properties, microarchitecture and shape. With regard to material properties, even if each spine behaves as a single calcite crystal with the *c*-axis oriented to its long axis [262]—as shown by polarized light microscopy [89], x-ray diffraction [107], and electron backscatter

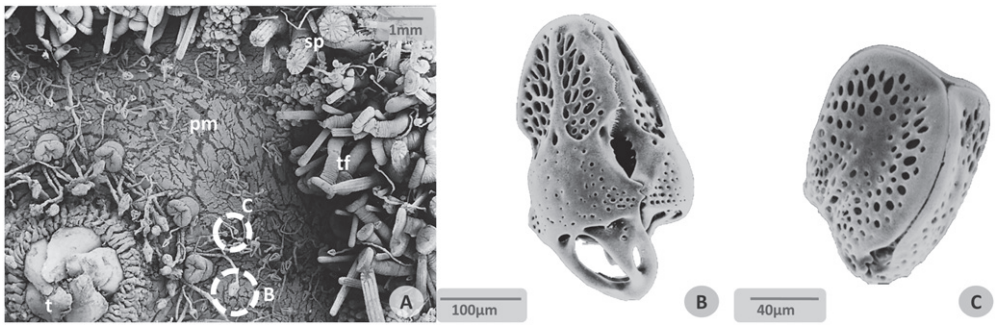

Figure 8. *SEM micrographs of pedicellariae.* (A) Oral view of *Paracentrotus lividus* showing the peristomial membrane area including the mouth with five teeth, spines, tube feet and pedicellariae. Bar = 1 mm. (B) Detail of ophicephalous pedicellaria tip. Bar = 100 μm. (C) Detail of triphyllous pedicellaria tip. (B) and (C) are identified in (A) with dotted circles. Bar = 40 μm. p = pedicellariae, pm = peristomial membrane, t = tooth, tf = tube foot, sp = spine.

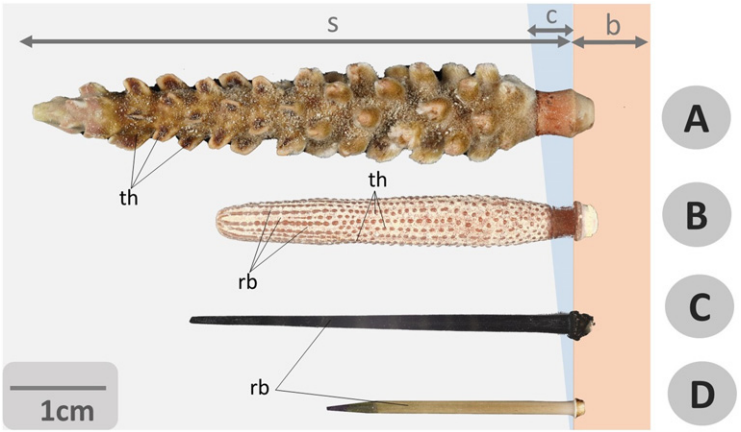

Figure 9. *Photographs of echinoid spines.* A general comparative view of spines from different species of cidaroid and camarodont regular sea urchins: relevant differences in shape, size and structure (including external, reliefs and tubercles) of shaft, tip and base are well evidenced. (A) *Chandrocidaris giganteus* (Cidaroida), (B) *Phyllacantus imperialis* (Cidaroida), (C) *Echinothrix diadema* (Camarodonta), (D) *Echinometra lucunter* (Camarodonta). Bar = 1 cm, s = c = collar, b = base, rb = ribs, s = shaft, th = thorns.

diffraction [132]—it has a mesocrystalline structure [99] consisting of a highly oriented array of nanocrystals embedded in a matrix of ACC and macromolecules [95–103, 110, 263–265]. The presence of ACC and intracrystalline macromolecules determines a typical conchoidal fracture behaviour resulting in increased fracture resistance and structural flexibility, as shown in the other skeletal parts [95–99, 110–113, 116, 121]. The material composition within the spine is highly variable (particularly the magnesium concentration), implying diverse mechanical properties in terms of elastic moduli, hardness and stiffness, and is significantly higher in the septa rather than in the spine central core [61, 132, 133]. *Apropos* the microarchitecture, spine stereom types greatly vary from species to species and along the same spine [54, 132, 133]. This leads to a very specific structural behaviour regarding the stress pattern distribution and resistance, as shown by the mechanical tests, such as three-point bending [54, 132, 266] and bulk compression tests [61, 133, 258]. Spine growth lines have also been shown to possess a mechanical significance and their presence could enhance resistance to larger force values [54, 59, 61, 67, 123, 133, 267–269]. Spines can display a peculiar morphology (widely recurrent in nature e.g. feather shafts and plant stems) consisting mainly of a hollow cylindrical porous structures, well known for their efficient mechanical advantage related to high strength-to-weight ratio [270]. In addition, many spines are characterized by sets of radial elements such as wedges [54, 59, 123], barbs and bridges, optimizing stress distribution [54, 65, 123, 135], increasing bending stress resistance [259] and preventing fracture propagation [43, 65, 132, 135, 271, 272]. In particular, in *Centrostephanus rodgersii,* a detailed analysis of spine behaviour under compression, tension and torsion loads by means of micro-CT scan and FE-Analysis has led to the identification of stress concentration patterns within spines and their role as mechanical supports [135].

In addition to the true musculo-skeletal appendages, tube feet (or podia) may also be considered because they are intrinsically related to the endoskeleton and their soft wall can include skeletal spicules [273]. Each tube foot consists of an

extensible hollow cylindrical stem with a terminal adhesive disc that includes small calcareous ossicles (rosette) [273–275]. Symmetrical pairs of podia (often used in taxonomic work) [276] emerge from the ambulacral plate test pores [25] and are moved hydraulically [277–280]. These podia are an integral part of the internal water vascular system whose major function is respiration [77], attachment [33, 277–282] and locomotion on different substrates [283], as well as, having a significant involvement in climbing, righting, covering [33], photoreception [284], food handling, burrow-building, and chemo/mechano-sensory reception [285]. The specific tube foot attachment/detachment mechanisms are related to disc adhesive and de-adhesive secretions [281, 282], whereas stem extension, flexion and retraction are caused by typical hydraulic mechanisms [277–279] involving the employment of MCT [282]. As revealed by Santos and co-workers [280–285], the adhesive secretion is composed of inorganic material (45.5%), proteins (6.4%), neutral carbohydrates (1.2%) and lipids (2.5%). The adhesive strength (force per unit area) ranges from 0.09 to 0.54 MPa [277, 279, 282]. However, the adhesive and tensile strength and overall attachment capabilities change according to the number of tube feet involved [278, 279, 286, 287], species and population analysed [278], animal body size and shape, substratum and hydrodynamic conditions [255, 278, 279, 286, 287].

6. Biomimetic applications

The term biomimetics identifies an interdisciplinary approach that combines the understanding of natural structures, systems and processes with their abstraction and translation into technological applications [69, 71–74, 288]. Biomimetics is neither an imitation of nature nor a mere copy of forms, but rather it is an in-depth comprehension and translation of natural working-principles (e.g. constructional principles of organisms), which can optimize structures in building constructions, industrial products and technical processes [74–76].

The biomimetic process is supported by a series of analogies between biological and technical structures enabling the transfer of solutions on functional bases [289–292]. Indeed, organisms and artefacts are often faced with similar problems, such as the need to increase structural stability and resistance (skeleton/frame), pressure drag reduction (streamline shape and ribbing surfaces of marine animals/hull of boats) and reaction to external conditions (nastic movement of plants/dynamic facades) [45, 103, 293]. Hence, by understanding and modelling the adaptive principles of organisms, functional solutions for innovative design inspirations or 'bioinspirations' can be identified stimulating technical implementations [69, 71, 74–76, 289–292]. Nevertheless, the constructional design of organisms is subjected to different factors such as heritage constraints and morpho-functional adaptations to biotic and abiotic factors [28]. Hence, structural and functional solutions adopted by organisms are often neither the most advantageous nor the most adapted in any situation and context, since they represent a compromise respect to evolutionary constraints [28]. A specific contextualization and optimisation of biomimetic technical solutions is therefore required and can be performed through an interdisciplinary collaboration between biology and other scientific fields (e.g. engineering, design, architecture, material science, etc) with the aid of specific tools, such as 'computer-aided design' (CAD), 'computer-aided optimization', knowledge database and algorithms [294, 295]. Consequently, the abstracted, interpreted and contextualized biological principles can lead to new inspirations for the improvement of structures and/or processes based on analogies of functions [28, 69, 71, 74–76, 288–291, 295, 296].

On the other hand, biological structures significantly differ from artificial ones in various important aspects such as: growth process generating structures with full functionality and integrity at all stages of life [158, 297]; use of basic autochthonous and sustainable materials usually characterized by heterogeneity, anisotropy and hierarchy that determine multiple functions and emerging properties [45, 109, 158, 298]; integration in the environment and ability to interact with biotic and abiotic components [299]. On pair with analogies, these differences can also lead to new design perspectives and opportunities [66, 76, 288, 300], e.g. growing structures of material ecology [301, 302] responsive dynamic façades for building constructions [288], and hybrid design products [303, 304].

The biomimetic procedure is carried out in different steps and tools [for review see 74]. Although the methods adoptable in this field are different and numerous, they can be allocated in two types of approaches: *bottom-up* and *top-down* [305, 306]. The bottom-up approach begins by identifying adaptive functional solutions in biological species, followed by the identification of the most suitable design and technological area for their transfer. This approach in literature has also been defined in diverse ways: *solution-based*, *solution-driven*, *biology push*, *biomimetics by induction* and *biology to design*. The top-down approach begins from the analysis of complex technical problems to the pursuing in nature of biological models offering novel solutions. In literature, this approach is also also known as: *problem-driven*, *problem-based*, *challenge to biology*, *technology pull* and *biomimetics by analogy* [69, 71–74,305, 306].

A general *bottom-up* is here simplified in five key steps [74]; in addition, a case study on *Paracentrotus lividus*'s test is used as an example [141, 165].

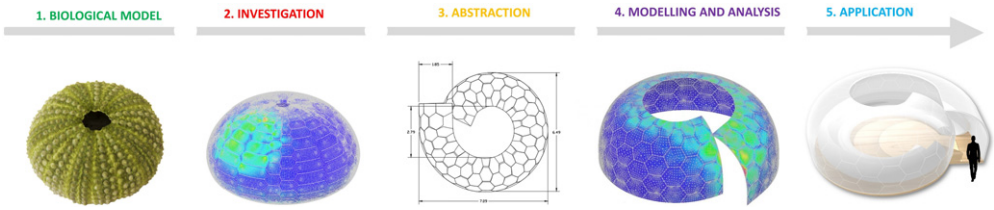

Figure 10. *Biomimetic process.* A five-step scheme of the biomimetic solution transfer: from a biological model to a technical application as exemplified by the *Paracentrotus lividus* case study. (1) Identification of a biological model: *P. lividus* test. (2) Investigation of structures, performances and functions of the biological model: a finite element analysis of the discontinuous shell structure divided into rigid hexagonal plates and semi-flexible joints. (3) Abstraction of functional mechanisms and design principles: a discontinuous shell structure with semi-flexible joints reduce bending moments. (4) Modelling and analysis determining and optimising the artificial system based on the biomimetic design principle: a 3D model of a bioinspired plexiglass open shell. (5) Biomimetic design application: the final implementation, manufacturing and testing of a bioinspired building construction (images designed by Gabriele Pontillo, Simona Landi, Lisa Vitale, Ilenia Rubino, Pasquale Ciardiello, Alessandro Fusaro of University of Campania 'Luigi Vanvitelli').

(1) *Identification of a biological model*, usually identifiable on the basis of an analogy of function and of problem solving related to the final application: *P. lividus* test model as a shell structure enduring environmental mechanical stress. (2) *Investigation* of the structure, performance and function of the biological model: FEA of the discontinuous shell structure divided into rigid hexagonal plates and semi-flexible sutures. (3) *Abstraction* of functional mechanisms and design principles: a discontinuous shell structure with semi-flexible joints reducing bending moments. (4) *Modelling and analysis* to determine and optimize the artificial system based on the biomimetic design principle: developed in design sketches and concepts, the abstracted principle is then implemented in a 3D model of a bioinspired shell structure. The technological implementation includes the choice of material, form and structure supported by virtual simulations and validations, with particular attention and adaptation to the final use. (5) *Application* and manufacturing of the bioinspired artefact: realization and final acceptance test of the pavilion inspired by *P. lividus* test (figure 10).

This process is not frequently linear due to constraints, context and scaling difficulties [288]. In this regard, the dimensional scale is a crucial factor: organisms have highly different working principles based on their dimensional realm [109, 307]. A direct scaling of the biological solution to the design dimension is not always possible, particularly in building constructions that concern not only size but also materials, external loading, life cycle, required safety range etc [288]. For this reason, the abstracted principles need to be usually translated, redesigned and contextualized to be successfully applied as new technical solutions [74, 305].

In all these approaches, knowledge integration and interdisciplinary methods and tools are essential for investigation and designing of biologically inspired structures. The study of biomimetics embraces both life and engineering disciplines [72, 289, 308]. Although, the functional characteristics and processes of nature conducting to the design of new innovative artefacts are immeasurable (e.g. bio-mineralization, growth processes and regeneration), bio-mechanical aspects are the most studied and implemented in the biomimetic field. A series of mechanical principles based on physical-mathematical laws appear to govern the structure–function relationship in organisms, as in artificial structures [45, 288]. Hence, the physical-mathematical approach can successfully describe bio-structures and their mechanical problems and performances. As shown by d'Arcy Thompson (1917), this biomechanical approach has been applied for decades [109, 158, 292, 293, 309–311]. Nevertheless, the contemporary advances in computational imaging acquisition, virtual simulation and manufacturing, together with the increased instrumental biological analysis resolution, lead to new developments for inter-disciplinary mechanical studies and biomimetics [71, 164, 295, 312]. Both biological structures and principles can be digitally analysed in depth at a micro- and nanoscale and better transferred into a multitude and various constructions and industrial products [295, 301–304, 313]. Consequently, biological structures are converted and analysed as 2D/3D models and directly connected to the technical process, becoming archetypes and/or guides for the genesis of the products [66, 295]. This creates a supporting process with efficacious tools for designers, engineers and scientists in the transition from real (organism) to digital (2D/3D archetype) and from digital (3D model) to the real entity (physical building, device or product), involving digital manufacturing techniques, which reproduce in a rigorous and functional way the analogous strategies and mathematical laws of nature [289].

These biomimetic methods and tools enable not only a successful transfer and unique application, but also a deeper understanding of biological structures, their bauplan and evolutionary process. This

enhancing knowledge of the biological realm based on biomimetic approaches is referred to as 'reverse biomimetics'. In particular, it can be conceived as an interactive spiral where the results achieved by the biomimetic approach lead to a more detailed understanding of the biological systems, representing the basis for further investigation and conducting to eventual new transfers and developments in biomimetic products [305].

In this complex framework, the skeletal components and mechanical properties of the echinoid constructional design have revealed a high potential in transferring functional bioinspired solutions into new diverse technical applications [27, 55–58, 64, 258]. Recent studies have shown how the echinoid structure can be digitally investigated generating 3D models and applying FE-analyses to identify possible structural and mechanical principles [54–58, 64, 138, 216]. In addition, based on their primary function, skeletal components have found a major and coherent field of technological application from engineering and architecture to robotics, biomedical and material sciences.

6.1. Engineering and architecture

Echinoids have a long history as inspiring models for engineering structures. This interest has recently increased, in particular regarding rotationally symmetrical constructions, defined as *echinodomes* [314, 315]. Detailed analyses of these structures including their mechanical advantages and limits have been technically described and generally well understood. Different load conditions, such as self-weight, snow loads, wind and hydrostatic loads, which can generate over- or under-pressure, can be calculated adapting constructions to specific mechanical needs and functions [315]. Echinodomes have been applied to several constructions including long-term storage containers for gas and liquid fuels such as automobile and aircraft gasoline, mineral oil, and other volatile substances [315]. The advantages of echinodomes are specifically due to their thin-shelled and double-curved architecture that results in mechanical behaviour predominantly following the membrane theory, i.e. in-plane membrane stress, reduced bending stress [315–318].

Additional studies have not only focussed on the overall shape of an echinoid test, but also on specific working principles that have recently been implemented in civil engineering. Grun *et al* [64, 319, 320] provided an overview on echinoid skeletal strategies in building constructions, by identifying in the skeleton various structural working principles on different hierarchical levels and their transfer into demonstrators. These are architectural constructions providing a proof-of-concept of specific functional aspects. Transferred structural principles based on echinoid skeleton include: (1) mosaic-arranged plates, where three plates meet in one point in order to avoid straight edges, which may cause kinking; (2) clypeasteroid-type plates, interconnected by skeletal protrusions leading to secure plate interlocking; (3) fibre-connected plates; (4) lightweight constructions; and (5) double-wall constructions as found in *Clypeaster rosaceus* [27, 64].

Both structural elements and processes leading to specific echinoid morphologies have been investigated [64]. Plate distribution has been optimized using the echinoid skeleton as a role model [64, 321] and high-performance structures, identified and analysed, have been abstracted and transferred in various ways into demonstrators. For example, the ICD/ITKE Research Pavilion 2011 (figure 11(A)) [64, 321, 322] has well demonstrated the application of three structural principles among those cited above: (1) mosaic-arranged modules, where three modules meet in one point; (2) single hollow modules, made from multi-elements reflecting a lightweight construction; (3) modules interconnected by comb-joints. Similarly, a building construction in the form of the *Landesgartenschau Exhibition Hall* 2014 was realized (figure 11(B)) [64, 321, 323–326]. A second ICD/ITKE Research Pavilion developed in 2015 (figure 11(C)) focussed on (1) modules arrangement; (2) comb-joint refinement; (3) material differentiation using textile connections; (4) light-weight construction; (5) a double-shelled structure; (6) an evolutionarily optimized growth algorithm based on the echinoid growth process by plate addition [64, 321]. In 2018, the Rosenstein Timber Pavilion was exhibited demonstrating further developed, high-performance characteristics based on echinoid skeleton, focussing on improved plate connections and optimized plate distribution [323]. Furthermore, these characteristics have also inspired the BUGA Wood Pavilion (2019, ICD/ITKE University of Stuttgart) (figure 11(D)), which was realized combining a new digital design approach for shape-funding structures with an automated robotic manufacturing using wood, thus receiving the German Design Award 2020 in the 'Excellent Architecture' category [327]. As a final example, the Rosenstein Pavilion was realized in 2019 as a functional graded concrete shell structure inspired by the stereom of *Heterocentrotus mammillatus* spines. In particular, the spine structure was investigated as a main biological model for the designing of a new functional graded porosity of a concrete shell. The abstracted principle lead to a structural efficiency improvement of the porous pavilion through a functional distribution of material in accordance to a dominant stress state, resulting 40% lighter [328].

6.2. Robotics

Various studies were carried out in the robotic sector from the analysis of echinoid biology and structures to the development of new robotic designs [329]. As an example, a sea urchin-like robot was

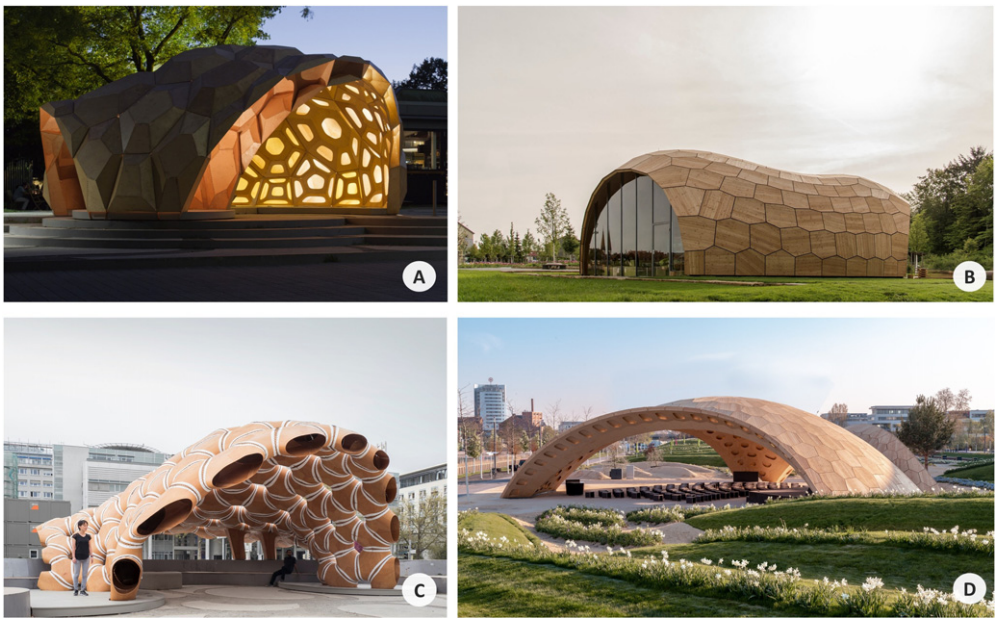

Figure 11. *Echinoids in Architecture*. Research pavilions and building constructions inspired by both morphological and mechanical principles of the genera *Clypeaster* and *Phyllacantus*. (A) ICD/ITKE Research Pavilion 2011. (B) Landesgartenschau Exhibition Hall 2014. (C) ICD/ITKE Research Pavilion 2015–16. (D) BUGA Wood Pavilion 2019 (© Photo A–D curtesy of Prof. Jan Knipper, curtesy of Prof. Jan Knipper, Institute of Building Structures and Structural Design, University of Stuttgart.

designed as a new exploration platform enhancing access to unstructured environments or dangerous places [330]. Based on tube feet and spine locomotion a flexible spherical rolling robot was developed with retractable linear actuators and pendulum-driven mechanisms. Both strategies intended to overcome the locomotion difficulties of spherical robots on irregular surfaces [330]. Echinoderm tube feet have been a source of inspiration for a wide range of soft robotic actuators [331–333]. For example, studies based on tube feet models have resulted in a magnetically controlled crawling mechanism [334] and suction device optimized for grasping rough surfaces with a rapid release mechanism [335].

An interdisciplinary team of engineers and marine biologists from the Jacobs School of Engineering (University of San Diego, California USA) used the Aristotle's lantern to develop a space exploration robot with a new gripping device for sediment sample collection (figure 12) [336]. Starting from the analysis of the opening and closing mechanism of the lantern system and the bio-exploration of keeled and non-keeled teeth, a bioinspired model was built and tested via FEA determining the efficiency of the lantern-like mechanism and confirming the structural importance of the keel in the reinforcement of the sea urchin's tooth [336].

6.3. Biomedical engineering

An optomechanical biopsy device for minimally invasive surgery was realized [337] adopting the lantern's ability to simultaneously scrape and engulf food in alternating and combined movements of opening/protrusion and closing/retraction following Scarpa's pioneering bionic model [338, 339]. The prototype was implemented as an extrudable steel tube (0.15 mm thickness and 4.3 mm diameter) provided with a cutting device, i.e. a crown-shaped system characterized by triangular teeth, designed to perform an accurate biopsy in less than a millisecond (figure 13) [337].

In the biomimetic industrial design field, especially in the biomedical sector, a recent study on the mechanical design of *P. lividus* test was carried out by an Italian team (Hybrid Design Lab, University of Campania 'Luigi Vanvitelli' and Department of Structures for Engineering and Architecture, University of Naples Federico II) [141, 165, 340]. As an example, the identified adaptive solutions of the test, as a modular system guaranteeing high integrity and structural stability in different stress conditions, were transferred into the design of two different biomedical devices: an arm-tutor and a cranial harmonizer. Shape and structure of the biological models were abstracted and applied, according to principles of functional analogy, and reproduced in parametric 3D CAD models responding to specific innovation needs expressed by users and medical experts, these are: (1) lightness, ensured by a controlled porous arrangement mimicking stereom structure; (2) resistance and stability, obtained by a discontinuous structure consisting of hexagonal modules connected by semi-flexible material reflecting the modular plated structure of *P. lividus* test and its low flexural stiffness at the sutures; (3) breathability, ensured by the high structural porosity and modular subdivision, reducing the presence of closed spaces; (4) free customization for

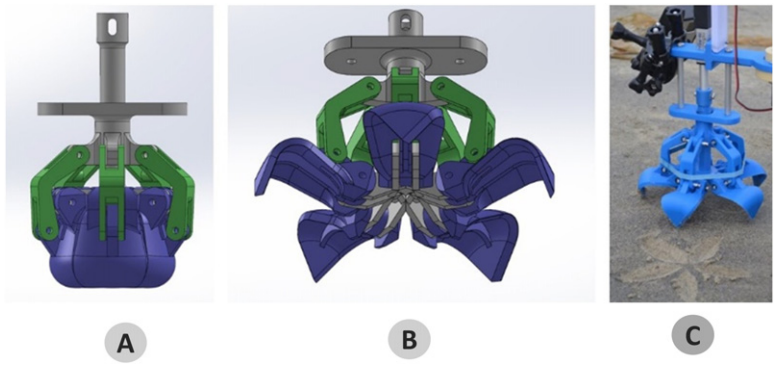

Figure 12. *Echinoids in robotics*. Gripping device for sediment sample collection inspired by Aristotle's lantern. Computer aided design images of the bioinspired device (A) closed, (B) fully opened. (C) 3D printed bioinspired device in collecting different types of sand on the beach. This image is adapted from [336].

different therapeutic needs and personal preferences, provided by an elevated versatility of shapes, geometries, colours and styles obtainable by parametric designs and digital manufacturing [340].

Pedicellariae-like devices have also been developed into new versatile tools in micromanipulation and micro-robotics fields for healthcare. Leigh and co-workers [341] designed bioinspired forceps using micro-stereolithography creating a pneumatic chamber that opens and closes the jaws by changing pressure using a syringe. The device can be used for functional grasping of microparticles and in addition can be activated hydraulically exhibiting a self-healing behaviour (isolating the damaged regions and maintaining the hydraulic mechanism efficiency) [341].

6.4. Material science

Echinoid spines revealed an important potential for innovative bio-inspired applications due to their sophisticated lightweight structure and material properties, in combination with strategic failure behaviour, high impact resistance and high-energy absorption [59, 61, 65, 133, 258, 342].

In particular, the calcitic microstructure of echinoid spines inspired: (1) new porous biomaterials useful for prosthetic applications, especially for synthetic teeth and bone replacement [343]; (2) optimized microporous vascular prostheses [344]; (3) bone implant materials obtained from the conversion of sea urchin spines to Mg-substituted tricalcium phosphate [345]; (4) model preparation of new materials by combination of crystals, polymers and functional molecules [135]; (5) a macroporous copper with greater mechanical properties [346]; (6) new functionally graded concrete [258].

In particular, the echinoid microstructure was deeply studied as a functional model to create new prosthetic materials. During the 70's, Weber *et al* [343] successfully replicated the skeletal structure of the *Heterocentrotus* spines in epoxy resin and in sodium silicate. In particular, they recognized in the arrangement of the echinoid 3D microstructure some important characteristics, which transferred into new functional prosthetic materials, were able to provide structural strength and proficient surface for tissue growth. In this regard, the stereom was identified as an optimized construction ensuring a good permeability and functional porosity, as well as a periodic minimal surface structure, in which the interface between calcite and the organic phase offers maximum contact for crystal growth [116]. Following studies involved a direct conversion from echinoderm material to bioimplant materials [345, 347]. In particular, based on a hydrothermal conversion, the spines of the echinoids *H. mammillatus* and *Heterocentrotus trigonarius* have been converted in Mg-substituted tricalcium phosphate for bone implant, maintaining the interconnected porous structure with a good bioactivity and osteoconductivity. Currently, high-resolution and advanced techniques in tissue engineering are able to reproduce new artificial scaffolds with a controlled porosity at micro and nanoscale; thus, these bioinspired solutions can be more effectively transferred creating new opportunities to realize innovative synthetic or hybrid materials [348, 349].

In addition, different studies on the cidaroid *Phyllacanthus imperialis* and *H. mammillatus* spines were carried out, showing how the specific arrangement of porous material, associated with different densities and architectures, allows these species to have extremely light and resistant structures identified as ideal models for the realization of new aluminium ceramic and concrete materials [59, 65, 67, 139, 261].

Lightweight structural ceramics have also been developed using the echinoid skeletal plates to template the synthesis of effective porous materials. As an example, porous gold structures with nearly regular 15 μm channels were prepared by coating skeletal plates with gold and dissolving them and leaving the original structural form [350, 351]. These materials with a pore dimension comparable to optical wavelengths could be applied for their optical properties or used as catalyst supports.

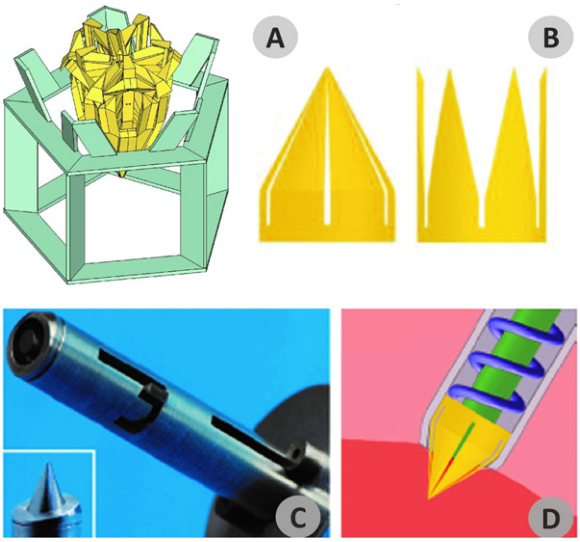

Figure 13. *Echinoids in bioengineering*. Optomechanical biopsy device inspired by Aristotle's lantern. (A) Drawing of the Aristotle's lantern bionic model. (B) Crown-shaped system characterized by triangular teeth in closed and opened positions. (C) Prototype implemented as an extrudable steel tube thick 0.15 mm and 4.3 mm in diameter. (D) Drawing of the bionspired device during surgical activity. This image is adapted from [336].

These examples highlight how biological principles can be successfully abstracted and transferred into technical applications [308]. Moreover, in a reverse biomimetic view, these analyses also provided a more detailed insight on morphology, function and integration of an organism in its ecosystem [46, 58, 269]. In particular, this allows a better understanding of an organism's adaptation to its environment, the evolutionary pathway of its structure, and its ecological and paleontological implementation [352, 353]. For example, the comprehension of the structural design, skeletal strength and weaknesses of the echinoid test consents to interpret taphonomic processes and the potential preservation of the echinoid taxa [56]. Such knowledge can help ecologists and palaeontologists to better assess the effect of taphonomic filters and biases on echinoid communities helping to determine e.g. if predatory drill holes or other biotic traces can promote the potential preservation of an echinoid [354] or lead to a loss of information.

7. Conclusion

In the course of time, the original constructional design of the echinoid endoskeleton has attracted the attention of researchers from different scientific fields due to its unique morphology, structure and material properties. Currently, these features reveal a great potential for biomimetic applications, thus motivating further investigations. This review presents a comprehensive synthesis of important studies on mechanical design and principles of echinoid skeletal structures, emphasised the efficiency of the endoskeleton at different hierarchical levels. Each constructional element of the echinoid's skeleton demonstrated to have a major application as a biological role model: the test in building construction; Aristotle's lantern and pedicellariae in grabbing devices; tube feet in robotic locomotion systems; spine stereom and biomineral composition in innovative materials. Contemporary technological advances in computational imaging, numerical simulation and fabrication have paved the way to a new era for the study of mechanical principles in organisms and their functional transfer [64, 295, 301–304, 340, 355]. Mechanical strategies and performances of the various components can be highlighted by means of different types of digital advanced techniques, such as high-resolution x-ray microcomputed tomography, imagine analysis, 3D modelling and FEA. These technologies ensure high fidelity in the acquisition of biological models, great reliability of results and high reproducibility of complex geometry and structures through the new frontiers of digital manufacturing techniques [64, 164, 301–304, 319, 356, 357].

Consequently, a new virtual biology is emerging capable to provide novel answers to questions concerning the morphology, function and evolution of living and fossil species [164, 356, 357]. In this regard, studies of mechanical design in organisms are just at an initial phase. Nonetheless, according to present literature, there is evidence of a significant increase in research [46, 55, 57, 59, 124, 135, 217, 218] regarding new future integrations between cutting-edge computer science and biology. In conclusion, this review aims to illustrate how the constructional design of echinoids reflects animal adaptations to specific mechanical needs related to different environmental stresses and lifestyles, which abstracted and transferred into engineering and industrial design,

provide functional solutions improving structures, processes, and human health.

Funding

This work was supported by the Department of Engineering, University of Campania "Luigi Vanvitelli", PhD program [National Operational Program (PON) "Research and Innovation" (R & I) 2014–2020]. Tobias B Grun's work was supported by National Science Foundation grants EAR SGP-1630475 and EAR SGP-1630276.

Acknowledgments

The Authors thank Prof. Arch. Mario Buono (University of Campania Luigi Vanvitelli, Aversa, Italy), the Zoological Station Antorn Dohrn (Naples, Italy) and the Hybrid Design Lab, (Naples, Italy) for their support. They also express thanks to John Slapcinsky (University of Florida, Florida Museum, Invertebrate Zoology) for the access to the echinoid spine collection; Ms. Laurajean Carbonaro-Tota for the English revision.

ORCID iDs

Valentina Perricone https://orcid.org/0000-0002-1410-2695

References

[1] Lefebvre B *et al* 2013 *Palaeobiogeography of Ordovician Echinoderms* vol 38 (London: Memoirs, Geological Society) pp 173–98
[2] Boivin S, Saucède T, Laffont R, Steimetz E and Neige P 2018 Diversification rates indicate an early role of adaptive radiations at the origin of modern echinoid fauna *PloS One* **13** e0194575
[3] Kier P M and Grant R E 1965 *Echinoid Distribution and Habits, Key Largo Coral Reef Reserve, Florida* vol 149 (Washington: Smithsonian Institution) pp 1–68
[4] Kroh A and Smith A B 2010 The phylogeny and classification of post-Palaeozoic echinoids *J. Syst. Palaeontol.* **8** 147–212
[5] Mortensen T 1927 *Handbook of Echinoderms of the British Isles* (London: Humpherey Milford Oxford University Press)
[6] Mortensen T 1930 Bothriocidaris and the ancestry of echinoids *Vidensk. Medd. Dansk Naturh. Foren.* **90** 313–52
[7] Mortensen T 1935 *A Monograph of the Echinoidea, II* (Copenhagen: C. A. Reitzel)
[8] Mortensen T 1937 Some echinoderm remains from the Jurassic of Wurttemburg: Det. Kgl.Dansk Vidensk. Selskab *Biol. Medd.* **13** 1–28
[9] Mortensen T 1940 *A Monograph of the Echinoidea, III* (Copenhagen: C. A. Reitzel)
[10] Mortensen T 1948 *A Monograph of the Echinoidea, IV* (Copenhagen: C. A. Reitzel)
[11] Mortensen T 1952 *A Monograph of the Echinoidea V* (Copenhagen: C. A. Reitzel)
[12] Saucède T, Mooi R and David B 2007 Phylogeny and origin of Jurassic irregular echinoids (*Echinodermata: Echinoidea*) *Geol. Mag.* **144** 333–59
[13] Smith A B, Gale A S and Monks N E A 2001 Sea-level change and rock-record bias in the Cretaceous: a problem for extinction and biodiversity studies *Paleobiology* **27** 241–53
[14] Durham J W and Melville R V 1957 A classification of echinoids *J. Paleontol.* 242–72
[15] Philip G M 1965 Classification of echinoids *J. Paleontol.* **39** 45–62
[16] Oldfield S C 1976 Surface ornamentation of the echinoid test and its ecologic significance *Paleobiology* **2** 122–30
[17] Solovjev A N 2015 Heterochrony and heterotopy in the phylogeny of sea urchins *Paleontol. J.* **49** 1582–96
[18] Lang A 1896 *Text-Book of Comparative Anatomy* (London: MacMillan)
[19] Durham J W 1966 Classification *Treatise on Invertebrate Paleontology, Echinodermata* ed R C Moore (Boulder, Lawrence: Geological Society of America and University of Kansas Press) pp 270–95
[20] Kier P M 1965 Evolutionary trends in Paleozoic echinoids *J. Paleontol.* **39** 436–65
[21] Jackson R T 1912 Phylogeny of the Echini with a revision of Palaeozoic species *Memoirs of the Boston Society of Natural History* Vol 7 (Boston: The Society) pp 1–491
[22] Loven S 1874 Etudes sur les echinoıdees *Kongliga Swenska Wetenskaps Academiens Handlingar* **11** 1–91
[23] Seilacher A 1979 Constructional morphology of sand dollars *Paleobiology* **5** 191–221
[24] Solovjev A N 2014 Symmetry, asymmetry, and dissymmetry in echinoids *Paleontol. J.* **48** 1237–42
[25] Smith A B 1980 The structure, function and evolution of tube feet and ambulacral pores in irregular echinoids *Palaeontology* **23** 39–83
[26] Allasinaz A 1995 *Paleontologia generale e sistematica degli invertebrati* (Genova: ECIG)
[27] Nebelsick J H, Dynowski J F, Grossmann J N and Tötzke C 2015 Echinoderms: hierarchically organized light weight skeletons *Evolution of Lightweight Structures: Analyses and Technical Applications* ed C Hamm (Berlin: Springer) pp 141–56
[28] Seilacher A and Gishlick A D 2014 *Morphodynamics* (Boca Raton, FL: CRC Press)
[29] Ghiold J 1979 Spine morphology and its significance in feeding and burrowing in the sand dollar, *Mellita quinquiesperforata* (*Echinodermata: Echinoidea*) *B. Mar. Sci.* **29** 481–90
[30] Mooi R 1986 Structure and function of clypeasteroid miliary spines (*Echinodermata, Echinoides*) *Zoomorphology* **106** 212–23
[31] Telford M and Mooi R 1986 Resource partitioning by sand dollars in carbonate and siliceous sediments: evidence from podial and particle dimensions *Biol. Bull.* **171** 197–207
[32] Smith A B 1980 The structure and arrangement of echinoid tubercles *Philos. Trans. R. Soc.*, B **289** 1–54
[33] Lawrence J 1987 *A Functional Biology of Echinoderms* (Baltimore: John Hopkins University Press)
[34] Coppard S E, Kroh A and Smith A B 2012 The evolution of pedicellariae in echinoids: an arms race against pests and parasites *Acta Zool.* **93** 125–48
[35] De Ridder C and Lawrence J M 1982 Food and feeding mechanisms: Echinoidea *Echinoderm Nutrition* ed M Jangoux and J M Lawrence (Rotterdam: Balkema) pp 57–115
[36] Mooi R 1990 Paedomorphosis, Aristotle's lantern, and the origin of the sand dollars (*Echinodermata: Clypeasteroida*) *Paleobiology* **16** 25–48
[37] Kier P 1974 Evolutionary trends and their functional significance in the post-paleozoic echinoids. *J. Paleontol.* **48** 1–95
[38] Smith A B 1984 *Echinoid Palaeobiology. Special Topics in Palaeontology* (London: Allen & Unwin)
[39] Cavey M J and Märkel K 1994 Echinodermata *Microscopic Anatomy of Invertebrates* ed F W Harrison (New York: Wiley) pp 345–400

[40] Guidetti P and Mori M 2005 Morpho-functional defences of Mediterranean Sea urchins, *Paracentrotus lividus* and *Arbacia lixula*, against fish predators *Mar. Biol.* **147** 797–802

[41] Lawrence H M 2001 *Edible Sea Urchins: Biology and Ecology* (Amsterdam: Elsevier)

[42] Nichols D 1967 *The Origin of Echinoderms* (London: Symposia of the Zoological Society of Academic Press)

[43] Strathmann R R 1981 The role of spines in preventing structural damage to echinoid tests *Paleobiology* **7** 400–6

[44] Telford M and Harold A S 1982 Lift, drag and camber in the northern sand *Echinoderms* 235–45

[45] Wainwright S A, Biggs W D, Currey J D and Gosline J M 1976 *Mechanical Design in Organism* (London: Edward Arnold Publishers)

[46] Grun T B and Nebelsick J H 2018 Structural design of the minute clypeasteroid echinoid *Echinocyamus pusillus R. Soc. Open Sci.* **5** 171323

[47] Von Uexkull J 1899 Die Physiologie der Pedicellariae *Z. Biol.* **37** 334–403

[48] Jensen M 1984 Functional morphology of test, lantern and tube feet ampullae system in flexible and rigid sea urchins (*Echinoidea*) *Echinodermata* ed B F Keegan and B D S O'Connor (Rotterdam: Balkema) pp 281–8

[49] Andrietti F, Carnevali M D C, Wilkie I C, Lanzavecchia G, Melone G and Celentano F C 1990 Mechanical analysis of the sea-urchin lantern: the overall system in Paracentrotus lividus *J. Zool.* **220** 345–66

[50] Andrietti F, Carnevali M D C and Wilkie I C 1993 A biomechanical comparison of the lantern of the cidarid sea-urchin Stylocidaris affinis with the typical camarodont lantern *J. Zool.* **231** 595–610

[51] Candia Carnevali M D, Wilkie I C, Lucca E, Andrietti F and Melone G 1993 The Aristotle's lantern of the sea-urchin *Stylocidaris affinis* (*Echinoida, Cidaridae*): functional morphology of the musculo-skeletal system *Zoomorphology* **113** 173–89

[52] Carnevali M D C, Bonasoro F and Melone G 1991 Microstructure and mechanical design in the lantern ossicles of the regular sea-urchinParacentrotus lividusiA scanning electron microscope study *Bolletino di zoologia* **58** 1–42

[53] Lanzavecchia G, Candia Carnevali M D, Melone G, Celentano F C and Andrietti F 1988 Aristotle's lantern in the regular sea urchin *Paracentrotus lividus*. I. Functional morphology and significance of bones, muscles and ligaments *Echinoderm Biology* (Rotterdam: Balkema) pp 649–62

[54] Grossmann J N and Nebelsick J H 2013 Comparative morphological and structural analysis of selected cidaroid and camarodont sea urchin spines *Zoomorphology* **132** 301–15

[55] Grun T B, Von Scheven M, Bischoff M and Nebelsick J H 2018 Structural stress response of segmented natural shells: a numerical case study on the clypeasteroid echinoid *Echinocyamus pusillus J. R. Soc., Interface* **15** 20180164

[56] Grun T B, Mancosu A, Belaústegui Z and Nebelsick J H 2018 The taphonomy of Clypeaster: a paleontological tool to identify stable structures in natural shell systems *neues jahrb geol palaontol abh* **289** 189–202

[57] Grun T B and Nebelsick J H 2018 Structural design of the echinoid's trabecular system *PloS One* **13** e0204432

[58] Grun T B and Nebelsick J H 2018 Technical biology of the clypeasteroid echinoid *Echinocyamus pusillus*: a review *C. T. Geo.* **7** 247–54

[59] Lauer C, Grun T B, Zutterkirch I, Jemmali R, Nebelsick J H and Nickel K G 2018 Morphology and porosity of the spines of the sea urchin *Heterocentrotus mamillatus* and their implications on the mechanical performance *Zoomorphology* **137** 139–54

[60] Philippi U and Nachtigall W 1996 Functional morphology of regular echinoid tests (*Echinodermata, Echinoida*): a finite element study *Zoomorphology* **116** 35–50

[61] Presser V, Schultheiß S, Berthold C and Nickel K G 2009 Sea urchin spines as a model-system for permeable, light-weight ceramics with graceful failure behavior. Part I. Mechanical behavior of sea urchin spines under compression *J Bionic Eng* **6** 203–13

[62] Telford M 1981 A hydrodynamic interpretation of sand dollar morphology *Bull. Mar. Sci.* **31** 605–22

[63] Telford M 1985 Domes, arches and urchins: the skeletal architecture of echinoids (*Echinodermata*) *Zoomorphology* **105** 114–24

[64] Grun T B, Dehkordi L K F, Schwinn T, Sonntag D, von Scheven M, Bischoff M and Nebelsick J H 2016 The skeleton of the sand dollar as a biological role model for segmented shells in building construction: a research review *Biomimetic Research for Architecture and Building Construction* (Berlin: Springer) pp 217–42

[65] Klang K *et al* 2016 Plants and animals as source of inspiration for energy dissipation in load bearing systems and facades *Biomimetic Research for Architecture and Building Construction* (Berlin: Springer) pp 109–33

[66] Knippers J, Nickel K G and Speck T 2016 *Biomimetic Research for Architecture and Building Construction* (Berlin: Springer)

[67] Presser V, Schultheiß S, Kohler C, Berthold C, Nickel K G, Vohrer A, Finckh H and Stegmaier T 2011 Lessons from nature for the construction of ceramic cellular materials for superior energy absorption *Adv. Eng. Mater.* **13** 1042–9

[68] Wester T 1984 *Structural Order in Space: The Plate-Lattice Dualism* (Copenhagen: Plate Laboratory, Royal Academy of Arts, School of Architecture)

[69] Speck O, Speck D, Horn R, Gantner J and Sedlbauer K P 2017 Biomimetic bio-inspired biomorph sustainable? An attempt to classify and clarify biology-derived technical developments *Bioinsp. Biomim.* **12** 011004

[70] ISO 18458:2015 2015 Biomimetics—Terminology, Concepts and Methodology, International Organization for Standardization

[71] Bhushan B 2009 Biomimetics: lessons from nature-an overview *Philos. Trans. R. Soc.,* A **367** 1445

[72] Gebeshuber I C and Drack M 2008 An attempt to reveal synergies between biology and mechanical engineering *Proc. Inst. Mech. Eng., Part* C **222** 1281–7

[73] Gebeshuber I C, Gruber P and Drack M 2009 A gaze into the crystal ball: biomimetics in the year 2059 *Proc. Inst. Mech. Eng., Part* C **223** 2899–918

[74] Fayemi P E, Wanieck K, Zollfrank C, Maranzana N and Aoussat A 2017 Biomimetics: process, tools and practice *Bioinspiration Biomimetics* **12** 011002

[75] Vincent J F V, Bogatyreva O A, Bogatyrev N R, Bowyer A and Pahl A-K 2006 Biomimetics: its practice and theory *J. R. Soc., Interface* **3** 471–82

[76] Benyus J M 1997 *Biomimicry: Innovation Inspired by Nature* (New York: Quill-William Morrow)

[77] Nichols D 1962 *Echinoderms* (London: Hutchinson & Co)

[78] Märkel K, Kubanek F and Willgallis A 1971 Polykristalliner Calcit bei Seeigeln (*Echinodermata, Echinoidea*) *Z Zellforsch* **119** 355–77

[79] Okazaki K 1975 Spicule formation by isolated micromeres of the sea urchin Embryo *Am. Zool.* **15** 567–81

[80] Märkel K and Röser U 1983 Calcite-resorption in the spine of the echinoid *Eucidaris tribuloides Zoomorphology* **103** 43–58

[81] Benson S C, Benson N C and Wilt F 1986 The organic matrix of the skeletal spicule of sea urchin embryos *J. Cell Biol.* **102** 1878–86

[82] Märkel K 1990 Biomineralization in echinoderms *Echinoderm Research* ed C de Ridder, P Dubois, M C Lahaye and M Jangoux (Rotterdam: Balkema) pp 276–82

[83] Märkel K, Röser U, Mackenstedt U and Klostermann M 1986 Ultrastructural investigation of matrix-mediated biomineralization in echinoids (*Echinodermata, Echinoida*) *Zoomorphology* **106** 232–43

[84] Smith A 1990 Biomineralization in echinoderms *Skeletal Biomineralization: Patterns, Processes and Evolutionary Trends* ed J G Carter (Princeton, NJ: Van Nostrand Reinhold) pp 413–43

[85] Killian C E and Wilt F H 2008 Molecular aspects of biomineralization of the echinoderm endoskeleton *Chem. Rev.* **108** 4463–74

[86] Clarke F W and Wheeler W C 1917 The inorganic constituents of marine invertebrates *U.S. Geol. Surv. Prof. Pap.* **102** 1–56

[87] Raup D M 1966 The endoskeleton *Physiology of Echinodermata* ed R A Boolootian (New York: Wiley) pp 379–95

[88] Smith A, Clark D, Lamare M, Winter D and Byrne M 2016 Risk and resilience: variations in magnesium in echinoid skeletal calcite *Mar. Ecol.: Prog. Ser.* **561** 1–16

[89] Solovjev A N 2014 Echinoid skeleton *Paleontol. J.* **48** 1540–51

[90] Weber J N 1969 The incorporation of magnesium into the skeletal calcites of echinoderms *Am. J. Sci.* **267** 537–66

[91] Ebert T A 2007 Growth and survival of Postsettlement sea urchins *Edible Sea Urchins: Biology and Ecology* ed J M Lawrence (Amsterdam: Elsevier) p 529

[92] Hermans J, Borremans C, Willenz P, André L and Dubois P 2010 Temperature, salinity and growth rate dependences of Mg/Ca and Sr/Ca ratios of the skeleton of the sea urchin *Paracentrotus lividus* (Lamarck): an experimental approach *Mar. Biol.* **157** 1293–300

[93] Ma Y, Cohen S R, Addadi L and Weiner S 2008 sea urchin tooth design: an 'all-calcite' polycrystalline reinforced fiber composite for grinding rocks *Adv. Mater.* **20** 1555–9

[94] Nichols D and Currey J D 1968 The secretion, structure, and strength of echinoderm calcite *Cell Structures and its Interpretation* ed S M McGee and K F A Ross (London: Edward Arnold) pp 251–61

[95] Berman A, Addadi L, Kvick A, Leiserowitz L, Nelson M and Weiner S 1990 Intercalation of sea urchin proteins in calcite: study of a crystalline composite material *Science* **250** 664–7

[96] Herman A, Addadi L and Weiner S 1988 Interactions of sea-urchin skeleton macromolecules with growing calcite crystals- a study of intracrystalline proteins *Nature* **331** 546–8

[97] Nissen H-U 1969 Crystal orientation and plate structure in echinoid skeletal units *Science* **166** 1150–2

[98] Towe K M 1967 Echinoderm calcite: single crystal or polycrystalline aggregate *Science* **157** 1048–50

[99] Seto J *et al* 2012 Structure-property relationships of a biological mesocrystal in the adult sea urchin spine *Proc. Natl Acad. Sci.* **109** 3699–704

[100] Albéric M, Bertinetti L, Zou Z, Fratzl P, Habraken W and Politi Y 2018 The crystallization of amorphous calcium carbonate is kinetically governed by ion impurities and water *Adv. Sci.* **5** 1701000

[101] Beniash E, Aizenberg J, Addadi L and Weiner S 1997 Amorphous calcium carbonate transforms into calcite during sea urchin larval spicule growth *Proc. R. Soc. London, Ser.* B **264** 461–5

[102] Magdans U and Gies H 2004 Single crystal structure analysis of sea urchin spine calcites: systematic investigations of the Ca/Mg distribution as a function of habitat of the sea urchin and the sample location in the spine *ejm* **16** 261–8

[103] Weiner S 1985 Organic matrixlike macromolecules associated with the mineral phase of sea urchin skeletal plates and teeth *J. Exp. Zool.* **234** 7–15

[104] Swift D M, Sikes C S and Wheeler A P 1986 Analysis and function of organic matrix from sea urchin tests *J. Exp. Zool.* **240** 65–73

[105] Barrett C R, Nix W D and Tetelman A S 1973 *The Principles of Engineering Materials* (Englewood Cliffs, NJ: Prentice-Hall) p 554

[106] Bandyopadhyay-Ghosh S 2008 Bone as a collagen-hydroxyapatite composite and its repair *Trends Biomater. Artif. Organs* **22** 116–24

[107] Currey J D 1999 The design of mineralized hard tissues for their mechanical function *J. Exp. Biol.* **202** 3285–94

[108] Gilbert P U P A and Wilt F H 2011 Molecular aspects of biomineralization of the echinoderm endoskeleton *Molecular Biomineralization: Aquatic Organisms Forming Extraordinary Materials* ed E G Müller (Berlin: Springer) pp 199–223

[109] Vogel S 2013 *Comparative Biomechanics: Life's Physical World* (Princeton, NJ: Princeton University Press)

[110] Lauer C, Haußmann S, Schmidt P, Fischer C, Rapp D, Berthold C and Nickel K G 2020 On the relation of amorphous calcium carbonate and the macromechanical properties of sea urchin spines *Adv. Eng. Mater.* **22** 1900922

[111] Merino M, Vicente E, Gonzales K N and Torres F G 2017 Ageing and degradation determines failure mode on sea urchin spines *Mater. Sci. Eng.*, C **78** 1086–92

[112] Albéric M *et al* 2018 Interplay between calcite, amorphous calcium carbonate, and intracrystalline organics in sea urchin skeletal elements *Cryst. Growth Des.* **18** 2189–201

[113] Aizenberg J, Hanson J, Koetzle T F, Weiner S and Addadi L 1997 Control of macromolecule distribution within synthetic and biogenic single calcite crystals *J. Am. Chem. Soc.* **119** 881–6

[114] Smith A B 1980 Stereom microstructure of the echinoid Test. *Spec. Pap. Palaeontol.* **25** 1–324

[115] Bather F A 1891 Stereom *Nature* **43** 345

[116] Donnay G and Pawson D L 1969 X-ray diffraction studies of echinoderm plates *Science* **166** 1147–50

[117] Raup D M 1965 Crystal orientations in the echinoid apical system *J. Paleont.* **39** 934–51

[118] Killian C E *et al* 2009 Mechanism of calcite co-orientation in the sea urchin tooth *J. Am. Chem. Soc.* **131** 18404–9

[119] Metzler C E *et al* 2011 Self-sharpening mechanism of the sea urchin tooth *Adv. Funct. Mater.* **21** 682–90

[120] Metzler R Z, Addadi L and Weiner S 1997 Design strategies of sea urchin teeth: structure, composition and micromechanical relations to function *Philos. Trans. R. Soc. London, Ser.* B **352** 469–80

[121] Emlet R B 1982 Echinoderm calcite: a mechanical analysis from larval spicules *Biol. Bull.* **163** 264–75

[122] Presser V, Gerlach K, Vohrer A, Nickel K G and Dreher W F 2010 Determination of the elastic modulus of highly porous samples by nanoindentation: a case study on sea urchin spines *J. Mater. Sci.* **45** 2408–18

[123] Grossmann J N and Nebelsick J H 2013 Stereom differentiation in spines of *Plococidaris verticillata, Heterocentrotus mammillatus* and other regular sea urchins *Echinoderms in a Changing World* ed C Johnson (London: Taylor & Francis) pp 97–104

[124] Müter D, Sørensen H O, Oddershede J, Dalby K N and Stipp S L S 2015 Microstructure and micromechanics of the heart urchin test from x-ray tomography *Acta Biomater.* **23** 21–6

[125] Emson R H 1985 Bone idle—a recipe for success? *Echinodermata* ed B F Keegan and B D S O'Connor (Rotterdam: Balkema) pp 25–30

[126] Nichols D 1967 The uniqueness of the echinoderms *Symp. Zool. Soc. Lond.* **20** 209–29

[127] Paul C R C 1977 Evolution of primitive echinoderms *Developments in Palaeontology and Stratigraphy* vol 5 (Amsterdam: Elsevier) pp 123–58

[128] Valentin H G 1841 Anatomie des Echinodermes *Monographies d'Echinodermes vivants et fossils* ed I Agassiz (Neuchatel: Petitpierre) pp 1–126

[129] Jensen M 1972 The ultrastructure of the echinoid skeleton *Sarsia* **48** 39–48

[130] Regis M B 1977 Organisation microstructurale du stereome de l'Echinoide *Paracentrotus lividus* (Lamarck) et ses eventuelles incidences physiologiques *C. R. Acad. Sei. Paris* **285** 189–92

[131] Stock S R, Nagaraja S, Barss J, Dahl T and Veis A 2003 X-ray microCT study of pyramids of the sea urchin *Lytechinus variegatus J. Struct. Biol.* **141** 9–21

[132] Moureaux C, Pérez-Huerta A, Compère P, Zhu W, Leloup T, Cusack M and Dubois P 2010 Structure, composition and mechanical relations to function in sea urchin spine *J. Struct. Biol.* **170** 41–9

[133] Presser V, Kohler C, Živcová Z, Berthold C, Nickel K G, Schultheiß S, Gregorová E and Pabst W 2009 Sea urchin spines as a model-system for permeable, light-weight ceramics with graceful failure behavior. Part II. Mechanical behavior of sea urchin spine inspired porous aluminum oxide ceramics under compression *J Bionic Eng* **6** 357–64

[134] Regis M B and Thomassin B A 1985 Macro-and microstructure of the primary spines in asthenosoma varium grube (*Echinothuridae: Echinoidea*): affinities with the diadematidae and toxopneustidae *Echinodermata* (Rotterdam: Balkema) pp 321–32

[135] Tsafnat N, Fitz Gerald J D, Le H N and Stachurski Z H 2012 Micromechanics of sea urchin spines *PloS One* **7** e44140

[136] Becher S 1914 Über statische Strukturen und kristalloptische Eigentümlichkeiten des Echinodermenskeletts *Verh. dtsch. zool. Ges.* **24** 307–27

[137] Becher E 1924 Über den feineren Bau der Skelettsubstanz bei Echinoiden, insbesondere über statische Strukturen in derselben *Zool. Jb. (Anat.)* **41** 179–244

[138] Chen T T 2011 Microstructure and micromechanics of the sea urchin, *Colobocentrotus atratus Ph.D Dissertation,* Massachusetts Institute of Technology

[139] Lauer C, Sillmann K, Haußmann S and Nickel K G 2018 Strength, elasticity and the limits of energy dissipation in two related sea urchin spines with biomimetic potential *Bioinsp. Biomim.* **14** 016018

[140] Ellers O, Johnson A S and Moberg P E 1998 Structural strengthening of urchin skeletons by collagenous sutural ligaments *Biol. Bull.* **195** 136–44

[141] Marmo F, Perricone V, Langella C, Pontillo G and Rosati L 2019 Bioinspired design of shell structures: a lesson from echinoids *Proc. of IASS Annual Symposia* (International Association for Shell and Spatial Structures (IASS)) 1–7

[142] Currey J D 1962 Strength of bone *Nature* **195** 513–4

[143] Gordon J E 1980 Biomechanics: the last stronghold of vitalism *The Mechanical Properties of Biological Materials, Symposia of the Society for Experimental Biology, Number XXXIV* (Cambridge: Cambridge University Press)

[144] Oaki Y and Imai H 2006 Nanoengineering in echinoderms: the emergence of morphology from nanobricks *Small* **2** 66–70

[145] Weber J, Greer R, Voight B, White E and Roy R 1969 Unusual strength properties of echinoderm calcite related to structure *J. Ultrastruct. Res.* **26** 355–66

[146] Dubois P and Chen C P 1989 Calcification in echinoderms *Echinoderm Stud.* **3** 109–78

[147] Duncan P M 1882 On some points in the morphology of the test of the temnopleuridae *Zool. J. Linn. Soc.* **16** 343–58

[148] Pearse J S and Pearse V B 1975 Growth zones in the echinoid skeleton *Am. Zool.* **15** 731–51

[149] Telford M 1985 Structural analysis of the test of *Echinocyamus pusillus* (O. F. Müller) *Echinodermata: Proc. of the Fifth Int. Echinoderm Conf.* (Galway 24–29 September 1984) ed B F Keegan and B D S O'Connor (Rotterdam, The Netherlands: Balkema) 353–60

[150] Mihaljević M, Jerjen I and Smith A B 2011 The test architecture of Clypeaster (*Echinoidea, Clypeasteroida*) and its phylogenetic significance *Zootaxa* **2983** 21–38

[151] Wester T 2002 Nature teaching structures *Int. J. Space Struct.* **17** 135–47

[152] Chakra M A and Stone J R 2011 Classifying echinoid skeleton models: testing ideas about growth and form *Paleobiology* **37** 686–95

[153] Zachos L G 2009 A new computational growth model for sea urchin skeletons *J. Theor. Biol.* **259** 646–57

[154] Zachos L G 2015 Holistic morphometric analysis of growth of the sand dollar *Echinarachnius parma* (*Echinodermata: Echinoidea: Clypeasteroida*) *Zootaxa* **4052** 151–79

[155] Dafni J 1986 A biomechanical model for the morphogenesis of regular echinoid tests *Paleobiology* **12** 143–60

[156] Ellers O 1993 A mechanical model of growth in regular sea urchins: predictions of shape and a developmental morphospace *Proc. R. Soc. London, Ser.* B **254** 123–9

[157] Raup D M 1968 Theoretical morphology of echinoid growth *J. Paleont.* **42** 50–63

[158] Thompson D A W 1917 *On Growth and Form* (Cambridge: Cambridge University Press)

[159] Ellers O and Telford M 1992 Causes and consequences of fluctuating coelomic pressure in sea urchins *Biol. Bull.* **182** 424–34

[160] Dafni J 1986 Echinoid skeletons as pneu structures *Konzepte SFB* **230** 9–96

[161] Märkel K 1981 Experimental morphology of coronar growth in regular echinoids *Zoomorphology* **97** 31–52

[162] Wilkie I C 1984 Variable tensility in echinoderm collagenous tissues: a review *Mar. Freshwater Behav. Physiol.* **11** 1–34

[163] Johnson A S, Ellers O, Lemire J, Minor M and Leddy H A 2002 Sutural loosening and skeletal flexibility during growth: determination of drop-like shapes in sea urchins *Proc. R. Soc. London, Ser.* B **269** 215–20

[164] Rayfield E J 2007 Finite element analysis and understanding the biomechanics and evolution of living and fossil organisms *Annu. Rev. Earth Planet. Sci.* **35** 541–76

[165] Marmo F, Perricone V, Pontillo G, Langella C and Rosati L 2020 Learning from nature: the echinoid strategy to design a lightweight and resistant shell structure *Proc. of the 1st Italian Workshop on Shell and Spatial Structures* (25–26th June 2020) web meeting (https://sites.google.com/view/iwss2020) (Accessed: 1 August 2020)

[166] Candia Carnevali M D, Lanzavecchia G, Melone G, Celentano F C and Andrietti F 1988 Aristotle's lantern in the regular sea urchin *Paracentrotus lividus*. II. Biomechanical approach to the interpretation of movement *Echinoderm Biology* ed R D Burke, P V Mladenov, P Lambert and R Parsley (Rotterdam: Balkema) pp 663–72

[167] Savriama Y and Gerber S 2018 Geometric morphometrics of nested symmetries unravels hierarchical inter-and intra-individual variation in biological shapes *Sci. Rep.* **8** 18055

[168] Wilkie I C, Candia Carnevali M D and Andrietti F 1993 Variable tensility of the peristomial membrane of the sea-urchin *Paracentrotus lividus* (lamarck) *Comp. Biochem. Physiol., Part A: Mol. Integr. Physiol.* **105** 493–501

[169] Wilkie I C, Candia Carnevali M D and Andrietti F 1994 Microarchitecture and mechanics of the sea-urchin peristomial membrane *Ital. J. Zool.* **61** 39–51

[170] Ellers O and Telford M 1991 Forces generated by the jaws of clypeasteroids (*Echinodermata: Echinoidea*) *J. Exp. Biol.* **155** 585–603

[171] Markel K 1970 Morphologie der Seeigelzahne. IV. Die Zahne von Laganum und Clypeaster (*Echinodermata, Echinoidea*) *Z Morph Tiere* **68** 370–89

[172] Jensen M 1985 Functional morphology of test, lantern, and tube feet ampullae system in flexible and rigid sea urchins (*Echinoidea*) *Proc. Int. Echinoderms Conf.* (Galway, Eire 1984) (Rotterdam: A. A. Balkema) 281–8

[173] Smith A B 1981 Implications of lantern morphology for the phylogeny of post-Palaeozoic echinoids *Palaeontology* **24** 779–801

[174] Leroi A M 2014 *The Lagoon: How Aristotle Invented Science* (London: Bloomsbury Publishing)

[175] Cuvier G 2012 *1817 Le Règne Animal* (English Version 1824: The Animal Kingdom, Edited by Edward Griffith) New edn (Cambridge: Cambridge University Press)

[176] Hoffmann C K 1871 Zur Anatomie der Echinen und Spatangen *Niederl Arch Zool* **1** 11–112
[177] Lovén S 1892 Echinologica *Bih Kong Svensk Vetensk Akadem Handl* **18** 1–74
[178] Tiedemann F 1816 Anatomie der Rohren-Holothurie, des pomeranzfarbigen Seesterns und des Stein-Seeigels *Landshut: Joseph Thomann* **7** 1–98
[179] Lawrence J M 2001 Function of eponymous structures in echinoderms: a review *Can. J. Zool.* **79** 1251–64
[180] Birenheide R 1992 The sea urchin lantern coelom: a circulatory system *Echinoderm Research 1991* ed L Scalera-Liaci and C Canicatti (Rotterdam: Balkema) pp 67–72
[181] Cobb J L S and Laverack M S 1966 The lantern of *Echinus esculentus* (L.) I. Gross anatomy and physiology *Proc. R. Soc. London, Ser.* B **164** 624–40
[182] Schick J M 1983 Respiratory gas exchange in echinoderms *Echinoderm Studies 1* ed M Jangoux and J M Lawrence (Rotterdam: Balkema) pp 67–110
[183] Salter S J S 1861 On the structure and growth of the tooth of Echinus *Philos. Trans. R. Soc. London* **151** 387–40
[184] Andrietti F, Candia Carnevali M D and Wilkie I C 1992 Mechanical analysis of the lantern movement in the cidarid sea-urchin *Stylocidaris affinis* (Phil.): comparison with a typical camarodont lantern *Echinoderm Research 1991* ed L Scalera-Liaci and C Canicatti (Rotterdam: Balkema) pp 95–8
[185] Birenheide R, Tsuchi A and Motokawa T 1996 To be stiff or to be soft–the dilemma of the echinoid tooth ligament. II. Mechanical properties *Biol. Bull.* **190** 231–6
[186] Jensen M 1974 The Strongylocentrotidae (Echinoidea), a morphologic and systematic study *Sarsia* **57** 113–48
[187] Markel K and Titschack H 1969 Morphologie der Seeigelzahne. I. Der Zahn von Stylocidaris affinis (Phil.) (*Echinodermata, Echinoidea*) *Z. Morph. Tiere* **64** 179–200
[188] Markel K 1969 Morphologie der Seeigelzahne. II. Die gekielten Zahne der Echinacea (*Echinodermata, Echinoidea*) *Z. Morph. Tiere* **66** 1–50
[189] Markel K 1970 Morphologie der Seeigelzahne. III. Die Zahne der Diadematoida und Echinothuroida (*Echinodermata, Echinoidea*) *Z. Morph. Tiere* **66** 189–211
[190] Markel K 1974 Morphologie der Seeigelzahne. V. Die Zahne der Clypeasteroida (*Echinodermata, Echinoidea*) *Z Morph Tiere* **78** 221–56
[191] Markel K 1970 The tooth skeleton of *Echinometra mathaei* (Blainville) (*Echinodermata, Echinoidea*) *Annot Zool Japon* **43** 188–99
[192] Wilkie I C, Candia Carnevali M D and Bonasoro F 1998 Organization and mechanical behaviour of myocyte-ligament composites in a sea-urchin lantern: the compass depressors of *Stylocidaris affinis* (*Echinodermata, Echinoida*) *Zoomorphology* **118** 87–101
[193] Wilkie I C, Candia Carnevali M D and Andrietti F 1998 Mechanical properties of sea-urchin lantern muscles: a comparative investigation of intact muscle groups in *Paracentrotus lividus* (Lam.) and *Stylocidaris affinis* (Phil.) (*Echinodermata, Echinoidea*) *J. Comp. Physiol.*, B **168** 204–12
[194] Wilkie I C, Candia Carnevali M D and Bonasoro F 1992 The compass depressors of *Paracentrotus lividus* (*Echinodermata, Echinoida*): ultrastructural and mechanical aspects of their variable tensility and contractility *Zoomorphology* **112** 143–53
[195] Ellers O and Telford M 1997 Muscles advance the teeth in sand dollars and other sea urchins *Proc. R. Soc. London, Ser.* B **264** 1525–30
[196] Ribeiro A R, Barbaglio A, Benedetto C D, Ribeiro C C, Wilkie I C, Carnevali M D and Barbosa M A 2011 New insights into mutable collagenous tissue: correlations between the microstructure and mechanical state of a sea-urchin ligament *PloS One* **6** e24822
[197] Wilkie I C, Fassini D, Cullorà E, Barbaglio A, Tricarico S, Sugni M and Carnevali M D C 2015 Mechanical properties of the compass depressors of the sea-urchin *Paracentrotus lividus* (*Echinodermata, Echinoidea*) and the effects of enzymes, neurotransmitters and synthetic tensilin-like protein *PloS One* **10** e0120339
[198] Ziegler A, Schröder L, Ogurreck M, Faber C and Stach T 2012 Evolution of a novel muscle design in sea urchins (*Echinodermata: Echinoidea*) *PloS One* **7** e37520
[199] Wilkie I C, Carnevali M C and Andrietti F 1996 Mechanical properties of the peristomial membrane of the cidaroid sea-urchin *Stylocidaris affinis J. Zool.* **238** 557–69
[200] Giesbrecht W 1880 Der feinere Bau der Seeigelzahne *Morph Jahrb* **6** 79–105
[201] Ma Y and Qi L 2010 Biomineralization of sea urchin teeth *Front. Chem. China* **5** 299–308
[202] Robach J S, Stock S R and Veis A 2005 Transmission electron microscopy characterization of macromolecular domain cavities and microstructure of single-crystal calcite tooth plates of the sea urchin *Lytechinus variegatus J. Struct. Biol.* **151** 18–29
[203] Stock S R, Barss J, Dahl T, Veis A and Almer J D 2002 X-ray absorption microtomography (micro-CT) and small beam diffraction mapping of sea urchin teeth *J. Struct. Biol.* **139** 1–12
[204] Stock S R 2014 Sea urchins have teeth? A review of their microstructure, biomineralization, development and mechanical properties *Connect. Tissue Res.* **55** 41–51
[205] Ziegler A, Stock S R, Menze B H and Smith A B 2012 Macro-and microstructural diversity of sea urchin teeth revealed by large-scale micro-computed tomography survey *Developments in X-ray Tomography VIII* vol 8506 (San Diego: International Society for Optics and Photonics) p 85061G
[206] Goetz A J, Griesshaber E, Abel R, Fehr T, Ruthensteiner B and Schmahl W W 2014 Tailored order: the mesocrystalline nature of sea urchin teeth *Acta Biomater.* **10** 3885–98
[207] Ma Y R, Weiner S and Addadi L 2007 Mineral deposition and crystal growth in the continuously forming teeth of sea urchins *Adv. Funct. Mater.* **17** 2693–700
[208] Robach J S, Stock S R and Veis A 2006 Mapping of magnesium and of different protein fragments in sea urchin teeth via secondary ion mass spectroscopy *J. Struct. Biol.* **155** 87–95
[209] Veis A, Barss J, Rahima M and Stock S 2002 Mineral related proteins of the sea urchin teeth: *Lytechinus variegatus Microsc. Res. Tech.* **59** 342–51
[210] Reich M and Smith A B 2009 Origins and biomechanical evolution of teeth in echinoids and their relatives *Palaeontology* **52** 1149–68
[211] Chen C P and Lawrence J M 1986 The ultrastructure of the plumula of the tooth of *Lytechinus variegatus* (*Echinodermata: Echinoidea*) *Acta Zool.* **67** 33–41
[212] Kniprath E 1974 Ultrastructure and growth of the sea urchin tooth *Calcif. Tissue Res.* **14** 211–28
[213] Jensen M 1979 Primary plates of sea urchin teeth (*Echinoidea*) *Vidensk. Meddr. Dansk Naturh. Foren.* **141** 7–27
[214] Laxminarayana R, Rodrigues S and Dickinson M 2012 Characterization of *E.chloroticus* sea urchin tooth using nanoindentation and SEM *Intern. J. Mod. Phys. Conf. Ser.* **6** 705–8
[215] Markel K, Gorny P and Abraham K 1977 Microarchitecture of sea urchin teeth *Forts. Zool.* **24** 103–14
[216] Espinosa H D, Zaheri A, Nguyen H, Restrepo D, Daly M, Frank M and McKittrick J 2019 *In situ* wear study reveals role of microstructure on self-sharpening mechanism in sea urchin teeth *Matter* **1** 1246–61
[217] Alderete N, Zaheri A and Espinosa H D 2019 A novel in situ experiment to investigate wear mechanisms in biomaterials *Exp. Mech.* **59** 659–67

[218] Gao H, Ji B, Jäger I L, Arzt E and Fratzl P 2003 Materials become insensitive to flaws at nanoscale: lessons from nature *Proc. Natl Acad. Sci.* **100** 5597–600

[219] Hermans J, Andre L, Navez J, Pernet P and Dubois P 2011 Relative influences of solution composition and presence of intracrystalline proteins on magnesium incorporation in calcium carbonate minerals: insight into the vital effects *J. Geophys. Res.* **116** G01001

[220] Klinger T S and Lawrence J M 1985 The hardness of the teeth of five species of echinoids (*Echinodermata*) *J. Nat. Hist.* **19** 917–20

[221] Ma Y, Aichmayer B, Paris O, Fratzl P, Meibom A, Metzler R A and Weiner S 2009 The grinding tip of the sea urchin tooth exhibits exquisite control over calcite crystal orientation and Mg distribution *Proc. Natl Acad. Sci.* **106** 6048–53

[222] Wang R 1998 Fracture toughness and interfacial design of a biological fiber-matrix ceramic composite in sea urchin teeth *J. Am. Ceram. Soc.* **81** 1037–40

[223] Carpenter W B 1847 Report on the microscopic structure of shells *Br Assoc Advan Sci Lond Rept* **17** 93–134

[224] Ebert T A 1967 Growth and repair of spines in the sea urchin *Strongylocentrotus purpuratus* (Stimpson) *Biol. Bull.* **133** 141–9

[225] Dubois P and Ameye L 2001 Regeneration of spines and pedicellariae in echinoderms: a review *Microsc. Res. Tech.* **55** 427–37

[226] Lewis J B 1968 The function of sfaeridia of sea urchins *Can. J. Zool.* **46** 1135–8

[227] Märkel K, Mackenstedt U and Röser U 1992 The sphaeridia of sea urchins: ultrastructure and supposed function (*Echinodermata, Echinoida*) *Zoomorphology* **112** 1–10

[228] Stauber M 1990 Functional morphology of the muscle-skeleton attachments in the pedicellariae of echinoids and asteroids *Echinoderm Research* 283–8

[229] Campbell A C 1973 Observations on the activity of echinoid pedicellariae: I. stem responses and their significance *Mar. Behav. Physiol.* **2** 33–61

[230] Campbell A C 1974 Observations on the activity of echinoid pedicellariae: II. Jaw responses of tridentate and ophicephalus pedicellariae *Mar. Behav. Physiol.* **3** 17–34

[231] Campbell A C 1976 Observations on the activity of echinoid pedicellariae: III. Jaw responses of globiferous pedicellariae and their significance *Mar. Freshw. Behav. Phy.* **4** 25–39

[232] Campbell A C and Rainbow P S 1977 The role of pedicellariae in preventing barnacle settlement on the sea-urchin test *Mar. Freshw. Behav. Phy.* **4** 253–60

[233] Campbell A C 1983 Form and function of pedicellariae *Echinoderm Studies* **1** 139–67

[234] Jensen M 1982 Pedicellariae in classification of echinoids *Echinoderms: Proc. of the Int. Conf.* ed J M Lawrence 111–5

[235] Haude R 1998 *Evolutionary Reconstruction of Primitive (Spinate) Echinoid Pedicellariae. Echinoderms: San Francisco* ed R Mooi and M Telford (Rotterdam: Balkema) pp 675–9

[236] Sladen W P 1880 On a remarkable form of pedicellaria and the functions performed thereby *Annals and Magazine of Natural History* **6** 101–14

[237] Brosseau O and Eléaume M 2001 Morphometric analysis of pedicellariae in Stylocidaris affinis (Philippi, 1845) (*Echinodermata, Echinoidea, Cidaridae*) using scanning electron microscopy (SEM) *Echinoderm Research* **2001** 137–42

[238] Kuwabara S 1994 Purification and properties of peditoxin and the structure of its prosthetic group, pedoxin, from the sea urchin *Toxopneustes pileolus* (Lamarck) *J. Biol. Chem.* **269** 26734–8

[239] Coppard S E and Campbell A C 2005 Taxonomic significance of spine morphology in the echinoid genera Diadema and Echinothrix *Invertebr. Biol.* **123** 357–71

[240] Coppard S E and Campbell A C 2006 Systematic significance of tridentate pedicellariae in the echinoid genera Diadema and Echinothrix *Invertebr. Biol.* **125** 363–78

[241] Mortensen T 1903 *Den Danske Ingolf Expedition. I-Echinoidea* (Copenhagen: H. Hagerup)

[242] Dubois P and Ghyoot M 1995 Integumentary resorption and collagen synthesis during regression of headless pedicellariae in *Sphaerechinus granularis* (*Echinodermata: Echinoidea*) *Cell Tissue Res.* **282** 297–309

[243] Campbell A C and Laverarck M S 1968 The response of pedicellariae from *Echinus esculentus* (L) *J. Exp. Mar. Biol. Ecol.* **2** 191–214

[244] Chia F S 1970 Histology of the globiferous pedicellariae of *Psammechinus miliaris* (*Echinodermata: Echinoidea*) *J. Zool.* **160** 9–16

[245] Oldfield S C 1975 Surface fine structure of the globiferous pedicellariae of the regular echinoid, *Psammechinus miliaris* Gmelin *Cell Tissue Res.* **162** 377–85

[246] Lambert A, De Vos L and Jangoux M 1984 Functional morphology of the pedicellariae of the asteroid *Marthasterias glacialis* (*Echinodermata*) *Zoomorphology* **104** 122–30

[247] Peters B H and Campbell A C 1987 Morphology of the nervous and muscular systems in the heads of pedicellariae from the sea urchin *Echinus esculentus* L *J. Morph.* **193** 35–51

[248] Smith D S, del Castillo J, Morales M and Luke B 1990 The attachment of collagenous ligament to stereom in primary spines of the seaurchin *Eucidaris tribuloides Tissue Cell* **22** 157–76

[249] Takahashi K 1967 The catch apparatus of the sea-urchin spine I. Gross histology *J. Fac. Sci. Univ. Tokyo, Sect. IV* **11** 109–20

[250] Wilkie I C 1996 Mutable collagenous tissues: extracellular matrix as mechano-effector *Echinoderm Studie* vol 5 ed M Jangoux and J M Lawrence (Rotterdam: AA. Balkema) pp 61–102

[251] Motokawa T 1983 Mechanical properties and structure of the spine- joint central ligament of the sea urchin, *Diadema setosum* (Echinodermata, Echinoidea) *J. Zool.* **201** 223–35

[252] Goodbody I 1960 The feeding mechanism in the sand dollar *Mellita sexiesperforata* (Leske) *Bio. Bull.* **119** 80–6

[253] Kowalewski M and Nebelsick J H 2003 Predation on recent and fossil echinoids *Predator–Prey Interactions in the Fossil Record* (*Topics in Geobiology Series*) (New York: Plenum Press/Kluwer)

[254] Verling E, Barnes D K A and Crook A C 2005 Smashing tests? Patterns and mechanisms of adult mortality in a declining echinoid population *Mar. Biol.* **147** 509–15

[255] Cohen-Rengifo M, Moureaux C, Dubois P and Flammang P 2017 Attachment capacity of the sea urchin *Paracentrotus lividus* in a range of seawater velocities in relation to test morphology and tube foot mechanical properties *Mar. Biol.* **164** 79

[256] George M N and Carrington E 2014 Spine reorientation influences drift particle capture efficiency in sea urchins *J. Exp. Mar. Bio. Ecol.* **461** 102–6

[257] Stewart H L and Britton-Simmons K H 2011 Streamlining behaviour of the red urchin *Strongylocentrotus franciscanus* in response to flow *J. Exp. Biol.* **214** 2655–9

[258] Toader N, Sobek W and Nickel K G 2017 Energy absorption in functionally graded concrete bioinspired by sea urchin spines *J. Bionic Eng.* **14** 369–78

[259] Burkhardt A, Hansmann W, Märkel K and Niemann H J 1983 Mechanical design in spines of diadematoid echinoids (*Echinodermata, Echinoidea*) *Zoomorphology* **102** 189–203

[260] David B, Stock S R, De Carlo F, Hétérier V and De Ridder C 2009 Microstructures of Antarctic cidaroid spines: diversity of shapes and ectosymbiont attachments *Mar. Biol.* **156** 1559–72

[261] Schmier S *et al* 2016 Developing the experimental basis for an evaluation of scaling properties of brittle and

'Quasi-Brittle' biological materials *Biomimetic Research for Architecture and Building Construction* ed J Knippers, K G Nickel, T Speck (Berlin: Springer) pp 277–94
[262] Su X, Kamat S and Heuer A H 2000 The structure of sea urchin spines, large biogenic single crystals of calcite *J. Mater. Sci.* **35** 5545–55
[263] Addadi L and Weiner S 1985 Interaction between acidic proteins and crystals: stereochemical requirements in biomineralization *Proc. Natl Acad. Sci. USA* **82** 4110–4
[264] Albeck S, Aizenberg J, Addadi L and Weiner S 1993 Interactions of various skeletal intracrystalline components with calcite crystals *J. Am. Chem. Soc.* **115** 11691–7
[265] Weiner S and Addadi L 1997 Design strategies in mineralized biological materials *J. Mater. Chem.* **7** 689–702
[266] Lu G, Lu G Q and Xiao Z M 1999 Mechanical properties of porous materials *J. Porous Mater.* **6** 359–68
[267] Dotan A and Fishelson L 1985 Morphology of spines of *Heterocentrotus mammillatus* (*Echinodermata: Echinoidae*) and its ecological significance *Echinodermata: Proc. of the Int. Echinoderm Conf.* ed B F Keegan and B D S O'Connor (Galway 24–29 Sept 1984) (Rotterdam: A.A. Balkema) pp 253–60
[268] Nickel K G *et al* 2008 Seeigelstachel als Modell Fur stoffdurchlassige Einschlagschutzsysteme *Bionik: Patente aus der Natur* eds A B Kesel, D Zehren BremenGTBB pp 29–39
[269] Regis M B and Thomassin B A 1983 Anomalies de structure des radioles de *Heterocentrotus mammillatus* (*Echinodermata: Echinoidea*) en microcosme *in vitro Mar. Biol.* **75** 89–98
[270] Karam G N and Gibson L J 1994 Biomimicking of animal quills and plant stems: natural cylindrical shells with foam cores *Mater. Sci. Eng.*, C **2** 113–32
[271] Stock S R, Carlo F and Ebert T A 2009 Bridges between radial wedges (septs) in two diadematid spine types *Echinoderms* (Boca Raton, FL: CRC Press) pp 263–326
[272] Stock S R, Ebert T A, Ignatiev K and De Carlo F 2006 Structures, structural hierarchy, and function in sea urchin spines *Developments in X-ray Tomography V* vol 6318 (San Diego: International Society for Optics and Photonic) p 63180A
[273] Smith A B 1979 Peristomial tube feet and plates of regular echinoids *Zoomorphologie* **94** 67–80
[274] Coleman R 1969 Ultrastructure of the tube foot wall of a regular echinoid, Diadema antillarum Philippi *Zeitschrift für Zellforschung und Mikroskopische Anatomie* **96** 162–72
[275] Florey E and Cahill M A 1977 Ultrastructure of sea urchin tube feet *Cell Tissue Res.* **177** 195–214
[276] Mooi R 1986 Non-respiratory podia of clypeasteroids (*Echinodermata, Echinoides*) *Zoomorphology* **106** 21–30
[277] Santos R and Flammang P 2006 Morphology and tenacity of the tube foot disc of three common European sea urchins species: a comparative study *Biofouling* **22** 187–200
[278] Santos R and Flammang P 2007 Intra- and interspecific variation of attachment strength in sea urchins *Mar. Ecol.: Prog. Ser.* **332** 129–42
[279] Santos R and Flammang P 2008 Estimation of the attachment strength of the shingle sea urchin, *Colobocentrotus atratus*, and comparison with three sympatric echinoids *Mar. Biol.* **154** 37–49
[280] Santos R, Hennebert E, Varela Coelho A and Flammang P 2009 The echinoderm tube foot and its role in temporary underwater adhesion *Functional Surfaces in Biology* (Berlin: Springer) vol 2
[281] Flammang P 1996 Adhesion in echinoderms *Echinoderm Studies* vol 5 ed M Jangoux and J M Lawrence (Rotterdam: Balkema) pp 1–60
[282] Santos R, Gorb S, Jamar V and Flammang P 2005 Adhesion of echinoderm tube feet to rough surfaces *J. Exp. Biol.* **208** 2555–67
[283] Ruppert E E, Fox R S and Barnes R D 2004 *Invertebrate Zoology* (Belmont, CA: Thomson-Brooks/Cole) pp 890–6
[284] Ullrich-Lüter E M, Dupont S, Arboleda E, Hausen H and Arnone M I 2011 Unique system of photoreceptors in sea urchin tube feet *Proc. Natl Acad. Sci.* **108** 8367–72
[285] Santos R, Barreto A, Franco C and Varela Coelho A 2013 Mapping sea urchins tube feet proteome—a unique hydraulic mechano-sensory adhesive organ *J. Proteomics* **79** 100–13
[286] Sharp D T and Gray I E 1962 Studies on factors affecting the local distribution of two sea urchins, *Arbacia punctulata* and *Lytechinus variegatus Ecology* **43** 309–13
[287] Märkel K and Titschack H 1965 Das Festhaltevermögen von Seeigeln und die Reißfestigkeit ihrer Ambulacralfüßchen *Sond Zeit Naturw* **10** 268
[288] Knippers J and Speck T 2012 Design and construction principles in nature and architecture *Bioinsp. Biomim.* **7** 7015002
[289] Gruber P 2011 *Biomimetics in Architecture* (Berlin: Springer)
[290] Nachtigall W 2002 *Bionik: Grundlagen und Beispiele für Ingenieure und Naturwissenschaftler* (Berlin: Springer)
[291] Lebedew J S 1983 *Architektur und Bionik* (Berlin, Germany: Verlag für Bauwesen)
[292] Vogel S 1998 *Cats' Paws and Catapults: Mechanical Worlds of Nature and People* (New York: WW Norton & Company) p 289
[293] Wainwright S A 1988 Form and function in organisms *Am. Zool.* **28** 671–80
[294] Deb K 2001 *Multi-Objective Optimization Using Evolutionary Algorithms* (New York: Wiley)
[295] Hamm C 2015 *Evolution of Lightweight Structures: Analyses and Technical Applications* vol 6 (Berlin: Springer)
[296] Vincent J F 2016 Biomimetics in architectural design *Intell. Build. Int.* **8** 138–49
[297] Goriely A 2017 Basic aspects of growth *The Mathematics and Mechanics of Biological Growth* (New York: Springer) pp 3–26
[298] Chen Q and Pugno N M 2013 Bio-mimetic mechanisms of natural hierarchical materials: a review *J. Mech. Behav. Biomed.* **19** 3–33
[299] Odum E P and Barrett G W 1971 *Fundamentals of Ecology* (Philadelphia, PA: Saunders)
[300] Vincent J 2009 Biomimetic patterns in architectural design *Archit. Des.* **79** 74–81
[301] Oxman N 2010 Material-based design computation *Doctoral Dissertation* Massachusetts Institute of Technology
[302] Oxman R and Oxman R 2014 *Theories of the Digital in Architecture* (Abingdon: Routledge)
[303] Oxman N 2010 Structuring materiality: design fabrication of heterogeneous materials *Arch. Des.* **80** 78–85
[304] Langella C and Perricone V 2019 Hybrid biomimetic design for sustainable development through multiple perspectives *GRID-Mimarlık Planlama ve Tasarım Dergisi* **2** 44–76
[305] Speck T, Speck O, Beheshti N and McIntosh A C 2008 Process sequences in biomimetic research *Design and Nature* **114** 3–11
[306] Cohen Y H and Reich Y 2016 *Biomimetic Design Method for Innovation and Sustainability* (Berlin: Springer)
[307] West G B 2017 *Scale: The Universal Laws of Growth, Innovation, Sustainability, and the Pace of Life in Organisms, Cities, Economies, and Companies* (London: Penguin)
[308] Drack M, Limpinsel M, de Bruyn G, Nebelsick J H and Betz O 2017 Towards a theoretical clarification of biomimetics using conceptual tools from engineering design *Bioinsp. Biomim.* **13** 016007
[309] Abzhanov A 2017 The old and new faces of morphology: the legacy of D'Arcy Thompson's 'theory of transformations' and 'laws of growth' *Development* **144** 4284–97

[310] Vogel S and Wainwright S A 1969 *A Functional Bestiary: Laboratory Studies about Living Systems* (Reading, MA: Addison-Wesley)
[311] Vogel S 1994 *Life in Moving Fluids: The Physical Biology of Flow* (Princeton, NJ: Princeton University Press)
[312] Cerrolaza M, Shefelbine S and Garzón-Alvarado D 2017 *Numerical Methods and Advanced Simulation in Biomechanics and Biological Processes* (New York: Academic)
[313] Oxman N 2011 Variable property rapid prototyping: inspired by nature, where form is characterized by heterogeneous compositions, the paper presents a novel approach to layered manufacturing entitled variable property rapid prototyping *Virt. Phys. Prototyp.* **6** 3–31
[314] Ibidapo O and Ab S 1981 Echinodome: some approaches to the analysis of the drop-shaped tank *Mech. Res. Commun.* **8** 47–54
[315] Bramski C 1981 *Rotations Symmetrische Tropfenförmige Behälter* (Berlin: Wilhelm Ernst and Sohn)
[316] Bletzinger K, Maute K, Reitinger R and Ramm E 2012 Institut für Baustatik, Universität Stuttgart *IUTAM Symp. on Optimization of Mechanical Systems: Proc. of the IUTAM Symp.* (Stuttgart, Germany 26–31 March 1995) vol 43 (Berlin: Springer) p 49
[317] Tamboli A, Xing M and Ahmed M 2000 Structural theory *Building Design and Construction Handbook* 6th edn ed F Merritt and J T Ricketts (NewYork: McGraw-Hill) pp 232–419
[318] Schodek D and Bechthold M 2015 *Structures* (London: Pearson)
[319] Grun T B, von Scheven M, Geiger F, Schwinn T, Sonntag D, Bischoff M, Knippers J, Menges A and Nebelsick J H 2017 Bauprinzipien und Strukturdesign von Seeigeln—Vorbilder für bioinspirierte Konstruktionen *Baubionik—Biologie Beflügelt Architektur* ed J Knippers, U Schmid and T Speck (Stuttgart: Naturkundemuseum Stuttgart) pp 82–9
[320] Grun T B, von Scheven M, Geiger F, Schwinn T, Sonntag D, Bischoff M, Kinppers J, Menges A and Nebelsick J H 2019 Building principles and structural design of sea urchins: examples of bio-inspired constructions *Biomimetics for Architecture* ed J Knippers, U Schmid and T Speck (Basel: Birkhäuser) pp 104–15
[321] Schwinn T, Sonntag D, Grun T, Nebelsick J H, Knippers J and Menges A 2019 Potential applications of segmented shells in architecture *Biomimetics for Architecture* ed J Knippers, U Schmid and T Speck (Basel: Birkhäuser) pp 116–25
[322] Knippers J, Menges A, Gabler M, La Magna R, Waimer F, Reichert S and Schwinn T 2013 From nature to fabrication: biomimetic design principles for the production of complex spatial structures *Advances in Architectural Geometry* ed L Hesselgren, S Sharma, J Wallner, N Baldassini, P Bompas and J Raynaud (Berlin: Springer) pp 107–22
[323] Schwinn T, Krieg DO and Menges A 2014 Behavioral Strategies: Synthesizing design computation and robotic fabrication of lightweight timber plate structures *Proc. 34th Ann. Conf. Association for Computer Aided Design in Architecture (ACADIA)* Los Angelespp 177–88
[324] Li J and Knippers J 2015 Segmental timber plate shell for the Landesgartenschau exhibition Hall in schwäbisch Gmünd—the application of finger joints in plate structures *Int. J. Space Struct.* **2** 123–39
[325] Krieg O D, Schwinn T, Menges A, Li J M, Knippers J, Schmitt A and Schwieger V 2015 Biomimetic lightweight timber plate shells: computational integration of robotic fabrication, architectural geometry and structural design *Advances in Architectural Geometry 2014* (Berlin: Springer) pp 109–25
[326] Schmitt A and Schwieger V 2015 *Quality Control of Robotics Made Timber Plates* (Sofia: Fédération Internationale Géometès) pp 17–21
[327] Sonntag D, Aldinger L, Bechert S and Knippers J 2019 Lightweight segmented timber shell for the Bundesgartenschau 2019 in Heilbronn *Proc. of IASS Annual Symposia* vol 2019 No. 26 (International Association for Shell and Spatial Structures (IASS)) 1–8
[328] Kovaleva D, Gericke O, Kappes J, Tomovic I and Sobek W 2019 Rosenstein Pavilion: design and structural analysis of a functionally graded concrete shell *Structures* **18** 91–101
[329] Stiefel K and Barrett G 2018 Sea urchins as an inspiration for robotic designs *J Mar Sci Eng* **6** 112
[330] Ocampo-Jiménez J, Muñoz-Meléndez A and Rodríguez-Gómez G 2014 Extending a spherical robot for dealing with irregular surfaces: a sea urchin-like robot *Adv. Robotics* **28** 1475–85
[331] Mao S, Dong E, Zhang S, Xu M and Yang J 2013 A new soft bionic starfish robot with multi-gaits *2013 IEEE/ASME Int. Conf. on Advanced Intelligent Mechatronics* (IEEE) pp 1312–7
[332] Shepherd R F, Ilievski F, Choi W, Morin S A, Stokes A A, Mazzeo A D, Chen W M and Whitesides G M 2011 Multigait soft robot *Proc. Natl Acad. Sci.* **108** 20400–3
[333] Umedachi T, Vikas V and Trimmer B A 2013 Highly deformable 3-d printed soft robot generating inching and crawling locomotions with variable friction legs *2013 IEEE/RSJ Int. Conf. on Intelligent Robots and Systems* (IEEE) pp 4590–5
[334] Bell M A, Pestovski I, Scott W, Kumar K, Jawed M K, Paley D A, Majidi C, Weaver J C and Wood R J 2018 Echinoderm-inspired tube feet for robust robot locomotion and adhesion *IEEE Robot. Autom. Lett.* **3** 2222–8
[335] Sadeghi A, Beccai L and Mazzolai B 2012 Design and development of innovative adhesive suckers inspired by the tube feet of sea urchins *Proc. of the IEEE Conf. on Biomedical Robotics and Biomechatronics (BioRob)* (Rome, Italy 24–27 June) pp 617–22
[336] Frank M B *et al* 2016 A protocol for bioinspired design: a ground sampler based on sea urchin jaws *J. Visualized Exp.* **110** e53554
[337] Jelínek F, Goderie J, van Rixel A, Stam D, Zenhorst J and Breedveld P 2014 Bioinspired crown-cutter—the impact of tooth quantity and Bevel type on tissue deformation, penetration forces, and tooth collapsibility *J Med Devices* **8** 041009
[338] Scarpa G 1985 Modelli di Bionica *Capire la Natura Attraverso i Modelli* ed V Rossi (Bologna, Italy: Zanichelli Editore S.p.A) pp 13–74
[339] Trogu P 2019 Giorgio Scarpa's model of a sea urchin inspires new instrumentation *Leonardo* **52** 146–51
[340] Perricone V and Pontillo G 2020 Echinoidesign: ricerca biunivoca applicata al riccio di mare *Bionica e Design: Carmelo di Bartolo e il centro ricerche ed esperienze memorabili da 30 protagonisti (A. Arruda)* (Sao Paulo: Blucher) pp 371–80
[341] Leigh S J, Bowen J, Purssell C P, Covington J A, Billson D R and Hutchins D A 2012 Rapid manufacture of monolithic micro-actuated forceps inspired by echinoderm pedicellariae *Bioinsp. Biomim.* **7** 044001
[342] Nickel K G, Klang K, Lauer C and Buck G 2018 Sea urchin spines as role models for biologic design and integrative structures *Highlights of Applied Mineralogy* (Berlin: de Gruyter & Co) pp 1–14
[343] Weber J N, White E W and Lebiedzik J 1971 New porous biomaterials by replication of echinoderm skeletal microstructures *Nature* **233** 337–9
[344] Hiratzka L F, Goeken J A, White R A and Wright C B 1979 *In vivo* comparison of replamine form, silastic, and bioelectric polyurethane arterial grafts *Arch. Surg.* **114** 698–702
[345] Vecchio K S, Zhang X, Massie J B, Wang M and Kim C W 2007 Conversion of sea urchin spines to Mg-substituted

tricalcium phosphate for bone implants *Acta Biomater.* **3** 785–93
[346] Lai M, Kulak A N, Law D, Zhang Z, Meldrum F C and Riley D J 2007 Profiting from nature: macroporous copper with superior mechanical properties *Chem. Commun.* **34** 3547–9
[347] Roy D M and Linnehan S K 1974 Hydroxyapatite formed from coral skeletal carbonate by hydrothermal exchange *Nature* **247** 220–2
[348] Sanchez C, Arribart H and Guille M M G 2005 Biomimetism and bioinspiration as tools for the design of innovative materials and systems *Nat. Mater.* **4** 277–88
[349] Piticescu R M, Cursaru L M, Ciobota D N, Istrate S and Ulieru D 2019 3D bioprinting of hybrid materials for regenerative medicine: implementation in innovative small and medium-sized enterprises (SMEs) *JOM* **71** 662–72
[350] Meldrum F C and Seshadri R 2000 Porous gold structures through templating by echinoid skeletal plates *Chem. Commun.* **1** 29–30
[351] Seshadri R and Meldrum F C 2000 Bioskeletons as templates for ordered, macroporous structures *Adv. Mater.* **12** 1149–51
[352] Drack M, Betz O and Nebelsick J H 2020 Konstruktionslehre, Bionik und phylogenetische Aspekte *Phylogenie, Funktionsmorphologie und Bionik* ed I Werneburg and O Betz (Tübingen: Scidinger Hall) pp 27–38
[353] Grun T and Nebelsick J 2020 Adaptation abgeflachter Seeigel an ihr Habitat und deren strukturelle Interpretation *Phylogenie, Funktionsmorphologie und Bionik* ed I Werneburg and O Betz (Tübingen: Scidinger Hall) pp 141–6
[354] Tyler C L, Dexter T A, Portell R W and Kowalewski M 2018 Predation-facilitated preservation of echinoids in a tropical marine environment *Palaios* **33** 478–86
[355] Langella C 2019 *Design e Scienza* (Trento: LIST Lab)
[356] Richmond B G, Wright B W, Grosse I, Dechow P C, Ross C F, Spencer M A and Strait D S 2005 Finite element analysis in functional morphology *The Anat. Rec.* **283** 259–74
[357] Dumont E R, Grosse I R and Slater G J 2009 Requirements for comparing the performance of finite element models of biological structures *J. Theor. Biol.* **256** 96–103