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A biomechanical approach to the ontogeny and phylogeny of echinoids

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INTRODUCTION

This paper reviews evidence concerning echinoid skeletal growth and morphology, reintroducing a 70-year-old approach, the biomechanical regulation of ontogenetic and phylogenetic skeletal morphogenesis.

The question whether shape is predetermined, selected to a well-defined set of environmental conditions; or plastic, responsive to a variable set of physical conditions by ontogenetic modification, is of cardinal importance in morphology. D'Arcy Thompson (1917, 1942, p. 15) was the first to show how,

> the forms of living things, and that of the parts of living things, can be explained by physical considerations . . . and no organic forms exist save such as are in conformity with physical and mathematical laws

and

> . . . it is not merely the nature of the motions . . . which we must interpret in terms of force, but also the conformation of the organism itself, whose permanence or equilibrium is explained by the interaction or balance of forces, as described in statics.

These pioneering ideas remained dormant for several decades, possibly because they could not be accommodated easily within the prevailing doctrine, that morphological adaptation is genetically determined. Thompson's mechanical analogies had been considered, at the most, as illustrations of the effective way natural selection eliminates those forms that do not conform to mechanical and economical principles of design.

The rapid progress in the fields of genetics and molecular biology held the promise that all possible phenotypic variability, of which natural selection makes use in evolution, will be amply accommodated within the unlimited capacity of the genome. And yet, after so many years of enormous efforts invested in these disciplines, one still wonders

> what controls the process of morphogenesis, or . . . how does a one-dimensional genetic code ultimately specify a tri-dimensional organism (Edelman 1984, p. 118).

A possible solution to this dilemma is that organisms yield to mechanical stimuli throughout their morphogenesis, and that the gene complement that favours such responsiveness is retained by selection (Bonner 1961). The expression of the genes is, according to this view, limited to the realm of constructive materials and regulative processes, whereas morphogenesis itself is self-organized, influenced by the internal constraints and the physico-mechanical external environment. Growing organisms follow mechanical principles and design, through which the nature of the constructional elements and materials affects their ultimate structural morphology (Stevens 1976; Wainwright *et al.* 1976), in processes that are largely independent of the direct control by the genome.

This is best illustrated by the prevalence of pneumatic structures in nature (Bach *et al.* 1976). Cells, organs, and frequently also whole organisms, assume the typical shape of the *pneu*—a globular or roundish inflated body, filled with fluid or gas, which is under higher than ambient

Echinoderm phylogeny and evolutionary biology (ed. C. R. C. Paul and A. B. Smith). Clarendon Press, Oxford, 1988.

hydrostatic pressure, and surrounded by a flexible strained membrane. The pneu paradigm is equally common among living and non-living forms, and is known for its being optimized by a mechanical force-balance. By adopting this principle organisms attain mechanical stability and save energy.

Echinoderms have a skeleton unlike that of any other invertebrate group. In contrast to the inert molluscan shell, or the ephemeral disposable arthropod carapace, they have a mesodermal endoskeleton, composed of skin-embedded plates, and an internal fluid-filled cavity, the coelom. Seilacher (1979) coined the term 'mineralized pneu' for permanently fixed pneus, such as egg-shells and foraminiferal chambers. The echinoid test consists of a still more complex form of pneu—a *plastic mineralized pneu.* Thompson (1917, 1942, p. 945) was the first to describe its pneumatic nature:

> The sea-urchin shell consists of a membrane, stiffened into rigidity by calcareous deposits, which constitute a beautiful skeleton of separate, neatly fitting ossicles. The rigidity of the shell is more apparent than real, for the entire structure is, in a sluggish way, plastic; inasmuch as each little ossicle is capable of growth, and the entire shell grows by increments to each and all of these multitudinous elements, whose individual growth involves a certain amount of freedom to move relative to one another; in a few cases the ossicles are so little developed that the whole shell appears soft and flexible. The viscera of the animal occupy but a small part of the space within the shell, the cavity being mainly filled by a large quantity of watery fluid, whose density must be very near to that of external sea-water. . . . While the sea-urchin is alive, an immense number of delicate tube-feet, with suckers at their tips, pass through minute pores in the shell, and, like so many long cables, moor the animal to the ground. They constitute a symmetrical system of forces, with one resultant downward, in the direction of gravity, and another outwards in the radial direction; and if we look upon the shell as originally spherical, both will tend to depress the sphere into a flattened cake . . . This is precisely the condition which we have to deal with in a drop of liquid lying on a plate; the form of which is determined by its own uniform surface-tension, plus gravity, acting against the internal hydrostatic pressure.

ECHINOID SKELETAL MORPHOGENESIS RESEARCH

Thompson's biomechanical approach concerning echinoid morphology was adopted by a few echinoderm students, whose morphometric observations seemed to conform with his hypotheses, while most students of morphology ignored it altogether.

In the last two decades echinoid skeletal research progressed appreciably. Many studies dealt with skeletal growth and allometry (Moss and Meehan 1968; Raup 1968; Kobayashi and Taki 1969; Régis 1969, 1973; Jensen 1969; Ebert 1967, 1975, 1982; Seilacher 1979; Smith 1980, 1984; Dafni 1980, 1983*b*; Dafni and Erez 1982, 1987*a,b*). Jensen (1972), Pearse and Pearse (1975), Märkel (1975, 1976, 1981) and Smith (1978, 198 used enhanced microscopy techniques to observe echinoid microstructure, while Weber *et al.* (1969), Emlet (1982) and Telford (1985) studied the mechanical design of the skeleton. Okazaki (1975) described the morphogenesis of normal and abnormal larval skeletons. Although all these students contributed immensely to our knowledge of both inherited and adaptable morphology, only few attempted to elucidate the regulatory mechanisms which determine echinoid skeletal morphogenesis.

Among the latter were Raup (1968), and Moss and Meehan (1967, 1968). Raup, an ardent supporter of Thompson's ideas, tried to formulate the growth process, using computer simulation. As to the factors which control skeletal growth, he believed that while rates of new plate addition and plate peripheral accretion are species-specific, skeletal morphology as a whole is a product of the ontogenetic development of the plate mosaic. H argued that

> growth (of plates) occurs around their periphery and is concentrated in those regions where pressure counter to this growth is lowest (p. 58).

In other words, the growth of echinoid plates is controlled by sutural compression. Moss and Meehan (1968), who found an analogy between the growth of echinoid tests and the growth of mammalian clavarial bones, believed that plate growth is triggered by surface tensional stresses rather than compression. They speculated that the individual echinoid plates, as well as the whole test, grow passively in response to the expansion of the enclosed living mass, which they termed 'functional matrix', a mechanically obligatory process.

The differential growth and downward shift of plates represent, according to Moss and Meehan (1968), ontogenetic changes in an internal reference register, rather than a real movement of plates.

Although Moss and Meehan's approach is more consistent with the pneu paradigm, close examination of test plates, and their design, indicates the existence of sutural compression in some areas of the test (Seilacher 1979; Telford 1985; Dafni 1986*a*), supporting Raup's proposition. It is argued below that sutural compression and tension are in fact two sides of the same coin.

Telford (1985) analysed the architectual design of the echinoid skeleton, comparing it to an arched dome, physically adapted to carry its own weight and sustain a variety of external forces. Loads, which weigh down the test dome are transformed, according to Telford's analysis, into compressional stresses in the radial (= longitudinal) direction and tensile stresses circumferentially. He argued that some allometric trends in growth of regular echinoids, namely growing taller with size and forming thicker radial ribs on the inner surface of the test, as well as the ample sutural collagen fibres lashed across the longitudinal sutures, all represent adaptations to minimize circumferential tension, which may tear the test at the sutures.

A somewhat different attitude is held by the author (Dafni 1986*a*). He views the echinoid test as a mineralized pneumatic structure, which is ontogenetically modified by means of differential growth. Growth, according to this hypothesis, is controlled by sutural stresses, tension, and to a lesser extent compression, brought about by either external or internal forces.

The plastic response of the coronal test to changes in the physico-mechanical environment, without endangering the structural stability, is enabled by the combination of compression-resistant mineral plates and flexibility of the sutural fibres, which are tensed during expansion. Hence, the articulated echinoid test combines the properties of a flexible pneu with those of a rigid mineralized pneu.

Environment influences echinoid growth inducing morphological plasticity, through resource allocation (Ebert 1980). Food deficiency was found to suppress growth rates, but at the same time cause exaggerated growth of food gathering apparatuses, possibly due to an energy trade-off between the various body components (Ebert 1980).

A BIOMECHANICAL MODEL OF ECHINOID GROWTH AND MORPHOGENESIS

Based on the above approach, a model has been presented, describing skeletal growth and morphogenesis of echinoid tests in terms of a biomechanical force-balance resulting from the pneu principle and the activity of various contractile and elastic tissue elements (Dafni 1986*a*). Essentially, this model integrates Moss and Meehan's (1968) and Raup's (1968) models. The principles of this model, as well as evidence supporting it, are summarized here to justify phylogenetic considerations presented later.

According to this model the echinoid test, characterized by an external plate armour, increases its volume owing to internal expansion, which forces the mineral plates apart, inducing growth and calcification along their free margins. During intensive growth, tension prevails throughout the coronal surface, whereas a non-growing mineralized pneu relies upon its skeletal framework for rigid support. Under the latter conditions the external static and loading forces are being absorbed by the combination of compression-resistant plates and tension-dispersing collagen fibres (Strathmann 1981; Telford 1985).

The various mechanical components of the model which affect the alleged 'stress-balance', controlling the peripheral growth of plates and, ultimately, the entire test morphology, are (Fig. 14.1): (1) the inner hydrostatic pressure; (2) the mechanical pull of the ambulacral tube-feet; (3) the tethering effect of mesenterial threads; and (4) the muscles of the Aristotle's lantern, which pull the lowermost part of the test centrally. A somewhat more passive role is played by the sutural collagen fibre system (Dafni 1986*a*), to keep the test plates together, and to enable plastic response.

The following aspects of the model have been observed or experimentally tested.

Tension-induced growth

Observations suggest that tensile stresses control the peripheral growth of test plates by forming sutural gaps, which are spanned by fast-growing

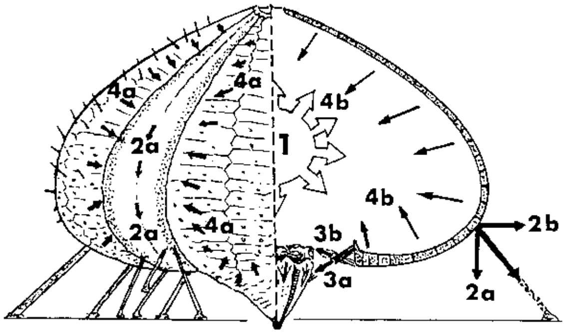

Fig. 14.1 Schematical presentation of the proposed model, showing the various components of force involved in echinoid morphogenesis, side view (left) and section (right): (1) expansion of the inner mass; (2) forces produced by the tubefeet; (3) lantern muscles (retractor and protractor); (4) mesenterial threads pulling at the plates in the plate level (4a) or centripetally (4b) (Dafni 1986*a*).

trabecular rods; and that trabecular growth ceases when compression develops along non-stretched sutures (Dafni 1986*a*). This has been tested experimentally by culturing skeletal explants in seawater and, using an artificial spring device, stretching their plates either along the horizontal (latitudinal) or the vertical (meridional) sutures. The pattern of uptake of ^{45}Ca of the stretched sutures, as well as the vertical/horizontal calcification ratio of vertically stretched explants were significantly greater than those of the non-stretched or horizontally stretched control, thus supporting this hypothesis (Dafni 1985).

Slow-growing, confined sutures are characterized by a denser trabecular mesh while rapid trabecular growth, in stretched sutures, usually yields a more spacious stereom (Dafni 1986*a*). It has also been shown that well-fed urchins produced a fast-growing well-aligned galleried stereom, whereas starved urchins produce a labyrinthic stereom with poorly-aligned trabeculae (Pearse and Pearse 1975). Since growth-lines are microstructurally defined as alternations between different stereom types, often showing different porosity (Smith 1980), and rapid growth is associated with sutural tensional stresses (Dafni 1985, 1986*a*), the various mesh sizes or alignment types may reflect different physico-mechanical sutural conditions.

Echinoid species with collagen embedded test plates, not confined to a tight mosaic, usually lack periodic growth-lines. This is consistent with Smith's (1980) observation that coronal plates of diadematoid and echinothurioid echinoids, with a more mouldable test, lack growth banding. It is also noteworthy that the peristomial plates of *Tripneustes*, fully enveloped by connective tissue, are roundish rather than polygonal, and have no growth-lines (J. Dafni, unpublished results). The scarcity of growth zones in the tightly-arranged cidaroid plates (Smith 1980), may be explained by their extremely slow growth (Ebert 1982).

Possible role of internal hydrostatic pressure

Internal higher-than-ambient pressure is an inherent property of the pneu paradigm. Furthermore, a flexible plate armour makes sense only if being hydrostatically supported (Seilacher 1986). It has been suggested (Dafni 1986*b*) that the flexibility [illegible] the sutural binding of the plates plays a decisive role during growth, when the internal mass expands, while their resistance to compression is exhibited mainly when the test is overwhelmed by external loads. The plate stereom seems to be well-adapted to these conditions, since porosity is known to reduce the difference between tensional and compressional strength (Emlet 1982). This dual function, a rapidly expanding structure interlocked by sutural fibres at one time and a dome-shaped solid armature of exceptional mechanical stability (Telford 1985) at other times, is perhaps the most remarkable structural property of the echinoid mineralized pneu. Hence, Telford's (1985) static model, implying morphological adaptation to external loads, and Dafni's (1986*a*) model, emphasizing the role of internal forces, do not conflict, since both apply to different states, or temporal phases, of the same structure.

Alternations from one state to another are associated with the echinoid's metabolism. Starvation, low temperature or physiological stress inhibit skeletal growth (Kobayashi and Taki 1969; Pearse and Pearse 1975; Dafni and Tobol in press), even causing 'negative growth' (Ebert 1967, 1968). Temporal growth fluctuations, recorded as growth-line patterns (Jensen 1969; Smith 1980), may well reflect fluctuations in the internal pressure. Moreover, since there is no conclusive evidence for peripheral resorption of plates (Märkel 1981), it is speculated that slight negative growth in the size order of < 5 per cent in the test diameter, described by several authors (Ebert 1967, 1968; Régis 1979; Dafni 1984), may result from reduction of the internal pressure and test shrinkage due to contraction of the sutural gaps.

Specialized metabolic processes are employed by various invertebrates in an effort to control their internal fluid pressure, thus controlling their body form and size under the different osmotic conditions, or for special functions (e.g. carapace shedding in arthropods, Prosser 1973).

In analogy to these animals, Dafni (1986*b*) suggested that higher than ambient internal hydrostatic pressures are obtained either by muscles, which brace the body wall and confine the internal fluid, or by maintaining internally higher osmotic pressures, that attract water inflow through the semi-permeable body wall. Rapid expansion of the test can also be obtained by temporarily reducing its surface tension, possibly by 'softening' the tensility of the sutural collagen fibres (see below).

Proving the existence of internal pressures is rather tricky. First, we already suggested that during periods of non-growth the sutural gaps close, which corresponds to a state of zero internal pressure. Secondly, these pressures may well be small, and act for relatively shorter periods. Thirdly, the plates themselves are enclosed in pneu-like capsules (see below) which further complicates the model. Confirming this model and measuring the pressures involved may be a challenging task.

Tube-feet activity

Thompson (1917) suggested that test profiles of sea urchins are modified by the mechanical interaction with the substratum, via the ambulacral tube-feet, and that stronger adherence yields flatter profiles (i.e. lower height *v.* horizontal diameter, H/D). Observations by Moore (1935), McPherson (1965), and Lewis and Storey (1984) support this hypothesis, showing that regular echinoids exposed to surf conditions, where firm adherence is essential, tend to be flatter than those living in low energy habitats. Similarly, Nichols (1982) found, in a biometric study among different populations of *Echinus esculentus*, a significant increase in H/D ratio with increasing water depth, possibly due to calmer water conditions.

Dafni (1983*a*) showed that two sub-species of *Tripneustes gratilla*, *T. g. gratilla*, and *T. g. elatensis*, differ in their typical habitat. *T. g. gratilla*, which inhabits seagrass meadows and sandy areas, has a typically high H/D and domed shape, while *T. g. elatensis*, which lives mainly in rocky shores, is flatter.

Testing Thompson's hypothesis, Dafni (1986*a*) transferred live urchins of the latter sub-species from their natural hard substratum into a sand-bottomed artificial habitat. As expected, they grew taller by ~ 5 per cent, while those which were carried back to their original habitat, after this treatment, showed a reversed trend. Moreover, the differential calcification pattern of these urchins was changed appreciably (Dafni and Erez 1987*b*). The hypothesis that the test profile is affected by tube-feet activity is supported also by the observation that abnormal echinoid tetramers, with only four ambulacra and, accordingly fewer functional tube-feet, are on the average taller than their normal conspecifics (Dafni 1986*a*).

Role of internal tethering elements

Ideal 'mineralized pneus' are expected to grow by uniform increase of each individual plate, in response to the expansion of the internal fluid (Moss and Meehan 1968). The actual pattern is anything but uniform; some plates grow rapidly in one peripheral direction, while in other directions they grow slowly or do not grow at all. Save for some species-specific differences, similar patterns are exhibited by most regular echinoids (Deutler 1926; Raup 1968; Märkel 1975, 1976, 1981; Dafni 1984; Dafni and Erez 1982, 1987*a*). According to the proposed model the internal pressure is transformed into a differential tensile stress pattern which determines plate growth pattern. The same process is shared by most species of regular echinoid (Dafni 1986*a*).

Dafni and Erez (1982) compared the plate peripheral patterns with the activity and spatial distribution of the ambulacral tube-feet and various tethering tissue elements, which, as suggested by earlier observations, pull the plates and affect their confinement patterns. Among the latter were lantern muscles and the mesenterial threads, which fasten the alimentary system to the inner surface of the coronal test (Dafni 1983*b*, 1986*a*). Using the radioisotope ^{45}Ca, they measured the calcification patterns of individual *T. gratilla* plates, along a vertical column, in all four directions. Assuming that test plates, arranged in 'close-packing' patterns (Raup 1968), grow more in tensed sutures than in compressed sutures, they transformed the measured rates into growth vectors, and studied their patterns (Fig. 14.2). They found that for the resultant vector of each plate there is a contractile element (mesenterial

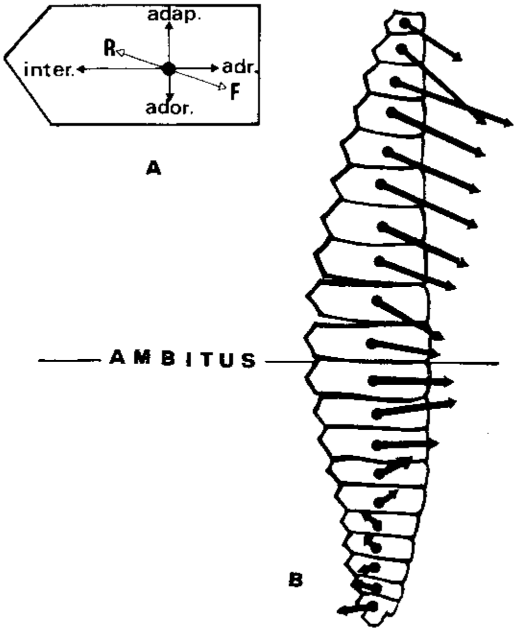

Fig. 14.2 (A) Vector addition of the differential calcification rates at the different directions in an interambulacral plate of *Tripneustes gratilla elatensis*. R, resultant growth vector, F–inferred tensional force vector. (B) Map of F vectors for plates along the interambulacral column (Dafni and Erez 1982).

thread or tube-foot), attached to the plate, which pulls the plate in a direction 180° to the growth direction. For example, an ambulacral plate, pulled downwards by tube-feet attached to it, will grow more in its upper margins. This analysis also confirmed observations, indicating a similar biomechanical effect caused by the mesenterial threads, owing to the presence of scattered muscle fibres in these threads (Dafni 1983*b*).

The homology between the mesenterial threads and the unique mesenterial muscles (Jensen 1985), that flex the elastic tests of various echinothuriid species, supports the hypothesis about the biomechanical role of the threads (Dafni 1983*b*). Indicative of the mesenterial pull are conspicuous protuberances on the internal surface of the interambulacral plates, where these threads are attached (Plate 14.1). Their orientation corresponds with that of the above-mentioned vectors (Dafni 1983*b*; Dafni and Erez 1987*b*).

These facts lead to the conclusion that these elements form an 'equilibrium of forces', which determines echinoid growth pattern. Hence, deformities in urchins exposed to pollution (Allain 1978; Dafni 1980, 1983*b*; Dafni and Erez 1987*b*), may well result from deviation from this equilibrium.

Although not treated in this analysis, lantern muscles also play a biomechanical role, pulling the lowermost part of the test, the peristome margin, internally. This pull is possibly counteracted by lantern growth, which limits peristome marginal growth, as indicated by the positive allometry of the lantern size, as compared to the peristome diameter (Dafni and Erez 1987*a*).

The soap-bubble analogy

This is another illustration of the biomechanical nature of echinoid plate growth. Thompson (19) and Raup (1968) pointed out the resemblance between echinoid plate patterns and soap-bubble configurations: equal-sized plates share straight suture lines, whereas unequal plates have curved sutures, with the smaller plates arching into their larger neighbours. The typical plate patterns greatly change ontogenetically, while they move downwards and change their size relative to their neighbours.

Using the pneu paradigm, the soap-bubble analogy of the plates is easily explained (Dafni 1986*a*); the highly porous plate is contained in a membrane-surrounded 'capsule', containing the quasi-fluid stroma, which serves as a template for calcification (Moss and Meehan 1967). Thus, the echinoid plates are continuously growing densely-packed pneus, fixed by calcification within the boundaries of their capsule, and the test as a whole is best described as a complex mineralized pneu. It has also been demonstrated that whole tests, as well as their dead, decalcified plate capsules, t[illegible] to retain their typical bubble-like form, owing to the flexible membrane and fluid content (Dafni 1986*b*) (Plate 14.2).

Although plate growth is controlled by the physico-mechanical relations between them, observations suggest that the plate plasticity is constrained by the mineral phase. When two neighbouring plates grow at different rates, the curvature of their common sutures usually reverses, as predicted by the soap-bubble analogy. Lowermost, non-growing coronal plates often fail to change their plate curvature, since this must involve resorption, which is extremely rare in echinoid tests (Dafni 1986*a*).

Pollution induced deformities

Skeletal deformities may serve as 'natural experiments', demonstrating the effect of regulatory factors on the developing body. Three types of echinoid deformities, developed in severely polluted sites, affecting the majority of *T. gratilla elatensis* populations there (Dafni 1980, 1983*b*; Dafni and Erez 1987*b*), were interpreted using the above model

(1) The extremely flat tests with aboral depression apparently resulting from a mechanical collapse of the aboral 'dome' (Dafni 1983*b*) (Plate 14.3).
(2) Five symmetrically arranged pits, superimposed on the aboral depression, coincidental with the uppermost attachment of the mesenterial threads to the test plates, appeared in many of the deformed tests. They are believed to be caused by internal tethering (Dafni 1983*b*).
(3) Another deformity, excessively tall and irregular-shaped urchins (Dafni 1980), was often accompanied by abnormal narrowing of the ambulacra, forming 'ambulacral pinches' (Koehler 1924; Jackson 1927; Moore 1974), which occurred in 69 per cent of the abnormally tall urchins (Plate 14.4). It has been suggested that the pinches result from a 'strangling effect', imposed by internal tethering (Dafni 1984; Dafni and Erez 1987*b*).

Deviations from radial symmetry

It has been suggested that deviation from the round symmetry of regular echinoids is associated with imperfect development of the ambulacral system (Chadwick 1924). Since the latter component produces a biomechanical effect, Dafni (1986*a*) proposed that the perfect pentaradial symmetry of regular echinoids corresponds to a symmetrical arrangement of the ambulacral system. He tested this hypothesis by inactivating one ambulacral ray of normal *T. gratilla elatensis*, severing the radial vessel and the associated neural system. The normal development of this ambulacrum was arrested, and the apical plate system became strongly oval. Consequently, the entire test became bilaterally symmetrical, with the damaged ambulacrum and the elongated apical diameter in the plane of symmetry. This was followed also by considerable skewedness and curving of the non-damaged ambulacra towards the damaged one (Plate 14.5).

Similarly, it has been shown that 'imperfect' tetramers, sea-urchins having four intact ambulacral rays, with a normal five-jawed lantern, always show a rudimentary fifth ambulacrum near the peristome, the growth of which was apparently impeded by physical damage during early post-larval ontogeny (Dafni 1986*a*).

OTHER ENVIRONMENTALLY-ASSOCIATED TRAITS

A number of additional morphological traits seem to be linked with the physico-mechanical environment.

Thicker tests

Echinoid species living in surf-exposed habitats tend to have thicker tests (Ebert 1982). Moreover, populations of the same species living in more exposed habitats usually have more massive tests than those from sheltered habitats (Moore 1935; Lewis and Storey 1984).

Thicker spines

Echinoids living in wave exposed reef habitats have thicker spines than conspecific populations inhabiting sheltered areas (Dotan and Fishelson 1985).

Roundness

The relationship between the long and short diameter in the oval-shaped echinoid *Echinometra lucunter* is also linked to the mechanical interaction between the test and the habitat (Lewis and Storey 1984).

PHYLOGENETIC CONSIDERATIONS

Teratological phenomena and experimentally induced deformities have often been used to provide evidence for a phylogenetic relationship between distantly related taxa, offering insight into evolutionary processes.

It is tempting to speculate, observing the striking resemblance of the abnormal *T. gratilla elatensis* phenotypes to those of more specialized echinoid taxa (e.g. irregulars), that these deformities actually 'mimic' phylogenetic development occurring in this group.

Jackson (1927) suggested that abnormal variation may serve as a clue to developmental processes. He grouped the various deformities in five types, related to phylogenetic trends:

(1) *arrested variation*—characters appearing in juveniles of one species, which are shared by adults of allied primitive species;
(2) *progressive variation*—not typical of the species, but which occurs typically in more specialized species;
(3) *regressive variation*—bearing characters of primitive species of the same lineage;
(4) *parallel variation*—variation shared by taxonomically unrelated species;
(5) *aberrant variation* that bears no resemblance to any known phylogenetic trend.

Jackson argued that even the aberrant variation is apt to follow definite lines of its own.

The following discussion highlights ontogenetic 'progressive variations' in the test shape among anomalous regulars, showing their correspondence to recognized phylogenetic trends among the Echinoidea. The rationale for this deduction is that the same constructional 'repertoire' is available for both processes.

Phylogenetic trends within the Echinoidea are discussed in greater detail by Durham (1966), Kier (1974) and Smith (1984). The present discussion is restricted to changes which affected the whole test and other characteristics related to our model.

ADAPTIVE RADIATION OF TEST MORPHOLOGY IN THE REGULARIA

Since earliest Palaeozoic echinoids ('Perischoechinoidea') were almost spherical (Durham 1966; Smith 1984), rigid or flexible (e.g. *Bothriocidaris* and *Eothuria*), it is safe to assume that echinoid phylogeny started with a non-specialized spherical archetype, evolving into the varied forms which inhabit today's marine environments.

Deviation from the globular archetype

Incorporation of the pneu paradigm into the echinoid archetype was facilitated by the flexible articulation of up to 3000 plates (Kier 1974). Hence, a major constraint ruling echinoid evolution was the mechanical balance emanating from the morphology (relative size, thickness, imbrication), ontogeny (vertical shift), and spatial organization of the plate shield. Other constraints which may have influenced this process were the pentamery imposed by the ambulacral pull; the mechanical properties and spatial arrangement of the alimentary system, festooned from the inner surface of the test; and possibly also the amount and organization of the sutural collagenous fibres, which provide echinoid tests with a varied degree of flexibility (Wilkie 1984).

While whole test morphology and plate close-packing patterns are biomechanically determined, the sculpture of the external surface and the shape of other skeletal appendages (spines, pedicellaria, etc.), as well as structures emanating from functional adaptation, are evidently under direct genetic control.

A perfect globular shape is of no advantage for epibenthic echinoids, because they must orient their body to the substratum for feeding, or stabilize it against external forces. It is, therefore, likely that the globular shape of Palaeozoic echinoids, several of which were probably elongated in the vertical axis (Kier 1966), may have been associated with a reclined posture, not unlike that of modern sea cucumbers.

Some globular species with long spines, such as the deep sea diadematoid *Plesiodiadema indicum*, display a stilt-like gait on the loose substratum (Durham 1966). Extant globular echinoids with short spines are known to cradle among seaweeds, clinging tenaciously to the algal tissue around them (Smith 1978). In both types there is no significant downward component of the ambulacral adherence. A similar tendency is shown by cidaroids, extant and extinct, whose feeble tube-feet emerge from a very narrow ambulacrum. They usually use their thick spines to fasten to rock crevices. Although both cradled and spine-supported urchins may become flattened owing to inwards pull by mesenterial threads and other tethering tissues, the plane of their ambitus is usually at mid-height (Dafni 1986*a*).

Effect of ambulacral system development

A conspicuous trend in the phylogeny of the Regularia is a progressive increase of ambulacral adherence. The tube-feet pores of early Palaeozoic (Ordovician) species, located next to the perradial (mid-ambulacral) suture, shifted later to their present position, at the adradial edge of the ambulacral plates (Kier 1966). A further development was the appearance of compound plates, with many pores pairs for each plate (Kier 1974).

However, the tendency to increase the circumferential angle of the ambulacral system prevailed throughout echinoid evolution. A morphometric survey (Dafni 1986*a*,*b*), in which 150 modern and fossil post-Palaeozoic rigid echinoid species from four orders were analysed, representing progressive evolutionary stages showed (Fig. 14.3):

(1) the mechanical efficiency of the ambulacra, represented by the relative breadth of the ambulacral system, increased, from 0.2 of the interambulacral breadth in the cidaroids, up to 0.6 in the most advanced group (Camarodonta);
(2) cidaroid species display an almost median ambitus, while in the other groups the ambitus is progressively lowered.

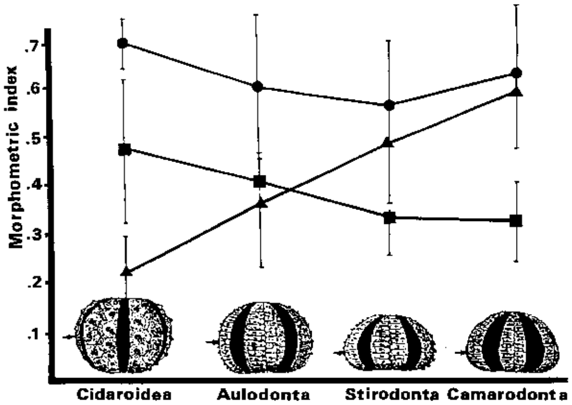

Fig. 14.3 Morphological indices among four regular echinoid orders: H/D ratio (●); ambulacral system relative breadth (▲); ambitus position (■). The breadth of the ambulacra in a typical representative of each order is emphasized by darkening. Vertical bars = SD (Dafni 1986*a*).

The morphometric survey failed, however, to show a significant trend in tallness (H/D ratio). This suggests that although lower H/D ratio generally reflects enhanced ambulacral adherence, this effect is probably restricted to ontogeny, whereas the related phylogenetic trend is lowering of the ambital line.

Adaptation to rock boring

An unusual test profile is shown by urchins of the tropical genus *Echinostrephus*. Their test is usually flat aborally and is markedly conical and tapering adorally (Fig. 14.4). The ambitus lies approximately at, or slightly above mid-height. This unique form is possibly an adaptation to infaunal life on a hard substratum. *Echinostrephus* live in perfectly round holes slightly larger than their size, which they bore deep into limestone rocks, using their short adoral spines and possibly also their jaws (Campbell *et al.* 1973). The longer aboral spines are apparently used for protection.

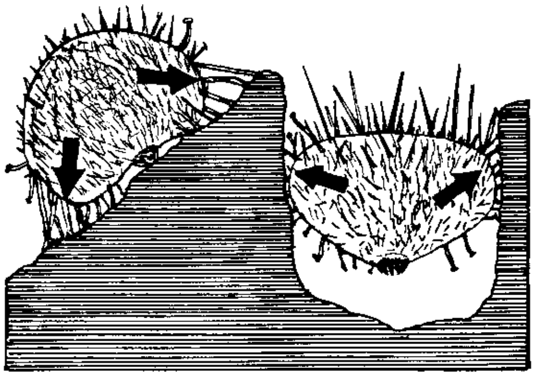

Fig. 14.4 A semidiagrammatic representation of a typical regular echinoid (left) and *Echinostrephus* shown in its natural habitat, bored holes in the rock. Arrows show the normal orientation of the ambulacral tube-feet, possibly affecting the test profile.

This unique profile reflects the continuous pull exerted by the ambulacral tube-feet sidewards, and toward the aperture, compared to the downwards orientation of most epifaunal echinoids. A similar profile is shown also by several other echinoid species such as *Heliocidaris erythrogramma armigera*, described by Mortensen (1943) as rock-boring, and the Jurassic cidaroid *Procidaris edwardsi*, whose habitat is unknown (Mortensen 1928).

Oral flattening in soft-bottom echinoids

Flattening of the subambital region is uncommon among regular echinoids. Yet it is shown by several Recent deep-sea regular genera, such as *Hebrocidaris*, *Baueria*, etc. (Mortensen 1935). These echinoids have a low ambitus, forming a sharp angle separating the domed aboral, from the flat adoral, side. This is evidently an adaptation to allow epibenthic locomotion on unconsolidated substrata.

This unusual flattening seems to be independent of ambulacral activity, since tube-feet adherence to the loose sediment is feeble, and their only means of locomotion are the short adoral spines. A similar phenomenon, shown by the holectypoids and holasteroids, marks an early stage in the evolution of irregular echinoids (Smith 1984).

The smaller subambital plates of those early irregulars, unlike those of modern sand-dollars (Seilacher 1979), indicate that their sharp ambital bending did not interrupt plate migration beyond the ambitus. Hence, the sutural binding of these plates must have changed its elasticity, yielding to the effect of gravity to form the sharp ambital angle, which never became fixed.

The variable tensility of echinoderm collagen (Wilkie 1984; Motokawa 1985) is a possible mechanism accounting for reversible oral flattening and ambital bending. It is possible that imbrication, found in plates of *Holectypus* and other irregulars (Jesionek-Szymanska 1968), facilitated sutural articulation of bending sutures.

TRENDS IN THE EVOLUTION OF IRREGULAR ECHINOIDS

The emergence of the Irregularia marks a transition from epibenthic to infaunal habit, accomplished through profound morphogenetic changes which took place within a relatively short period in the Mesozoic (Kier 1982).

Five evolutionary trends are relevant in this development.

Bilateral symmetry

Common to all irregular echinoids, this trend was heralded by the departure, in the Holectypoida, of the periproct from the apical region, moving downwards along interambulacrum 5 (Lovén's plane), well below the ambitus. In advanced irregular orders this was associated with elongation of the interambulacrum 5–ambulacrum III axis. In the Spatangoida, ambulacrum III became anterior and adapted to serve as a food-groove, while the periproct marks the posterior end. In several taxa this process was accompanied by arching forward of the paired ambulacra (Smith 1984).

Although it seems as if this chain of events started by the backward migration of the anus, anal migration and true bilateral symmetry are not necessarily linked. The tendency to move the periproct away from the apex was shown in groups, which are otherwise classified as regular echinoids, such as acrosaleniid species (Jesionek-Szymanska 1968).

It is speculated that in phylogeny, the excentric position of the periproct and bilateral orientation impair the mechanical balance between the ambulacra, producing a mechanical constraint on the perfect pentameral symmetry. This is supported by the frequent occurrence of teratologically induced 'bilateral' symmetry, apparently by damaging one ambulacrum (Plate 14.5), among a majority of almost perfect pentaradial specimens (Koehler 1924; Jackson 1927; Mortensen 1943; Dafni 1986*a*). It is plausible that ontogenetic 'bilateria' results from the same mechanical constraints which dominated bilateral symmetry in the evolution of irregular echinoids.

The observation that the ontogeny of irregular echinoids (e.g. spatangoids) starts with a slightly oval test with pentameral symmetry, and that periproctal shift and the typical bilateral symmetry are obtained during subsequent ontogenetic development (Gordon 1926), enables a comparison between the phylogenetic and teratologically induced bilateral phenomena.

Test flattening

Adoral flattening, shown by the earliest irregulars, developed into the extremely flat tests shown by the Clypeasteroida. It is reasonable to assume that this trend was primarily an adaptation to epibenthic life on soft substrata, as suggested for modern deep-sea regular echinoids, but later shifted to infaunal burrowing (Seilacher 1979). This development was facilitated by both a streamlined hydrodynamic design (Telford 1981) and constructional modification, such as sutural interlocking (Seilacher 1979) and magnetite accumulat (Chia 1973).

Two apparently antagonistic trends are exhibited here: (1) flattening by inner tether combined with yielding to gravity; and (2) creation of a supportive structure to prevent the entire collapse of the test. It is suggested that variable tensility of collagenous tissues may account for the former trend (see above), whereas the latter effect is discussed in the following section.

Internal pillar support

The introduction of vertical pillars across the coelomic cavity in the clypeasteroids, stiffened the test and enabled its infaunal way of life. Aside from fixing the flat profile of the test, it also arrested plate migration around the ambitus. In the suborder Scutellina the large marginal plates are folded around the ambitus, remaining in this position throughout adult life, whereas in the Clypeasterina the ambital margins consist of several narrow plates which are nevertheless fixed by the internal pillars (Seilacher 1979).

The origin of these pillars is obscure. Observations suggest their association with mesenterial threads (Dafni 1986*b*). In the epibenthic *Clypeaster rosaceus*, with an inflated test and relatively few pillars (Poddubiuk 1985), these pillars span the aboral interambulacra to the adoral interambulacra next to the lantern auricles (Plate 14.6). The orientation of the pillars is thus similar to that of the intestinal mesenterial threads of the Regularia (Dafni 1983*b*). Although in other clypeasteroids the pillars form a more complex pattern, the main connection is nevertheless between interambulacral plates in both sides of the ambitus. It is noteworthy that the pillars have a median suture (Seilacher 1979; Smith 1980), where the horizontal mesenteria are stabilized, appearing as if they are pierced by the pillars.

The association of the pillars with the mesenterial threads suggests that the latter may serve as guiding tissue, directing the aboral calcareous 'stalactites' towards the adoral 'stalagmites'. It also suggests that the same tissue which might have produced the inner tether has turned into a mechanical supportive structure simply by its mineralization.

Formation of the petals

In irregular echinoids the aboral ambulacra are typically adapted for gaseous exchange, whereas the lower, adoral ambulacra mainly became part of a highly complex food-gathering system. The aboral ambulacra are constricted at some distance from the apex, forming the flower-like petals, with narrow plates and specialized pores. Petals vary from one group to another within the Irregularia, and some variability in their shape is associated with the environmental conditions prevailing in the natural habitat (Smith 1984).

A striking similarity shows between petal constrictions and 'pinches' appearing in deformed urchins (Plate 14.4). First, they are found at about the same 'latitude', halfway between the ambitus and the apex; and secondly, it has been noticed that these constrictions usually coincide with the point where the foregut crosses the ambulacral ray (J. Dafni, unpublished observations). This further supports the hypothesis that they are produced by a biomechanical effect, the inward pull by mesenterial threads on either side of the ambulacra, which squeezed them together. Furthermore, it is suggested that 'pseudopetals' (Plate 14.7), consisting of five concurring pinches, that form under the specific pathologic conditions which characterize *T. g. elatensis* tall deformity (Plate 14.4), are a 'progressive variation' in Jackson's (1927) terminology. This suggestion can potentially be tested by observing the ontogeny of irregulars, in particular by studying the relations between the gut mesenteries and the development of petals at the early post-larval stage.

Brooding chambers in regular and irregular echinoids

Brooding chambers, in the form of coronal depressions, are a special adaptation found in cold-water echinoids (Hyman 1955). Philip and Foster (1971) listed several types of brooding chambers, ranging from a huge aboral cavity to five equal-sized depressions developed either within the petal region, or in other species-specific locations.

From a morphogenetical point of view these brooding chambers are 'natural deformities', rendered useful for this particular requirement. It is not surprising, therefore, that several of these shapes are reminiscent of abnormal depressions shown in deformed regular echinoids:

(1) A large, single aboral depression was typical for larger specimens of *T. g. elatensis*, possibly afflicted by calcification inhibitors (Dafni 1983*b*);
(2) small cavities at each of the ambulacral tips—occurring less frequently in both types of deformity (Plate 14.8).

The formation of these cavities can possibly be induced either by internal tethering or by localized 'softening' of the collagen links between adjacent plates, which allows them to grow excessively at the sutures and sag inwards.

CONCLUSIONS

Recently experimental observations have added to the hitherto descriptive skeletal research on the role of biomechanics. This review tries to explain the ontogeny and phylogeny of the echinoid skeleton in terms of continuous interaction of the genetically controlled structure with the physico-mechanical environment. Although the proposed model is still sketchy and roughly defined, it provides possible clues to the morphogenesis and constructional morphology of echinoids and other invertebrates with hard skeletons.

First, it defines the sort of structural modifications which are more likely to occur, either in normal or abnormal growth conditions, using universal laws and constructional principles.

Secondly, it links ontogenetic and phylogenetic changes, by assuming that the same constructional repertoire applies to both processes. Moreover, it seems that the ontogeny of advanced forms 'recapitulates' their phylogeny, simply because the growth process itself is self-organizing, and mainly depends on, or is controlled by, the constructional materials, which are similar, yet subjected to evolutionary changes.

Thirdly, this model enables us to put forward fruitful hypotheses for further experimental research, aiming to gain deeper insight into the constructional morphology of fossil and living forms.

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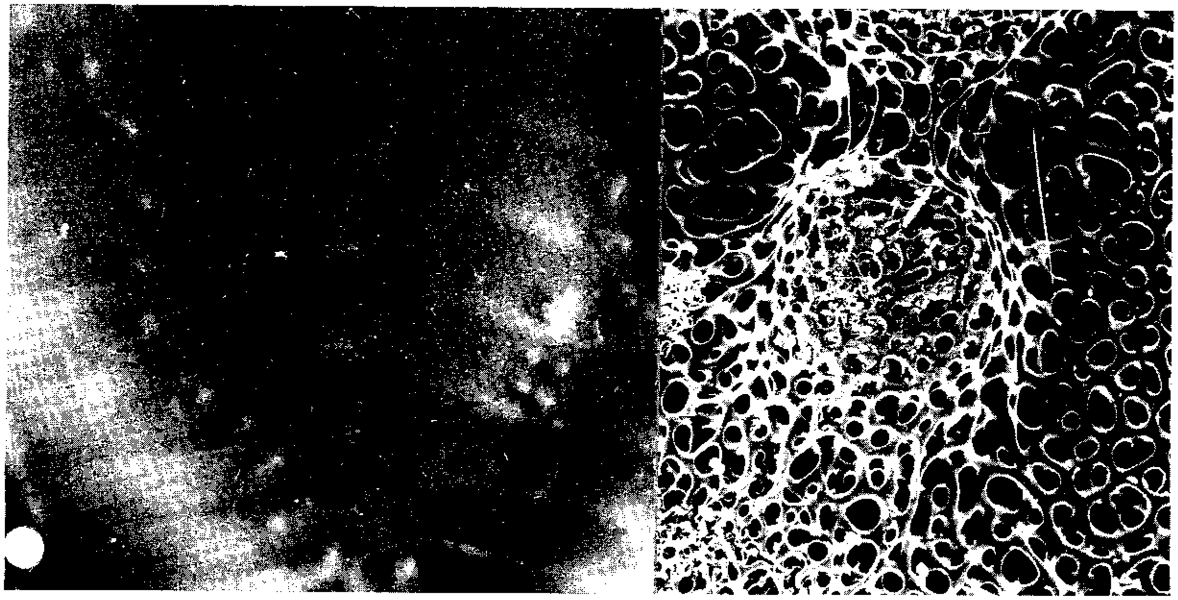

Plate 14.1 Left: The internal body wall of *Tripneustes gratilla elatensis*, showing large protuberances, serving for the attachment of mesenterial threads (x4.5). Right: The microstructure of such protuberances is enhanced by remodelling of surface trabeculae. Their orientation generally corresponds to the directions indicated by Fig. 14.2 (x90).

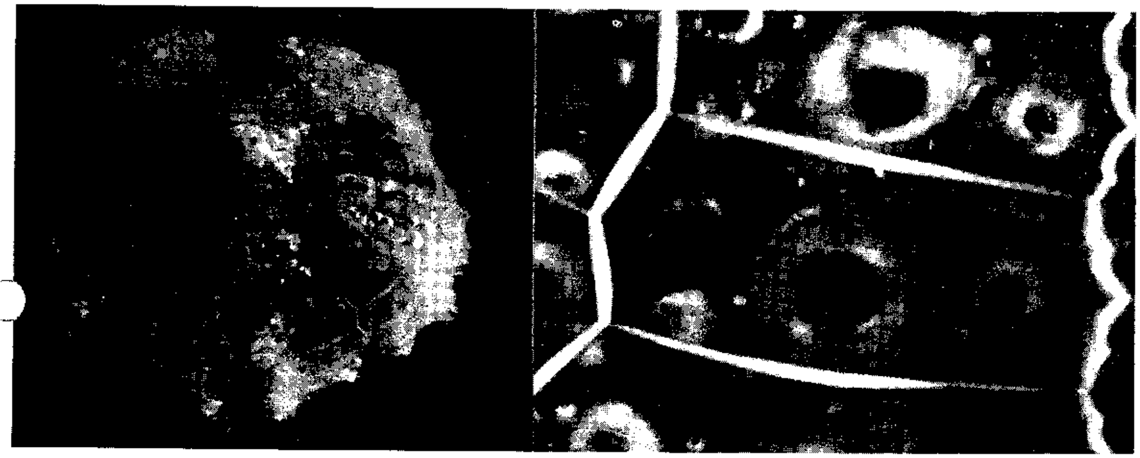

Plate 14.2. An EDTA treated regular echinoid *Psammechinus miliaris*, 25 mm horizontal diameter, submerged in water. Left: the decalcified test in a partly shrunken state following lowering of the water level (spines were removed to show the collagen sutures and internal organs). Right: interambulacral plate 'capsule' of the same, photographed under crossed nicols, showing the glowing light colour of sutural collagen bands (x8).

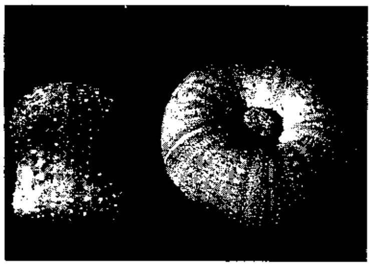

Plate 14.3. Two types of pollution-induced deformities in *Tripneustes gratilla elatensis.* Left: an abnormally tall specimen; right: aborally depressed urchin.

Plate 14.4. Deformed *Tripneustes gratilla elatensis* showing ambulacral 'pinches'.

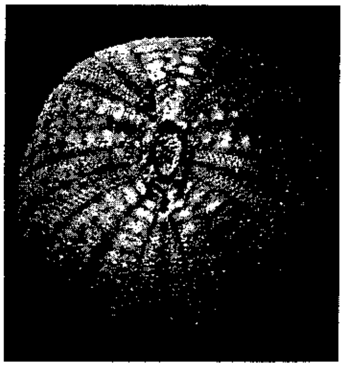

Plate 14.5. Test configuration of a *Tripneustes gratilla elatensis*, regenerated from experimental ambulacrum V immobilization. A plane of bilateral symmetry has developed due to impaired growth of the treated ambulacrum and subsequent elongation of the apical complex. Note arching of the adjacent ambulacral rays towards the treated one (Dafni 1986*a*).

Plate 14.6. Section of *Clypeaster rosaceus*, showing the internal supporting pillars, connecting interambulacral plates of the adoral and aboral sides.

Plate 14.7. Left: abnormal 'petaloid' formed by ambulacral pinching in deformed *Tripneustes gratilla elatensis* (35mmHD), compared with, right, the true petal of *Clypeaster humilis.*

Plate 14.8. Left: brood pouches in the petal of *Abatus cavernosus* (female, 25 mmHD), compared with, right, abnormally formed pits in the aboral tips of the ambulacra of a 72 mmHD *Tripneustes gratilla elatensis*.

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