

PENTAMERISM AND MODULARITY IN SEA URCHINS

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ABSTRACT

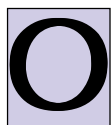
Fivefold symmetry is important in many scientific areas. In particular, five-part units or pentamerism is a basic pattern in the design of many animals and plants. Despite some efforts, a definite explanation of the abundance of this pentamerism is still missing. In this note we use sea urchins as working examples to propose some ideas, based on spatial efficiency arguments and the concept of modular systems, which can give clues to understand the advantages of a pentamer body plan partition in biological systems.

Key Words: Modularity, pentamerism, sea urchins.

RESUMEN

La simetría pentagonal resulta de importancia en muchas áreas de la ciencia. En particular, es conocido que un patrón básico en el diseño de muchos animales y plantas es pentámero, en el sentido de que se compone de cinco partes. A pesar de varios esfuerzos orientados a explicar este hecho, no existe una explicación definitiva para la abundancia del pentamerismo en la naturaleza. En esta nota usamos a los erizos de mar como ejemplos de trabajo para proponer algunas ideas, basadas en la partición eficiente del espacio y el concepto de sistema modular, que pueden ofrecer claves para entender las ventajas de una partición pentámera del plan corporal en sistemas biológicos.

Palabras Clave: Modularidad, pentamerismo, erizos de mar.



One of the most puzzling properties in many biological systems is the pentagonal symmetry. There are many notable examples of pentagonal symmetry in the members of the phylum Echinodermata, radiolarians, flowering plants and some fruits. In many cases radial symmetry is displayed but in some others it only remains a bilateral symmetry but the body is still divided into five parts, one of these parts lying along the mirror axis. These five-part units are common in both animal and plant design. We shall refer to both cases as pentamerism or pentamer symmetry. Despite of this abundance, there are few comments on pentamerism, with some important exceptions^{1,2}. In a pioneering work, Breder¹ shows that pentagonal symmetry is the basic pattern of flowers, dicotyledons, echinoderms, the vertebrate body section, the distal ends of tetrapod limbs, and of the oral armature of priapulids. Breder concludes “Five-partness, where it appears, is held to with great rigidity, even when extensive evolutionary change has taken

place. This does not seem to be the case to such a marked extent where other symmetries are concerned, as the coelenterates witness”.

The reasons for the success of pentamerism, where it appears, are not yet understood. It is in sea urchins (Figure 1a) where more hypotheses have been formulated, either on the origin of pentamerism (see Ref. 3 and references therein) or its robustness, based on mechanical or functional models⁴. If these hypotheses are true, however, they do not explain the occurrence and robustness of pentamerism in all other organisms. Breder¹ suggested that the origin of the stability of the pentamerism lies in the geometrical properties of the pentagon. López-Sauceda & Aragón⁵ suggested that in fact a geometrical property, the regularity, may be the reason for selecting certain symmetries but even it was no clear why the pentagonal symmetry is preferred in sea urchins. In this note, we retake this problem by using the concept of modular systems.

Some biological systems are characterized by properties that can be explained in terms of the relationships between entities inside

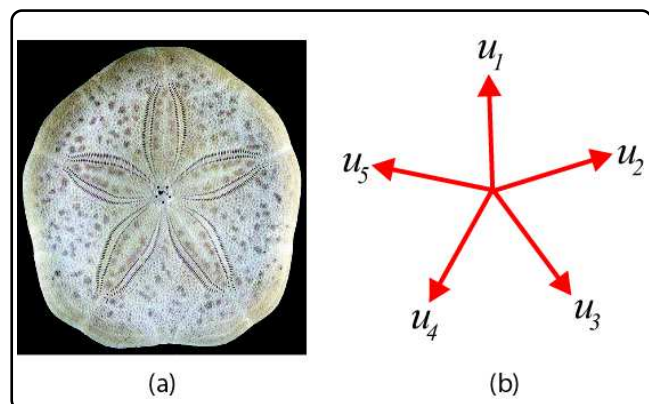


Figure 1. (a) Skeleton of a *laganum depressum* sea urchin. (b) Star of five vectors.

the system. It is assumed that organisms are composed by individual entities or *modules* and knowledge of modules and their integration is important to understand some properties of these organisms. The analysis of abstract entities into constituent elements, and their degrees of interaction among internal parts, represents a source of important information in terms of constrictions and evolvability. This approach is called modularity. This concept might be seen as a tool to infer features of the way organisms are built, for instance due to organizational principles of self-maintaining systems⁶, or it may be an “evolved property”⁷. The identification of structural and architectural modules is often a straightforward matter⁸, for instance, Eble⁹ points out “the parts and characters routinely identified by the morphologist reflect hypotheses of modularity based on observational or quantitative criteria, without reference to the generative mechanisms or the theoretical contexts to which modules relate”. One of the most basic levels, which conforms phenotypic features in animal evolution, is the body plan. Sea urchins have a pentamerally readily visible body plan, with either radial and/or bilateral symmetry (Figure 1a); such a partition defines an architectural space with some degree of interaction between parts. Our aim is the analysis of pentamerally body plan partitioning in order to understand not just the biological description of visible modules and their interactions, but to establish a plausible hypothesis in terms of spatial efficiency.

Measurements of regularity in a sample of living and extant sea urchins were carried out in López-Sauceda & Aragón⁵ by associating a set of five vectors, called a *star* (Figure 1b), to the five ocular plates in the apical disk; the regularity was associated with the eutacticity of the star. A given star of vectors $\{\mathbf{u}_1, \mathbf{u}_2, \dots, \mathbf{u}_N\}$ is said to be *eutactic* if it can be obtained by projecting an orthogonal set of N vectors $\{\mathbf{U}_1, \mathbf{U}_2, \dots, \mathbf{U}_N\}$ in a N -dimensional space¹⁰. That is, if P is an orthogonal projector then the star is eutactic provided that $P(\mathbf{U}_i) = \mathbf{u}_i$ for $i=1, 2, \dots, N$. From this definition, a measure of regularity can be proposed¹¹ and it was used to measure the regularity of the studied sea urchins. The analysis suggested a high degree of regularity (eutacticity) in the shape

of these organisms through their evolution. Rare deviations of regularity were measured in Holasteroida order, which seems to constitute a critical evolutive event in sea urchins evolution⁵. All these results provide strong evidence that the regularity of the five-vector stars associated with the studied samples was favored through evolution but no clues about the advantages of stars with five, instead of say six or four, vectors were available. Steps further were taken by López-Sauceda¹², who performed a numerical experiment, generating random bilateral stars with three, four, five, etc., vectors; the main idea was to determine if a star with a given number of vectors (hopefully five) could have more probability to be eutactic if its coordinates were chosen randomly, maintaining bilaterality. A statistical analysis of the obtained results yielded that stars with seven and eight vectors have more probability to be regular. If we just take into account the more frequently observed symmetries in Nature, those stars with four, five and six vectors have more probability to be regular if they are randomly generated, with a slight preference for pentagonal stars¹². The biological advantage of pentamerism, however, does not arise from these results and, even more, there was observed a tendency to prefer stars with seven and eight vectors. In order to pursue in this research, an approach based on modularity is now adopted. The main hypothesis is that regular (eutactic) pentagonal stars yield more homogeneous partitions of space.

A first step to verify the hypothesis was to define our modules that in this case are obtained by the following geometrical procedure (see Figure 2):

1. A random star S of N vectors, $\{\mathbf{u}_1, \mathbf{u}_2, \dots, \mathbf{u}_N\}$, is generated inside a circle of radius R .
2. In the same circle, a set of $\mathcal{P}$ of randomly generated points is inscribed with the restriction that no two points of $\mathcal{P} + S$ are closer than a certain distance r .
3. The Voronoi tessellation¹³ associated with the set of points $\mathcal{P} + S$ is calculated.
4. The Voronoi tessellation obtained in the previous step is partitioned as follows. Given a vertex $\mathbf{u}_i$ of the star S , the set of Voronoi polygons that are closer to $\mathbf{u}_i$ than to any other vertex $\mathbf{u}_j$ ($j \neq i$) are selected; this process is repeated for each vertex $\mathbf{u}_i$ ($i=1, 2, \dots, N$). Thus, the Voronoi tessellation is partitioned into N sub-tessellations or modules $L_1, L_2, \dots, L_N$.

Let A_i be the total area of the Voronoi polygons associated with the module L_i . Our main goal will now be to study the variation of total areas between modules L_i , $i=1, 2, \dots, N$, for partitions associated with regular and irregular stars; the larger variation, the less homogeneous the partition of the space is. In order to support the statistics, for each star S , generated at step 1, M sets of random points, $\mathcal{P}_1, \mathcal{P}_2, \dots, \mathcal{P}_M$, are generated and for each set, steps 2, 3 and 4, of the above procedure, are applied. Now, for a

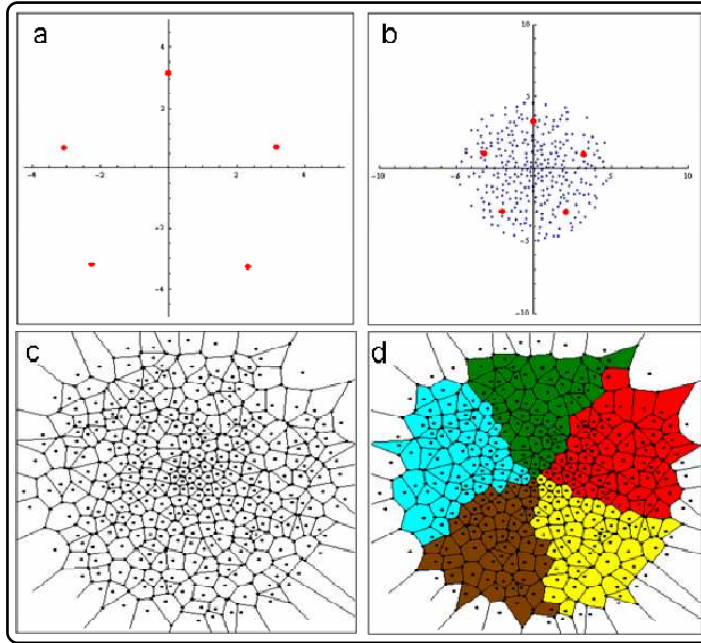


Figure 2. Graphical algorithm used to associate modules to a given vector star. Subfigures (a), (b), (c) and (d) corresponds to steps 1, 2, 3 and 4, respectively, of the procedure described in the main text.

given N (the number of vectors of the star) we generate E random regular stars, $S_1, S_2, \dots, S_E$, and the same number of irregular stars and the procedure already described is applied for each case. Therefore, let A_{mj}^e the total area of the module L_m of the star S_e , corresponding to the set of random points $\mathcal{P}_j$. The mean area of the module L_m is then

$$\bar{A}_m = \frac{1}{E} \sum_{e=1}^E \bar{A}_{mj}^e = \frac{1}{M \times E} \sum_{e=1}^E \sum_{j=1}^M A_{mj}^e,$$

and the standard deviation of the E mean areas corresponding to the Module L_m is

$$\sigma_m = \sqrt{\frac{1}{M \times E} \sum_{e=1}^E \sum_{j=1}^M (A_{mj}^e - \bar{A}_m)^2}.$$

With all this, the null hypothesis is that the standard deviation corresponding to regular star is the same that the standard deviation resulting from irregular stars. Stars with $N=3, 4, 5, 6$ and 7 vertices were considered and in all cases sets $\mathcal{P}_j$ with 300 pseudo-random points, with normal distribution, were generated. Other parameter values were $E=100$, $M=100$, $R=3$ and $r=0.5$. To avoid non-representative data, during the calculation of Voronoi tessellations, polygons with at least one vertex outside the convex hull were removed.

Since the standard deviation $\bar{\sigma}_m$ provides estimation of the area variability of module L_m , we performed an ANOVA to detect statistically significant differences on area variability of modules

corresponding to regular and irregular stars. From ANOVA (Figure 3) it can be observed that the variability in modules coming from partitions generated by irregular stars is considerably larger. This statistical difference is more noticeably when all modules from regular and irregular partitions are compared (Figure 3). Thus, the null hypothesis is rejected in 23 of 25 modules studied and, consequently, the area variability of modules obtained from regular stars is different than those obtained from irregular stars. Even more, regular stars yield modules with lower variability than modules coming from irregular stars. It should be pointed out that our experiment fails in the cases of modules L_1 in partitions with 3 modules and L_4 in partitions with 4 modules. In both cases, no statistically significant differences between partitions coming from regular and irregular stars were observed.

In the theory of modules the “interaction”, in the sense of efficiency, and “interference”, in the sense of inefficiency, are useful concepts. Interaction can be interpreted as physical contiguity of modules but interference, which also needs continuity, implies territory invasion between modules. The larger variability of size (or area) the more interference between contiguous modules. Paradoxically,

interference between modules is also required to exchange biological information; excessive interference, however, produces disorganization. With these ideas, we can retake the discussion about possible biological advantages of pentagonal arrangements. Modules with a high degree of independence have low possibilities to interact with its neighbors and, given its high organization (low variability), the resulting modular structure tends to be rigid, with low potential to change or, in biological terms, with low evolvability¹⁴.

Notice that from our results, it turns out that if the mean of $\bar{\sigma}_m$, denoted by σ_m , provides information about the variability of the area variability of modules, then the standard deviation of $\bar{\sigma}_m$ contains the information about the interaction between modules. By calculating this standard deviation (error bars in Figure 3), we get that structures with irregular modules have large values, thus implying large interference between modules. On the contrary, structures with regular modules have small values of standard deviations thus small interference between modules is measured. Finally, structures with five modules have intermediate values so neither large nor small interference between modules is assumed. These results are depicted in Figure 4 and can be interpreted as follows. Structures with three, four and six modules display excessive interference, thus disorganization. Arrangements with high degree of organization (eutacticity) such as those with seven modules have almost no interference so they are more rigid. Structures with five modules have a high degree of organization (eutacticity) and, at the same time, they show an adequate equilibrium between interference and rigidity, that can be interpreted as transformational potential. Consequently,

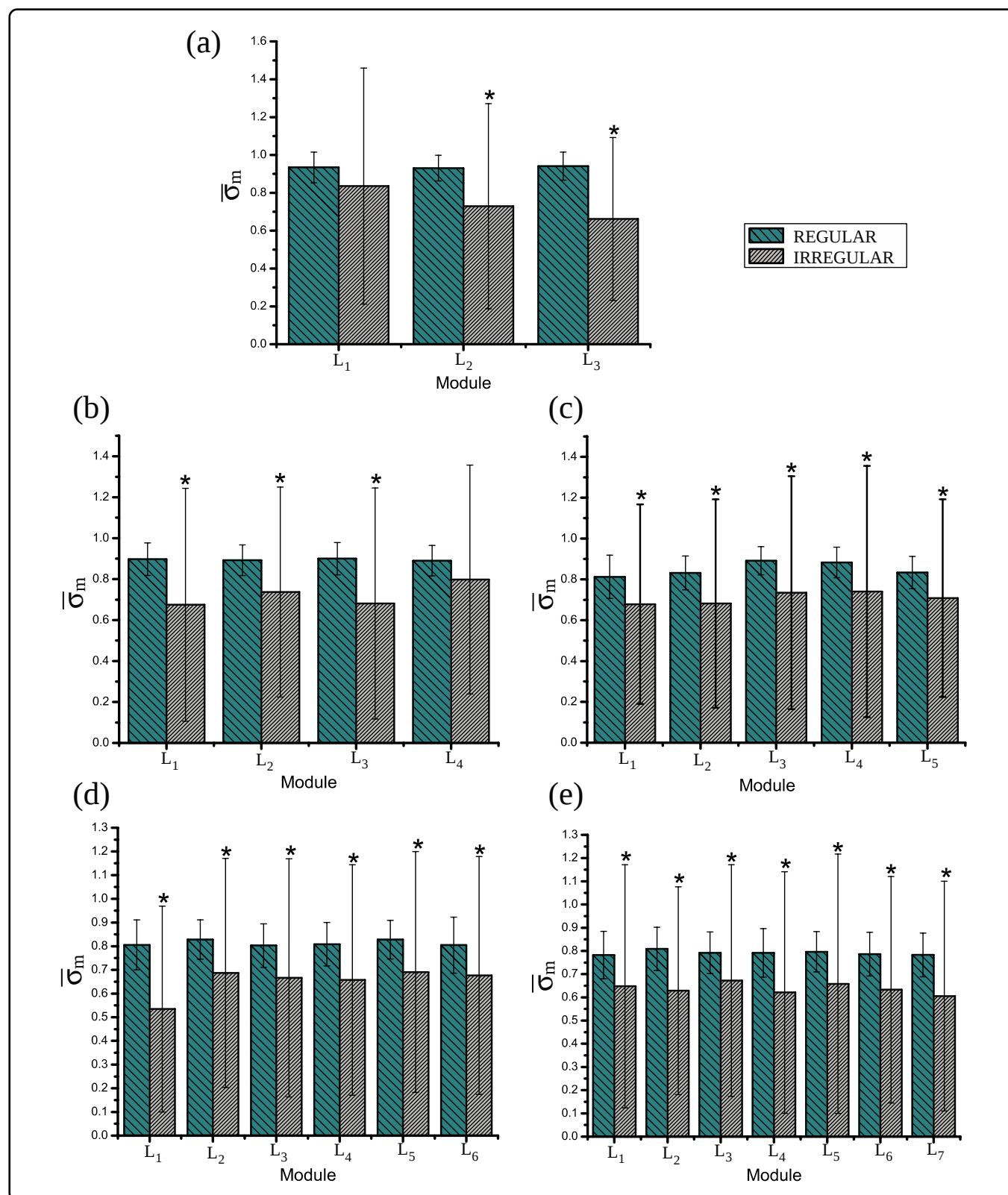


Figure 3. ANOVA of differences of area variability (mean of σ_m) for regular and irregular partitions of the space. Partitions with (a) Three modules (*: $P = 0.0001$), (b) Four modules (*: $P = 0.001$), (c) Five modules (*: $P = 0.05$), (d) Six modules (*: $P = 0.01$) and (e) Seven modules (*: $P = 0.01$).

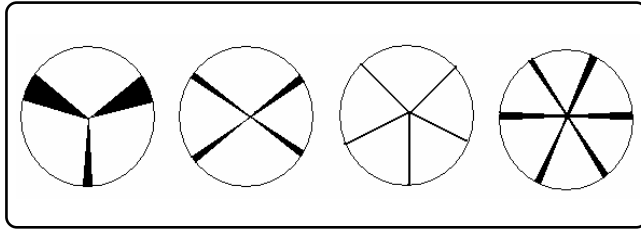


Figure 4. Graphical representation of interferences between modules, as inferred by the standard deviation of the mean of σ_m , for partitions with three, four, five and six modules. Shaded regions represent area interference. Partitions with seven vectors show almost no interference.

structures with five modules lie in the borderline between rigidity and disorganization; this particular equilibrium seems to be necessary to get an optimal balance between organization and evolvability.

Albeit much more work is needed, our approach seems to point along a promising direction in order to clarify the advantages of pentamerism in Nature. It would be interesting to mention the fact that pentagonal arrangements appear in other realms of science with the same property of lying in borderlines between ordered and disordered structures. In materials science, for instance, the atomic order of quasicrystals (with pentagonal symmetry, among others) lies between periodic and amorphous¹⁵. In the modern theory of dynamical systems, the transfer to chaos includes a passage through small regions, which are seeds of chaos; in Hamiltonian systems, these regions are called stochastic webs and examples with five and seven-fold symmetries have been found¹⁶.

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