**Eutacticity in sea urchin evolution**

J. López-Sauceda, J.L. Aragón*

*Departamento de Nanotecnología,*  
*Centro de Física Aplicada y Tecnología Avanzada,*  
*Universidad Nacional Autónoma de México,*  
*Apartado Postal 1-1010, Querétaro 76000, México.*

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**Abstract**

An eutactic star, in a $n$-dimensional space, is a set of $N$ vectors which can be viewed as the projection of $N$ orthogonal vectors in a $N$-dimensional space. By adequately associating a star of vectors to a particular sea urchin we propose that a measure of the eutacticity of the star constitutes a measure of the regularity of the sea urchin. Then we study changes of regularity (eutacticity) in a macroevolutive and taxonomic level of sea urchins belonging to the Echinoidea Class. An analysis considering changes through geological time suggests a high degree of regularity in the shape of these organisms through their evolution. Rare deviations from regularity measured in Holasteroida order are discussed.

**Key words:** Eutactic stars, Bilateral symmetry, Regularity, Sea urchins

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* Author for correspondence.
1 INTRODUCTION

This work is dealing with regularity, which is a property with deep implications in organisms. From the biological point of view regularity has been related with radial symmetry, and irregularity with bilateral symmetry (Coen, 1999). The heuristic value of radial and bilateral symmetry in biology account for taxonomic issues, however, symmetry as well as disruption symmetry have been an empirical and intuitive approach accounting for structural properties in organisms (Holland, 1988; Smith, 1997; Jan et al., 1999; Rasskin-Gutman et al., 2004; Knoblich, 2001).

From a mathematical point of view, the property of regularity of a geometric form has not been formalized. Based on previous results by Torres et al. (2002), we hypothesize that eutacticity provides a measure of regularity based in the following argument. A set of \( N \) vectors in \( \mathbb{R}^n \), with a common origin, is called a star and a star is said to be eutactic if it can be viewed as the projection of \( N \) orthogonal vectors in \( \mathbb{R}^N \). It turns out that stars associated with regular polygons, polyhedra or, in general, polytopes, are eutactic (Coxeter, 1973) and thus regularity and eutacticity are closely linked. A disadvantage of using eutacticity as a measure of regularity is that a star vector must be associated with the geometrical form under study. As we shall see, this is not a problem with echinoids. In fact, Torres et al. (2002) found that the flower-like patterns formed by the five ambulacral petals in 104 specimens of plane irregular echinoids (from Clypeasteroidea) are eutactic. Here we present a deeper study that overcome the restriction to plane irregular echinoids, using the five ocular plates (OP) to define the star vector. Additionally, we use a new criterion of eutacticity that provides a measure of the degree of eutacticity of a
star which is not strictly eutactic. With these tools we study the variability of eutacticity during geological time and to analyze pentamery variability during the evolution of sea urchins.

Sea urchins are pentameric organisms with an apical structure, called the apical disc (Melville and Durham, 1966). This structure includes five ocular plates (OP) that can fold the vector star associate with each sea urchin species (see Fig. 1 and Section 3 for a detailed description). In this work, we show that OP can be useful even in ovoid echinoids, such as Spatangoids, since the OP are almost tangential to the aboral surface (opposite to oral surface). Using the OP to define the star of vectors, we analyze the regularity and changes in a macroevolutive and taxonomic level in a collection of 157 extinct and extant sea urchins. We conclude that evolution has preserved a high degree of regularity and, consequently, that the apical disk is a homogeneous and geometrically stable structure through the geological time. Low values of regularity were recorded in some specific families and its biological consequences are discussed.

This paper is organized as follows. In Section 2 a mathematical introduction to the concept of eutactic star is presented. Section 3 describes the structure of the apical disc and its biological importance, making it the obvious choice to define a vector star which characterizes each specimen. Experimental methods and results are devoted to Section 4 and, finally, discussion and conclusions are presented in Section 5.
2 REGULARITY AND EUTACTIC STARS

Our main hypothesis is that the concept of regularity of a biological form may play an important role in the study of phenotypic variation in evolution. For this goal, one must first be able to establish a formal criterion defining regularity of a geometrical form, including a measure of how regular a form is. Mathematically, this property has not been defined and here, as a first step along this direction, we adopt the concept of eutacticity that, as we shall show, is closely related to regularity.

We shall deal with a set of \( N \) vectors \( \{a_1, a_2, \ldots, a_N\} \) in \( \mathbb{R}^n \), with a common origin, called *star*. In this case \( N > n \) so the set of vectors cannot be linearly independent. The star is called *eutactic* if its vectors are orthogonal projections of \( N \) orthogonal vectors in \( \mathbb{R}^N \), that is, there exist \( N \) orthogonal vectors \( \{u_1, u_2, \ldots, u_N\} \), in \( \mathbb{R}^N \), and an orthogonal projector \( P: \mathbb{R}^N \to \mathbb{R}^n \) such that

\[
P(u_i) = a_i, \quad i = 1, 2, \ldots, N.
\]

The notion of eutacticity (from the Greek *eu*=good and *taxy*=arrangement) was firstly introduced by the Swiss mathematician L. Schläfli (about 1858) in the context of regular polytopes. Later, Hadwiger (1940) noticed that the vectors of an eutactic star are projections from an orthogonal basis in higher dimensional spaces and proved that the star associated to a regular polytope is eutactic. Thus, eutacticity is associated with regularity and the remarkable properties of eutactic stars have been useful in different realms such as quantum mechanics, sphere packings, quasicrystals, graph and frame theory and crystal faceting (see Aragon et al. (2005) and references therein).
A well known necessary and sufficient condition for a star to be eutactic is due to Hadwiger himself, who proved that a star \( \{a_1, a_2, \ldots, a_N\} \) in \( \mathbb{R}^n \) is eutactic if and only if there is a real number \( \lambda \) such that

\[
\sum_{i=1}^{N} (x \cdot a_i) a_i = \lambda x,
\]

is fulfilled for all \( x \in \mathbb{R}^n \). In the special case where \( \lambda = 1 \), the star is said to be \textit{normalized eutactic}.

A more practical form of the eutacticity criterion is obtained if the so-called structure matrix \( A \) is introduced. Let \( A \) be the matrix whose columns are the components of the vectors \( \{a_1, a_2, \ldots, a_N\} \), with respect to a given fixed orthonormal basis of \( \mathbb{R}^n \). In this case, the matrix form of Hadwiger’s theorem states that the star represented by \( A \) is eutactic if and only if

\[
AA^T = \lambda I,
\]

for some scalar \( \lambda \) (here \( I \) is the \( n \times n \) unit matrix).

In this work we are dealing with stars measured in digital images of sea urchins and thus a reliable numerical criterion of eutacticity, suitable to work with experimental measurements, is need. Notice that a criterion such as (1) is not useful since experimental errors may produce a matrix which is not exactly the identity matrix \( I \). Thus, it is desirable to obtain a numerical criterion capable of measuring the degree of eutacticity of a star which is not strictly eutactic. This criterion has already been proposed (Aragon et al., 2005) and asserts that a star in \( \mathbb{R}^n \), represented by the structure matrix \( A \), is eutactic if
and only if

\[ \varepsilon = \frac{\text{Tr}(S)}{\sqrt{\text{Tr}(SS)}/\sqrt{n}} = 1, \]  

(2)

where \( S = AA^T \). Notice that the closer \( \varepsilon \) is to one, the more eutactic the star is. In the particular case of two-dimensional stars (\( n = 2 \)), it can be proved that \( 1/\sqrt{2} \leq \varepsilon \leq 1 \) (Aragon et al., 2005).

3 SE A URCHINS AND VECTOR STARS

In Torres et al. (2002), vector stars were associated to the petaloid ambulacra of plane irregular echinoids. It was reported that, for 104 specimens of the Natural History Museum of London, the pentagonal stars thus defined fulfill very accurately an eutacticity criterion. The calculations carried out in that work present two main restrictions: a) stars are associated to plane or almost plane sea urchin specimen and b) A eutacticity criterion was used that depends on the coordinate system and does not allow a measurement of the degree of eutacticity of stars which are not strictly eutactic. Here we overcome these restrictions by using the eutacticity criterion of (2) and using the five ocular plates (OP) to associate a star of vectors to each sea urchin. As we shall see in what follows, besides the biological importance of the OP, its use to define a star of vectors allows to study non planar echinoids.

The apical disc in sea urchins, encircled in Fig. 1, represents a crown of biological structures in the apex of the test (Melville and Durham, 1966). It is positioned in the aboral surface of the test and is conformed by five genital plates, five ocular plates and the madreporite. The OP are located at the
Fig. 1. Apical disc (encircled) showing landmarks (numbered) at ocular plates. The star vector is formed by vectors pointing to these landmarks, with common origin at the center of mass.

point of origin of the ambulacral zones. The biological relevance of ambulacra is given by the following reasons. Firstly, each ambulacra consist of two, or even more, columns of plates extending from the margin of an OP to the edge of the mouth. In most echinoids each mature plate is perforated by two pores forming a pore pair; each pore pair gives passage to one tube foot, which is connected internally with the water vascular system. Secondly, five ambulacra are a conspicuous sign of body plan pentamery in all extant and extinct sea urchins and, finally, ambulacral rays are seen as homologous structures in echinoderms. Thus we conclude, that OP has more biological implications as the origin of ambulacra than the end of petaloid ambulacra. In addition, the OP are almost tangential to the aboral surface and thus it is useful even for ovoid echinoids.
Table 1

List of the 47 families studied in this work. The number of specimens considered in this work is indicated between parenthesis.

| Radial families:          |
|---------------------------|
| Archaeocidaridae (1)      |
| Aspidisdematidae (1)      |
| Diademataceae (2)         |
| Echinometridae (2)        |
| Lissodiademataceae (1)    |
| Micropygidae (1)          |
| Parechinidae (1)          |
| Psychocidaridae (1)       |
| Saleniidae (1)            |
| Toxopneustidae (3)        |
| Toxopneustidae (3)        |
| Temnopleuridae (2)        |

| Bilateral families:       |
|---------------------------|
| Arachnoidae (5)           |
| Archiaciidae (3)          |
| Asterostomatida (1)       |
| Astriclypeidae (2)        |
| Brissidae (8)             |
| Cassiduloidae (12)        |
| Clypeasteridae (12)       |
| Clypeolampaidae (3)       |
| Collyritidae (4)          |
| Corystidae (1)            |
| Dendrasteridae (2)        |
| Disasteridae (3)          |
| Echinarchnidae (4)        |
| Eoscutellidae (1)         |
| Fibulariidae (4)          |
| Galeropygidae (4)         |
| Hemiasteridae (7)         |
| Holasteridae (2)          |
| Holectypidae (4)          |
| Laganidae (3)             |
| Loveniidae (1)            |
| Mellitidae (1)            |
| Micrasteridae (6)         |
| Neolampadidae (2)         |
| Neolaganidae (5)          |
| Nucleolitidae (3)         |
| Pliolampadidae (2)        |
| Pourtalesiidae (2)        |
| Pygasteridae (5)          |
| Protoscutellidae (2)      |
| Rotulidae (3)             |
| Scutellidae (4)           |
| Schizasteridae (9)        |
| Somaliasteridae (1)       |
| Spatangoidae (2)          |
| Toxasteridae (8)          |

We then define the star vector associated to a particular echinoid as the set of five vectors pointing to the OP with origin at the centroid. The star thus defined, allows us to test eutacticity in a wide range of echinoids and study changes in a macroevolutive and taxonomic level.
4 RESULTS

4.1 Variability in taxonomic groups

We have analyzed 157 extant and extinct specimens of sea urchins from the collection of the Instituto de Ciencias del Mar (Universidad Nacional Autónoma de México) and from images of The Natural History Museum of London website (http://www.nhm.ac.uk). As shown in Table 1, the analyzed sea urchins belong to 47 Families in a taxonomic group of 95 Families, according to the classification by Lebrun (2000). Eleven of these specimens are radial and thirty six bilateral. To each sea urchin we associate a vector star, with vectors pointing to the OP (shown in Fig. 1) and origin at the centroid. Measurements were carried out on digital images of aboral surfaces, analyzed using the morphometric software packages MakeFan6 (Zelditch et al., 2004) and tpsDig2 (Rohlf, 2006). With the former, the OP is digitized and the vector star coordinates are obtained by using the second program. Once the coordinates of the star vector are available, Eq. 2 is used to calculate the value of eutacticity of the star, i.e., $\varepsilon$.

Since one of our goals is to análize regularity of sea urchins through geological time, we must define a taxonomic group to define a phylogenetic reference in time. Taxonomic keys use the apical disk as a reference to describe the family level, thus family taxonomic level constitutes the best choice since it should have a low variability in the apical disk. In fact, as shown in Fig. 2, family level shows lower variability in eutactic values as compared to order. Hence, this taxonomic level was used to represent regularity in geological time.
Fig. 2. (a) Standard deviation of $\varepsilon$ per order: A) Clypeastroida, B) Cassiduoida, C) Holectypoida, D) Pygasteroida, e) Spatangoida, F) Holasteroida, G) Disasteroida. (b) Standard deviation of $\varepsilon$ per family (the bilateral families with the largest variations are only displayed.): A) Pygasteridae, B) Holectypidae, C) Cassiduloidae, D) Clypeasteridae, E) Arachnoidae, F) Fibulariidae, G) Neolaganidae, H) Rotulidae, I) Echinarchniiidae, J) Scutellidae, K) Collyritidae, L) Toxasteridae, M) Microasteridae, N) Brissidae, O) Hemiasteridae, P) Schizasteridae.
By organizing the values of eutacticity per family, we are able to carry out a formal statistical analysis. From the properties of eutacticity, we can deduce that radial families have a high degree of eutacticity (the stars form regular pentagons) and, consequently, no variability (up to experimental errors). Contrarily, high variability is expected in bilateral families.

Before proceeding with a statistical analysis of the eutacticity values per family, we have to take into account the possibility of a stochastic nature of eutacticity. In order to reject this possibility, an experimental set of two hundred randomly generated bilateral stars was considered. A formal statistical analysis must then include three groups: radial, bilateral and random stars. The values of $\varepsilon$ of the random sample yield a mean of 0.891026 with population standard error of 0.00604. Our experimental sample of radial stars yield a mean of 0.995187423 and standard deviation of 0.00526708. Finally, the experimental sample of bilateral stars gives a mean of 0.96499158 and standard deviation of 0.062079301. The Shapiro-Wilk test applied to our samples yields $W = 0.534789$ and $p < 0.0001$, for the joined radial and bilateral experimental sample, and $W = 0.853001$ and $p < 0.0001$, for the random sample. From this result we conclude that neither the experimental or random distribution are normal and thus a non parametric statistical analysis is needed. This non parametric test produces $\chi^2_{0.05} = 68.2774$ and $p < 0.0001$, consequently, the probability of finding random significant differences between radial, bilateral and random stars is lower that 0.0001. The possibility of a stochastic origin of regularity is thus rejected.

Now, concerning the analysis of the experimental sample per family, in Fig. 3, a scatter plot of the eutacticity values of the 47 families is shown. From the figure, it is observed that the lowest degree of regularity are recorded in Holasteri-
Fig. 3. Scatter plot of eutactic values in 47 Families of radial and bilateral sea urchins. The lowest degree of regularity are recorded in Holasteridae, Corystidae, Collyritidae, Pourtoalesiidae, Toxasteridae and Nucleolitidae. This observation will be revisited in the next Section. A Wilcoxon/Kruskal-Wallis analysis of the 47 families was carried out, yielding $\chi^2_{0.05} = 78.8904$ and $p<0.0001$. Consequently, differences between families are also accepted.

4.2 Eutacticity values through geological time

Here the variability of eutacticity per family through geological time is studied. The experimental sample includes extant and extinct specimens. Once again we have to take into account that radial echinoids are associated with nearly eutactic stars; the most primitive groups, like Paleozoic groups, are almost always totally radial. Contrarily, the eutacticity values of species from post-paleozoic groups are less uniform and thus more than two specimens per family are required. Fig. 4 shows the mean values of $\varepsilon$ at four geological time...
Fig. 4. Mean values of the eutacticity parameter ($\varepsilon$) of the experimental sample in four intervals of the geological time.

intervals, namely Paleozoic, Triassic-Jurassic, Cretaceous and Cenozoic. These scales were chosen because, according the paleontological records (Lebrun, 2000), at the beginning of each of these intervals there was a rise in the speciation rate; there was an increase in the numbers of families. As shown in Fig. 4, post-paleozoic sea urchins show the highest degree of variability. A statistical analysis, however, gives the values $\chi^2_{0.05} = 6.1418$ and $p(0.1049)$, implying that there are no statistical differences in regularity through geological time.

In Fig. 5 a plot of the eutacticity values, per family, through the geological time is shown. The lowest values of eutacticity are recorder firstly in early Mesozoic Collyritidae and low values continue with late Mesozoic and Cenozoic Holasteridae, Portuolesidae and Corystidae. As a matter of fact, all these families belong to the Holasteroida order which turns out to be the responsible of the prominent peak (F) in the standard deviation plot in Fig. 2(a). In order to have a better understanding of the singularity of Holasteroida order, in Fig. 6 an evolutive cladogram showing phylogenetic relationships between
orders is shown. In this cladogram a representative star, and the mean value of eutacticity per order, is included. It is clearly shown that the lowest values of regularity comes from Disasteroida and are recorded in Spatangoida and Holasteroida. In fact, from the measured values, we can say that Holasteroida is an “anti-eutactic” group, *i.e.*, mathematically irregular. Most living representatives of Holasteroida are deep-water inhabitants with exceedingly thin and fragile tests. Besides that we consider that regularity and irregularity constitute two important parameters to approach ecological and evolutive topics, the observed departure from regularity could have been a way to increase the amount of complexity in sea urchin morphology.

5 DISCUSSION

Traditionally, radial symmetry has been associated with regularity while bilateral symmetry with irregularity. In this work we propose the eutacticity as a measure of the regularity of a biological form which is independent of
Fig. 6. Evolutive cladogram of the class Echinoidea, depicted for illustrative purposes. A representative star of vectors and the mean value of eutacticity per order is included.

The of the radial or bilateral condition. With this hypothesis, we have shown that regularity has dominance over irregularity in sea urchins evolution; despite that variability increases over time, statistically sea urchins show a high degree of regularity. This regularity is nearly perfect in the most primitive groups, belonging to the paleozoic era, which were almost totally radial. A slight decreasing of regularity is observed in post-paleozoic sea urchins, with the notably exception of the Holasteroida order which seems to constitute a critical evolutive event in sea urchins evolution.

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