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# Simplified dynamic model for the motility of irregular echinoids

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Inspired by the locomotion mechanism of sea urchins, we study the locomotion of an irregular echinoid by means of a simplified dynamical model. We prove that if two conjectures are assumed, the geometrical arrangement of the five ambulacral petals of irregular echinoids should form a eutactic star in order to optimize motility. We firstly propose an adequate "measure" of eutacticity that allows us to to verify the statistical tendency to such a property for a representative collection of fossil specimens. Next, regarding dynamics, the biological advantage of eutactic stars is addressed as a minimal path problem. Finally, we study the stability of some eutactic stars under small perturbations.

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## I. INTRODUCTION

The concept of eutactic star arises in the study of regular polytopes [1,2]. The notion of *eutaxy* (from Greek *eu*=good, *taxy*=arrangement) is associated with regularity. Thus, it is not surprising that this property arises in different realms such as quantum mechanics [3–5], sphere packings [6,7], quasicrystals [8], graph and frame theory [9,10], and crystal faceting [11]. It has been suggested that the flower-like patterns displayed in the petaloid ambulacra of plane irregular echinoids [see Fig. 1(a)] generally occur as geometrical forms generated from eutactic stars [12]. Furthermore, it has also been observed that the morphospace of the above mentioned petals is fully occupied by extinct and living plane irregular echinoids. This was predicted for all geometrically accessible morphospaces, by Thomas *et al.* [13].

To further investigate the observed morphometric statistical tendency, we first need a numerically sound criterion to measure how close to eutacticity a given star is (Sec. II). Next, we have to verify if under this criterion the morphospace of plane irregular echinoid petals is statistically biased toward eutacticity (Sec. III). Finally, if this tendency is corroborated, one may ask if this geometrical property implies some biological advantage for these animals (Secs. IV and V).

## II. EUTACTIC STARS AND THEIR CHARACTERIZATION

Consider $M$ vectors $\{\mathbf{a}_1,\ldots,\mathbf{a}_M\}$ in $\mathbb{R}^n$ with $n<M$; such a set is called a *star*. We define a $n\times M$ matrix $A$ whose $i$th column is formed by the components of $\mathbf{a}_i$ with respect to the canonical basis in $\mathbb{R}^n$. By a theorem due to Hadwiger [1,8,10], a star is eutactic if and only if

$$AA^T=\lambda I, \tag{1}$$

for some real number $\lambda$. If $\lambda=1$, the star is called normalized eutactic. We say that $A$ is normalized eutactic if and only if the corresponding star is normalized eutactic. A convenient characterization of eutacticity that we will use later is given in the following [4]:

*Theorem*. A $n\times M$ matrix $A$ (with $n<M$) is normalized eutactic if and only if all of its singular values are one.

In Ref. [12], we proposed an alternative to the Hadwiger criterion, valid for planar lattices and that turns out to be dependent on the coordinate system. Briefly, the idea is that any two-dimensional star with $M$ vectors can be associated with two vectors in a $M$-dimensional space (see the discussion at the end of this section for details); if the star is eutactic, these two vectors are orthogonal and have the same norm. Here, we develop an alternative to the Hadwiger criterion (1), invariant under orthogonal transformations, and valid for stars in any dimension. Additionally, our criterion allows us to measure the degree of eutacticity of a star which is not strictly eutactic. Our goal is to produce an algorithm suitable for work with experimental measurements.

In the (real) vector space $M_{n\times n}$ of all $n\times n$ matrices with real entries, we can define the bilinear symmetric positive-definite form

$$\langle S,R\rangle=\mathrm{Tr}(S^TR).$$

By virtue of the Cauchy-Schwarz inequality, we can define the angle between the matrices $S$ and $T$ as that angle $\phi$

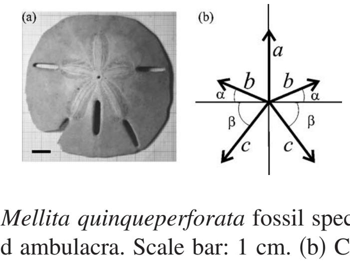

FIG. 1. (a) *Mellita quinqueperforata* fossil specimen displaying the five petaloid ambulacra. Scale bar: 1 cm. (b) Conventional representation of the ambulacra of irregular echinoids.

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$\in[0,\pi]$ that satisfies $\cos\phi=\langle S,T\rangle/\|S\|\|T\|$, where by $\|S\|$ we mean the norm induced by the inner product, namely $\|X\| = \sqrt{\langle X,X\rangle}$. If we define $S=AA^T$, Hadwiger's criterion becomes $S=\lambda I$, and we want to see what is the "angle" between $S$ and $I$, so

$$\cos\phi = \frac{\langle S,I\rangle}{\|S\|\|I\|} = \frac{\mathrm{Tr}(S)}{\sqrt{\mathrm{Tr}(SS)}\sqrt{n}}. \tag{2}$$

By the Cauchy-Schwarz inequality $\cos\phi=\pm1$ if and only if the vectors $S$ and $I$ are linearly dependent and, consequently, if and only if the star is eutactic. Thus, we propose $|\cos\phi|$ as a numerical measure of eutacticity. Notice that the expression (2) is invariant under scaling of $A$ and also under orthogonal transformations (change of the orthonormal basis).

The parameter $\cos\phi$ in (2) is capable of indicating the degree of eutacticity of a star which is not strictly eutactic, because the closer this quantity is to 1, the more eutactic the star is. This can be formalized as follows. Since we have already defined a bilinear symmetric positive-definite form in the vector space $M_{n\times n}$, let us consider the following decomposition of the "vector" $S$ as $S^{\parallel}$ and $S^{\perp}$: let $S^{\parallel}$ be the space spanned by the identity matrix $I$ (i.e., $S^{\parallel}=\lambda I$ for some real number $\lambda$) and let $S^{\perp}$ be the orthogonal complement. Clearly

$$S^{\parallel} = \frac{\langle S,I\rangle}{\|I\|^2} I = \left(\frac{\|S\|}{\|I\|}\cos\phi\right) I, \tag{3}$$

and $S^{\perp}=S-S^{\parallel}$. A simple calculation yields $\|S^{\perp}\|=\|S\|\sin\phi$, and thus for small values of $\phi$ we have $\cos\phi\approx1$ and $\sin\phi\approx0$. Consequently, for small values of $\phi, \|S^{\perp}\|$ is small and $S^{\parallel}$ is close to $S$. From (3), it is implied that $S\approx\lambda I$ for some real number $\lambda$. That is, small values of the angle $\phi$ imply that $\cos\phi$ is close to 1 and that the star is nearly eutactic.

For larger deviations of $\cos\phi$ from 1, we can use the geometric approach developed in Ref. [12] to show that $\cos\phi$ possesses a positive lower bound and, thus, $\cos\phi$ alone, without modulus, is a good measure of eutacticity. Consider, for example, the star formed by the following five arbitrary vectors in the plane: $\mathbf{a}_1=(a_{11},a_{12}), \mathbf{a}_2=(a_{21},a_{22}), \mathbf{a}_3=(a_{31},a_{32}), \mathbf{a}_4=(a_{41},a_{42}), \mathbf{a}_5=(a_{51},a_{52})$. According to Ref. [12], if the star formed by these vectors is eutactic, then the five-dimensional vectors

$$\mathbf{u} = (a_{11},a_{21},a_{31},a_{41},a_{51}),$$

$$\mathbf{v} = (a_{12},a_{22},a_{32},a_{42},a_{52})$$

have the same norm and are orthogonal. In this case, we also know that $\cos\phi=1$. Now, if the five-dimensional vectors $\mathbf{u}$ and $\mathbf{v}$ are not orthogonal, the star is not eutactic and the extreme case ("antieutacticity") occurs when these vectors are parallel. This can be only achieved with the following two-dimensional star: $\mathbf{a}_1=(a_{11},a_{11}), \mathbf{a}_2=(a_{21},a_{21}), \mathbf{a}_3=(a_{31},a_{31}), \mathbf{a}_4=(a_{41},a_{41}), \mathbf{a}_5=(a_{51},a_{51})$, (i.e., vectors with the same components). The application of (2) to this star yields $\cos\phi=1/\sqrt{2}$, which provides the lower bound for pentagonal stars in the plane. This argument can be easily generalized to stars formed by an arbitrary number of vectors $M(M>2)$ in the plane. Actually, similar arguments can be applied to stars in three dimensions, yielding $\cos\phi=1/\sqrt{3}$. By following the same procedure, it can easily be proven that for a star in a $n$-dimensional space, the lower bound is $\cos\phi=1/\sqrt{n}$. Observe that the value $\cos\phi=0$ can only be reached by a star in an infinite-dimensional space.

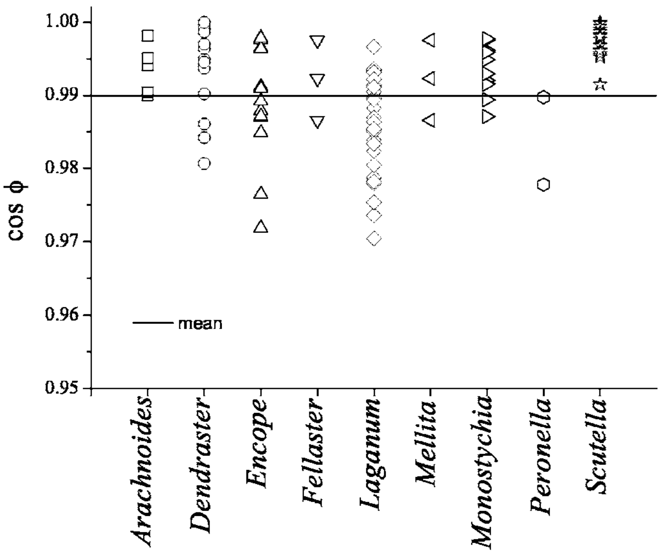

FIG. 2. Values of $\cos\phi$ for the 104 fossil specimens of the National History Museum of London. The studied echinoids fall into nine genera, indicated along the horizontal axis.

In this work, we shall consider stars formed by the five ambulacral petals of almost plane irregular echinoids. Thus, we study two-dimensional stars, and we are restricted to the case $N=5$ and $n=2$. Symmetries larger than 5 can be observed in echinoderms (notably sunstars) and these are treated in a similar fashion, but considering larger values of $N$.

## III. EUTACTICITY IN PLANE IRREGULAR ECHINOIDS

By using (2) we reanalyzed the experimental data of the 104 fossil specimens of the National History Museum of London, previously analyzed in Ref. [12] with a weak eutacticity criterion. Our results are shown in Fig. 2, where we can observe that the ambulacral patterns are all very close to being eutactic. The mean experimental value of $\cos\phi$ was 0.990 66 with a population standard deviation of 0.00 8617. To verify that this statistical tendency is not only the result of a random distribution of ambulacra during the evolution of these animals, without selection, only preserving bilaterality, we performed the following numerical experiment. Starting from the conventional plane representation of the ambulacra in irregular echinoids shown in Fig. 1(b), the values of the five free parameters ($a,b,c,\alpha$, and $\beta$) were chosen randomly in order to generate random echinoid-related stars, and we used criterion (2) to test the eutacticity of these stars. To account for the observed range of diametrical size values of the studied irregular echinoids, roughly between 1.5 and 10 cm, we used random values of $a,b$, and $c$ between 1 and 10. To preserve the actual existence of a *bivium* and a *trivium* of ambulacral petals [12], the values of $\alpha$ and $\beta$ ranged from 0

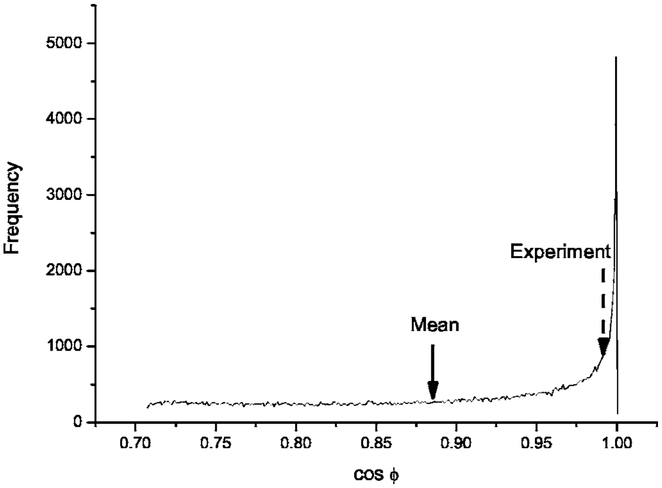

FIG. 3. Frequency distribution of cos $\phi$ values for 50 000 random stars. Arrows indicate the average of these numerical values and the average of the experimental data given in Fig. 2.

to $\pi/2$. In Fig. 3, the frequency distribution of cos $\phi$ values for 50 000 random stars is shown (for planar stars $1/\sqrt{2} \leqslant \cos\phi \leqslant 1$). The calculated mean value was $\overline{\cos\phi} = 0.893\,079$, with a population standard deviation of 0.09. Hence, the random eutacticity is clearly lower than the experimental one corresponding to measured irregular echinoids. Given this tendency, it is then natural to ask for the biological advantage that eutacticity may imply. We conjecture that it should be related to some structural adaptation facilitating the locomotion of these animals, which burrow just below the surface of sediments on the sea bottom.

## IV. DYNAMICS

Concerning locomotion, the five ambulacral petals [see Fig. 1(a)], are directly related, in a geometrical way, with the locomotive apparatus of irregular echinoids, and both of them exhibit similar geometrical morphology [14]. Thus, we simplified the locomotive apparatus by considering that the animal possesses five arms or legs, with the same disposition as the petaloid ambulacra of irregular echinoids.

As before, let $\{\mathbf{a}_1, \ldots, \mathbf{a}_M\}$ be a star in $\mathbb{R}^n$, with $n < M$, and let $A$ be its associated matrix. We will assume that $A$ has full row rank [Rank$(A) = n$] so the star spans the whole space $\mathbb{R}^n$. Now, let $\mathbf{P} \in \mathbb{R}^n$, be a goal location and consider the problem of reaching this target starting from the origin and using a locomotive apparatus represented by $A$. This is equivalent to the problem of finding $\mathbf{x}$ satisfying

$$A\mathbf{x} = \mathbf{P}. \tag{4}$$

There are many (infinite) solutions to this problem. In fact, if $A^*$ is the Moore-Penrose pseudoinverse [15] of $A$ then, since $AA^* = I$, one solution of (4) is

$$\mathbf{x}_0 = A^*\mathbf{P}.$$

This follows from the fact that, since $A$ has full row rank, it has a right inverse and this in turn implies that $A^*$ is a right inverse

$$A\mathbf{x}_0 = AA^*\mathbf{P} = I\mathbf{P} = \mathbf{P}.$$

The components of $\mathbf{x}$ (and of $\mathbf{x}_0$) indicate how many "steps" along vectors $\mathbf{a}_i$ one has to take in order to reach $\mathbf{P}$. Furthermore, the theory of pseudoinverses [15] indicates that $\mathbf{x}_0$ is the minimum norm solution, that is, $\|\mathbf{x}_0\|^2 \leqslant \|\mathbf{x}\|^2$ for any other solution $\mathbf{x}$. Having this in mind, it is adequate at this point to introduce a simplification, of the otherwise quite general motion problem, based on biological considerations. In particular, it seems justifiable that evolution seeks a configuration which permits minimal expenditure of energy for motion. This assumption can be reformulated as follows:

*Conjecture 1.* According to our simplified model, echinoids will move in such a way so as to minimize $\|\mathbf{x}\|^2$, i.e. the sum of the squares of the number of steps along the five vectors.

The minimal path problem previously stated is directly related with the following one: Find the extremes of

$$\Psi(\mathbf{P}) = \langle B^T\mathbf{P}, B^T\mathbf{P}\rangle, \tag{5}$$

subject to

$$\|\mathbf{P}\|^2 = 1,$$

where $B$ is a given real $n \times M$ matrix with $n < M$ with rank $n$ [16]. In order to use Lagrange's multiplier method to solve (5), we define the function

$$H(\mathbf{P},\lambda) = \langle B^T\mathbf{P}, B^T\mathbf{P}\rangle - \lambda(\|\mathbf{P}\|^2 - 1),$$

so the extreme points for the constrained problem are to be found among the extreme points of $H$.

The differential of $H$ can be calculated explicitly, yielding

$$dH(\mathbf{P},\lambda,\Delta\mathbf{P},\Delta\lambda) = 2\langle BB^T\mathbf{P}, \Delta\mathbf{P}\rangle - 2\lambda\langle \mathbf{P}, \Delta\mathbf{P}\rangle - \Delta\lambda\langle \mathbf{P}, \mathbf{P}\rangle + \Delta\lambda. \tag{6}$$

This means that extrema are to be found whenever $dH(\mathbf{P},\lambda,\Delta\mathbf{P},\Delta\lambda) = 0$ for all $\Delta\mathbf{P}$ and $\Delta\lambda$, so

$$BB^T\mathbf{P} - \lambda\mathbf{P} = 0, \tag{7a}$$

$$\langle \mathbf{P}, \mathbf{P}\rangle - 1 = 0. \tag{7b}$$

Thus, $\mathbf{P}$ must be an eigenvector of $BB^T$ and the Lagrange multiplier is the corresponding eigenvalue. But the $n$ eigenvalues of $BB^T$ are the squares of the $n$ singular values of $B$, and the eigenvectors of $BB^T$ are the left singular vectors of $B$. In short, the extreme points of $\Psi(\mathbf{P})$ subject to $\|\mathbf{P}\|^2 = 1$ are the left singular vectors of $B$. At an extreme point, the function $\Psi(\mathbf{P})$ has the value

$$\Psi(\mathbf{P}) = \langle BB^T\mathbf{P}, \mathbf{P}\rangle = \lambda\langle \mathbf{P}, \mathbf{P}\rangle = \sigma^2\|\mathbf{P}\|^2, \tag{8}$$

where $\sigma$ is a singular value of $B$.

Let us go back to original problem and consider the following: Find the extremes of

$$\|\mathbf{x}_0\|^2 = \|A^*\mathbf{P}\|^2, \tag{9}$$

subject to

$$\|\mathbf{P}\|^2 = 1.$$

By the previous results, with $B=A^*$, we conclude that the minimum of $\|\mathbf{x}_0\|^2$ is $(1/\sigma_1)^2$ whereas the maximum is $(1/\sigma_n)^2$, as it readily follows from the fact that the singular values of $A^*$ are the reciprocals of the singular values $(\sigma_1,\sigma_2,\ldots,\sigma_n)$ of $A$.

Now let us consider the possible advantage of eutacticity itself. Consider again the problem of reaching a given target $\mathbf{P}$ following certain steps $\mathbf{x}$ along a star contained in $A$ [Eq. (4)] and recall that $\|\mathbf{x}\|$ is taken as a measure of the "cost" of reaching the target. If the star were eutactic, the singular values would be equal, i.e., $\sigma_1=\sigma_2,\ldots=\sigma_n=\sigma$, where we have called $\sigma$ their common value. Then $\|A\mathbf{x}\|=\sigma\|\mathbf{x}\|=\|\mathbf{P}\|$ meaning that, in this case, the cost of reaching $\mathbf{P}(\|\mathbf{x}\|=\|\mathbf{P}\|/\sigma)$ depends exclusively on $\|\mathbf{P}\|$, the net distance to be traveled, and not on the direction of $\mathbf{P}$.

In summary, we have found that assuming minimal energy only yields The knowledge that the best direction to go and the best way to get there are given by singular values and vectors. With the further assumption that all directions should be equally cheap, we get eutacticity. Thus, we assume as conjecture the following:

*Conjecture 2*. The number of steps needed to reach a given $\mathbf{P}$ depends only on $\|\mathbf{P}\|$.

This has a peculiar implication: given an initial orientation for the five legs, the animal does not have to reorient itself in order to reach the destination at the same cost. From a biological point of view, the plausibility of this assumption is not completely clear. One can only invoke that the echinoid's lack of functional vision may imply that the animal does not needs to reorient its body depending on the position of the target.

## V. THE STABILITY OF EUTACTIC STARS

Finally, the eutacticity criterion (2) allows us to test the stability of some eutactic transformations [11,12,17] under small perturbations. We expect some eutactic transformations to be stable if biological evolutive systems have some preference for eutactic forms. Consider, for instance, the following eutactic transformation that is related with the morphospace of the plane irregular echinoids studied in Ref. [17]:

$$\mathbf{v}_1(\theta)=(-\cos^2\theta,-\sin\theta)/\sqrt{2},$$

$$\mathbf{v}_2(\theta)=(-\cos^2\theta,\sin\theta)/\sqrt{2},$$

$$\mathbf{v}_3(\theta)=(\sin^2\theta,\cos\theta)/\sqrt{2},$$

$$\mathbf{v}_4(\theta)=(\sin^2\theta,-\cos\theta)/\sqrt{2},$$

$$\mathbf{v}_5(\theta)=(\sin 2\theta,0)/\sqrt{2}.$$

The star formed by these vectors turns out to be eutactic for any value of $\theta$. In particular, for $\theta=\arctan(2)/2$, the vectors point to the vertices of a pentagon; for different values of this parameter, the pentagon is deformed but maintains bilateral symmetry. Now, we consider a small perturbation $\delta_j$ of the $j$th vector of the star, that is, the perturbed vector is $\mathbf{v}_j(\theta+\delta_j),j=1,\ldots,5$. By considering small perturbations ($\cos\delta_j\approx 1$ and $\sin\delta_j\approx\delta_j,j=1,\ldots,5$), after retaining terms up to order $\delta_j$, we obtain

$$\mathrm{Tr}(S)=2-\frac{1}{4}(\delta_1+\delta_2+\delta_3+\delta_4-4\delta_5)\sin(4\theta),$$

$$\mathrm{Tr}(SS)=2-\frac{1}{2}(\delta_1+\delta_2+\delta_3+\delta_4-4\delta_5)\sin(4\theta).$$

Thus, under criterion (2), the star is stable up to first order perturbations provided that $\delta_5=(\delta_1+\cdots+\delta_4)/4$, i.e., if $\delta_5$ is the arithmetic mean of the remaining perturbation factors. Since $\mathbf{v}_5$ is along the $y$ axis, the factor $\delta_5$ affects only the size of this vector. Thus, if arbitrary first order perturbations produce a noneutactic stars, it can become eutactic by an adequate rescaling of the vector $\mathbf{v}_5$.

In other words, we have a degree of freedom allowing the preservation of eutacticity under arbitrary first order perturbations $\delta_1,\ldots,\delta_4$.

An interesting observation comes from the analysis of a pentagonal star. The $j$th coordinate of a this star is $[\cos(2\pi j/5),\sin(2\pi j/5)]$, where $j=0,\ldots,4$, and one can verify that $\mathrm{Tr}(S)=5$ and $\mathrm{Tr}(SS)=25/2$, thus $\cos\phi=5/(\sqrt{25/2}\sqrt{2})=1$ as expected since the pentagonal star is eutactic. Consider now a small perturbation $\delta_j$ of the $j$th coordinate of the star, that is, the perturbed star has coordinates $[\cos(2\pi j/5+\delta_j),\sin(2\pi j/5+\delta_j)]$, where $j=0,\ldots,4$. The matrix $S$ can be evaluated and we obtain $\mathrm{Tr}(S)=5$, without restrictions on the perturbation factors $\delta_j$. To calculate $\mathrm{Tr}(SS)$, we consider small perturbations to get

$$\begin{aligned}\mathrm{Tr}(SS)=\frac{25}{2}&+\sum_{j=0}^{4}\delta_j^2-\left(1+\sqrt{5}\right)\delta_1\delta_2+\left(-1+\sqrt{5}\right)\delta_2\delta_4\\&-\left(1+\sqrt{5}\right)\delta_3(\delta_2+\delta_4)+\left(-1+\sqrt{5}\right)\delta_1(\delta_3+\delta_4)\\&-\delta_0\big(\delta_1+\sqrt{5}\delta_1+\delta_2-\sqrt{5}\delta_2+\delta_3\\&-\sqrt{5}\delta_3+\delta_4+\sqrt{5}\delta_4\big)+\mathcal{O}(3,4).\end{aligned}$$

Clearly, by retaining terms up to order $\delta_j$, we obtain $\mathrm{Tr}(SS)=25/2$. Thus $\cos\phi=1$, and the star is eutactic up to first order perturbations. As it is well known, irregular echinoids appear in a late geological period, compared with regular ones. This evolutive persistence of regularity agrees with the fact that a pentagonal star remains eutactic even under these first order perturbations.

## VI. CONCLUSIONS

It is expected that the property of eutacticity, or regularity, may arise in different realms. In this work, we explore the possible biological advantages that eutacticity may imply for movement by irregular echinoids. First of all, a reliable numerical criterion for eutacticity adequate for experimental measurements is proposed. This criterion is capable of measuring how closely the eutacticity criterion is satisfied in experimental measurements and allows us to test both the statistical tendency toward eutacticity of irregular echinoids and the stability of some eutactic stars under small perturbations. The biological advantage of eutacticity was addressed as a minimal path problem. By simplifying the anatomy of echinoids, we consider an echinoid possesing five arms and postulate the following two conjectures:

(1) In our simplified model, echinoids move in such a way so as to minimize the sum of the squares of the number of steps along the five "legs."

(2) The number of steps needed to reach a given target depends only on the net distance to be traveled.

If these two conjectures are true, the geometrical arrangement of the five petaloid ambulacra of regular or irregular echinoids should form a eutactic star in order to optimize locomotion from point to point in space.

Finally, it is suitable to remark that all the stars considered in this work have bilateral symmetry. Bilaterality is present in most of the biological systems. In echinoids, the problem of the relationship between the evolution of bilateral symmetry and the presence of a locomotor anterior end is experimentally studied in Ref. [18]. Given this relevance of bilaterality, the relationship between bilaterality and eutacticity is a topic that deserves a deeper independent study, which would be the subject matter of a future publication.

## ACKNOWLEDGMENTS

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$$\sup_{\|\mathbf{P}\|=1}\{\Psi(\mathbf{P})\} = \sup_{\mathbf{P}}\left\{\Psi\left(\frac{\mathbf{P}}{\|\mathbf{P}\|}\right)\right\},$$

and it should be noticed that (i) the set $V=\{\mathbf{P}\,|\,\|\mathbf{P}\|=1\}$ is a closed and bounded subset of $\mathbb{R}^n$ and, consequently, compact; (ii) the function $\Psi$ is continuous. Then, by a well-known theorem of calculus, the function $\Psi$ attains its maximum and its minimum in $V$.

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