

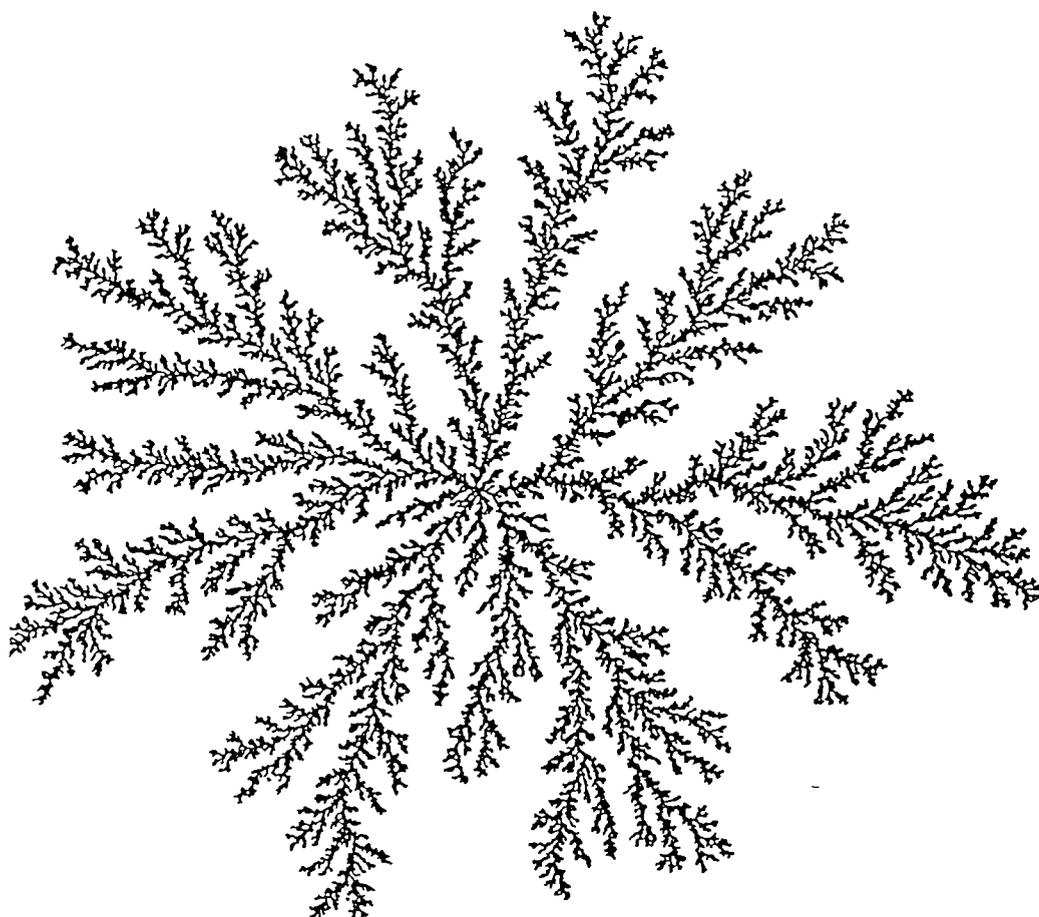
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DLA fractal cluster
of 10^6 particles

VOLVOX: A SIMPLE EXAMPLE FOR SPONTANEOUS SYMMETRY BREAKINGS

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Abstract: *Three spontaneous symmetry breakings of Volvox aureus are discussed from the viewpoint of symmetry.*

1. THE PROBLEM

Volvox is worth for mention when the topic is the evolution of symmetries. Some reasons are listed below; the statements are not new at all, for details see any textbook of phytology.

Some *Volvoces* are as spherical as possible, having so $E(3)$ or at least $SO(3)$ symmetry, the hypothetical starting point of form evolution (Lukács, 1993b; Bérczi, Lukács, and Molnár, 1993). While *Volvocaceae* do not possess true tissues, in the advanced colonies (*coenobia*) two different kinds of cells exist (vegetative and sexual) and the pattern does not follow the spherical symmetry of the shape. So in this simple “plant” at least three (probably correlated) spontaneous symmetry breakings are manifested.

The problem is important, since *Volvox* is an excellent analogy of the intermediate evolutionary steps leading to *Metaphyta*. *Volvox* is only an analogy, a product of parallel evolution; still its ancestral *Flagellatae* must have belonged to the same subregnum of *Sarcomastigota* as the ancestors of *Metaphyta* and *Metazoa* (Cavalier-



Smith, 1987). The obvious animal counterpart is *Mesozoa* (e.g., *Dicyema*), but there at least one symmetry breaking is absent, the sexual cell being at the symmetry center.

2. BROKEN SYMMETRIES: FACTS

Volvox aureus consists of some thousands of *flagellates* located on a surface of a sphere, kept together by a jelly and connected by plasma bridges. First all seem equivalent green vegetative cells, able to reproduce *themselves*: the small proto-colonies descend into the central part of the sphere, grow, and finally leave the mother colony, disrupting it. But in some stages a *few* cells transform themselves into sexual ones (SPONTANEOUS SYMMETRY BREAKING (LATER ON SSB) 1: SIMILAR CELLS HAVE DIFFERENT FATES; SSB2: THE TRANSFORMATION CHOOSES SOME POINTS ON A SYMMETRY SURFACE), either into larger ova, or dissolving into (say 2⁷) sperm cells (SSB3: THE GAMETES FROM SIMILAR CELLS ARE DIFFERENT); one colony produces only one kind of gametes, although both the original vegetative cells and the male and female *Volvores* are similar. The diploid zygote is the ancestor of a new colony.

Certainly these symmetry breakings have natural explanations, but still beyond the horizon. However we hope to be able to single out the *directions* in which they lie.

3. ENTROPIES

All the differences and symmetry breakings come from either evolution or ontogeny. A traditional and permanent idea is the existence of some 'merit' continuously growing. For such, physics suggests entropy-like quantities; see e.g., (Eigen, 1971; Lukács, 1990). Recently Martinás and Molnár have suggested a formal axiomatic framework for a thermodynamic-type formalism to be applied in biology (Martinás and Molnár, 1991). The axioms are obviously devoid of self-contradictions, being direct derivatives of the first 3 Callen axioms of Gibbsian thermodynamics (Callen, 1960). However, for us, it is hopeless to derive the above mentioned spontaneous symmetry breakings from such an axiomatic formalism. First, pure axioms very seldom lead to specific results. Second, the simplest living systems have dozens of simultaneous reactions, involving hundreds of material components. While an entropy, ekaentropy, entropy production, progress function or anything else may quite be a function of these components, their densities, currents or change rates, and may tend to extremum, at this number of independent variables no practical thermodynamic calculation seems possible. Finally, our *guess* (reasoning below) is that *two* different (but possibly connected) analogons of entropy are behind this problem. We will colloquially use here the idea of entropy-like quantities, because it is easy to visualize the possibility of *spontaneous* symmetry breaking if *anything* is to be maximized: e.g., when the symmetric configuration is not the maximum but, the minimum (Lukács, 1993a).

Now about the two extremum principles. It is easy to accept that natural selection maximizes *something* determining survival (Eigen, 1971; Lukács, 1990). But it is the survival of genetic information, not of soma, so the quantity, called here \mathcal{Q} , seems

to depend on the genetic information (as, e.g., *allele* frequencies). On the other hand, mature individuals, carrying and propagating this information, are results of ontogenic changes, during which a (partially unknown) extremum principle of the thermodynamics of open systems must hold (Glansdorff and Prigogine, 1971), called here U , depending on matter concentrations and currents. Therefore Q differs from U . (The rather exotic notation emphasizes the lack of definite forms and prevents any premature identification to thermodynamic quantities or to the 'progress function' Z of (Martínás and Molnár, 1991) whose connection to these quantities are utterly awkward.) *Compatibility* relations (of still unknown structure) must exist between Q and U , since the ontogenic changes have genetic determination.

Since no serious suggestion has ever been made for the forms of extreme quantities, now we may proceed through the 3 spontaneous symmetry breakings, backwards.

4. ON THE DIMORPHISM OF GAMETES

We chisel the details of this point, being the less hopeless without the nonexistent complete description. But first let us repeat some common opinion that sexual procreation is preferred for mixing independent genomes; then selection is faster so Q grows faster. Then consider cells of mass M dividing into *unequal* gametes $M_{\pm} = M - (\pm X)$, X having a distribution $p_i(X)$, i for generations. The p_i is genetically determined and its parameters roughly average in mixing, so in the usual 'reaction kinetic' approach

$$p_{i+1}(X_+)p_{i+1}(X_-) \approx C_{i+1}p_i(X_+)p_i(X_-)Q(X_+, X_-) \quad (4.1)$$

where C is a normalising constant and Q expresses the chance to meet *and* survive (so $Q(X_+, X_-)$ is a poor 2-variable 'projection' of Q). Q grows with growing zygote lifetime, so with M_{\pm} , but also with relative velocities. At constant propelling force in a resistant medium the acceleration is inversely proportional to mass, while stationary velocities decrease with the size in a way depending on details. For simplicity we take $v_{\pm} \sim 1/M_{\pm}$. So the product of lifetime and flux is growing with unequal divisions $M_{\pm} > 0$. Eq. (4.1) can be approximately evaluated assuming Gaussian distributions with constant width σ and mean Y_i ; then it is a single recursive equation for Y_i . The Figure shows a calculation in the simplest model with some arbitrary choice of parameters

$$x \equiv \gamma v_{\text{rel}}; \quad \gamma = M_+ + M_-; \quad v_{\text{rel}} = (v_+^2 + v_-^2)^{1/2}; \quad Q = \text{th } x \quad (4.2)$$

$$v_{\pm} = (M_{\pm} - m)/(0.1 + M_{\pm}(M_{\pm} - m)); \quad M = 1, m = 0.1, \sigma = 0.2$$

(everything in dimensionless units). Here m is the irreducible mass of the gamete, with $M_{\pm} > m$ there is no fuel; the chosen form of v_{\pm} is to get small v in the neighbourhood of m . With the present parameter values and functional forms the sexual dimorphism tends to $\langle X \rangle \approx 0.67$; different parameters lead to different $\langle X \rangle$'s. THE SYMMETRIC GAMETE CONFIGURATION IS UNSTABLE.

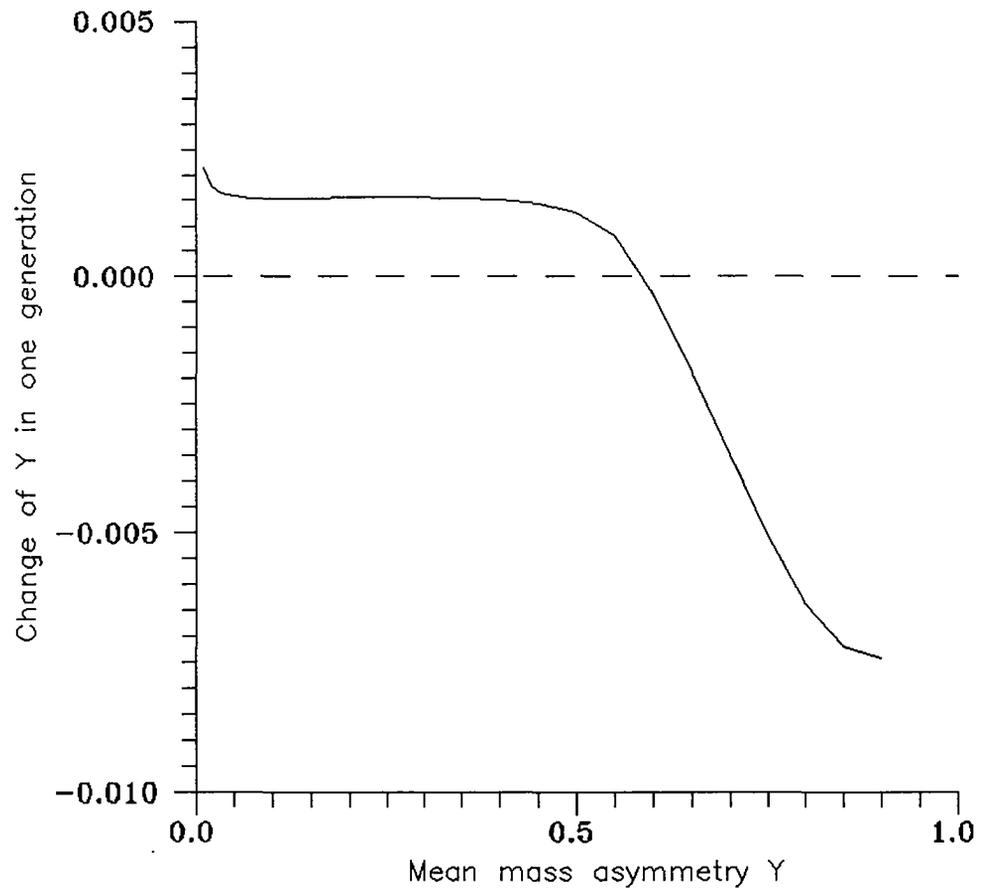


Figure: Change of the mean asymmetry Y vs. Y with the model and parameters of (4.2). Different parameters would lead to different stable point.

5 SPECIAL POINTS ON A SYMMETRIC SURFACE

Some few cells are selected for sexual fate, we do not know how. But cases are known in physics when currents or dissipation lead to asymmetric spatial pattern in a symmetric geometry. The most familiar example is *turbulent* mechanical flow of velocity v , density ρ and viscosity η between infinite plates separated by L . The symmetric *laminar* flow is stable if

$$R \equiv \rho v L / \eta < R_{crit} \sim 1160 \quad (5.1)$$

where R is the Reynolds number. Above R_{crit} the plane-symmetric pattern is unstable.

Now, Prigogine showed examples for spatial pattern formation in open thermodynamic systems. Details are pointless until somebody shows a relevant approach to describe *Volvox* in the thermodynamics of open systems, since the specific pattern is very model-dependent; however a nonsymmetric pattern of *something* (e.g., a concentration) may appear on the symmetric surface of *Volvox*. Complete spatial symmetry is broken via *U*.

6. DIFFERENT FATES OF EQUIVALENT CELLS

This last symmetry breaking now has got its natural explanation. *Q* prefers a few sexual cells. Then *Volvox* can adapt (*Q*) that slight differences of some concentrations be able to trigger transition into sexual activity, and the spatial pattern has been generated by *U*. (Maybe a stage of ageing is also needed, which is again *U*.)

7. CONCLUSIONS

The description of even such a simple organism as a spherical *Volvox* by thermodynamics of open systems is beyond the present horizon. Formal approaches give little help. Still, the picture seems *qualitatively* coherent and at some minor points *semiquantitative* treatment is not utterly impossible. Computer simulations of *Volvox* utilizing the listed symmetry breaking rules are going to start.

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