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SELF-ORGANIZING MORPHOGENETIC MECHANISMS AS PROCESSORS OF EVOLUTION

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ABSTRACT

Many organismic shapes and ornamentations are analogous to self-organizing patterns in the non-biological world. It is suggested that responsible processes become first serendipitously "adopted" by developmental systems and then "tamed" by Darwinian selection as soon as a specific function has been acquired. Yet, taming can only reduce, but not eliminate, the unpredictability of the dynamic systems at the local level.

Keywords: Morphodynamics, Inorganic and Organic Pattern Formation, Dynamic Systems, Evolutinary Theory.

RESUMEN

Muchas de las características de la forma y de la ornamentación de los organismos son análogas a las pautas auto-organizativas en el mundo inorgánico. Se sugiere que los procesos responsables de ello son "adoptados" por los sistemas en desarrollo, al principio, de un modo que, para definirlo, podríamos usar el conocido término "serendipity"; luego son "domados" por selección darwinista tan pronto como adquieren una función específica. Sin embargo, la doma puede sólo reducir, pero no eliminar, la impredecibilidad de los sistemas dinámicos a nivel local.

Palabras clave: Morfodinámica, Formación de Patrones Inorgánicos y Orgánicos, Sistemas Dinámicos, Teoría Evolutiva.

INTRODUCTION

Ever since it was discovered that dynamic systems produce fascinatingly ordered patterns in physical reality and on computer screens (see Gleick 1987 for a popular treatment), naturalists have been wondering about the meaning of chaos for biological diversity. Equally, the symmetries involved in the smooth spiral of a *Nautilus* shell, the hexagonal meshwork of radiolarian skeletons, the regular dome shape of an echinoid test have counterparts in the physical world (D'Arcy Thompson, 1917). We may discard such similarities as fortuitous, but we may also assume that similar rules are at work in the physical and the living world. In the second view, many biological structures become "self-organized" in the sense that the genome does not code for them directly in the mode of a specified blueprint, but turns on autonomous morphogenetic mechanisms by creating the right developmental environment at the right time and place. To emphasize this quasi-autonomy, such mechanisms and their results are called "epigenetic"; but because dynamic self-organization and genetic causations are inseparably coupled, the distinction is largely a matter of view point. In the present essay I advocate for the epigenetic perspective and claim that the recognition of self-organizing mechanisms does have an explanatory value in development and evolution. I also use the term "morphodynamics" in place of the more restricted concept of constructional morphology (Seilacher, 1970). In the morphodynamic view, the old triangle of phylogenetic, fabricational and functional constraints is transformed into a tetrahedron by addition of the "effective environment" (Fig. 1), i.e. the set of environmental factors, and their relative importance, that are recognized by, and relevant for, a particular group of organisms and their developmental and evolutionary transformations.

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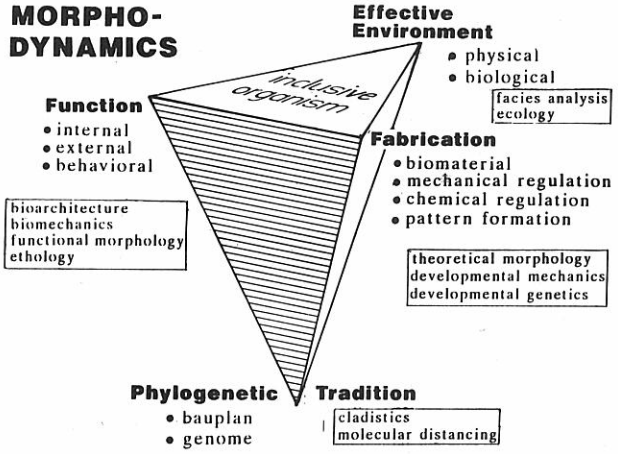

Figure 1. By including the effective environment, the concept of biological morphodynamics expands the original triangle of constructional morphology (shaded). Also listed are relevant processes and structures and established avenues of research (in boxes).

A. WORKING PROCEDURES

Visual recognition and comparison of patterns is the firs step in every analysis. At this stage, drawing specimens with the camera lucida is a great help, because it sharpens our sense for repetition. Such observations show that patterns are real, but vary between individuals, between ontogenetic stages and even between the right and left sides of bilaterally symmetrical organisms (Fig. 2). Int the latter case, genetic mutants could hardly be responsible for the difference, unless being somatic and therefore without consequences for the offspring. If desired, morphometric methods may be applied. They add numerical rigor and, when used not as a blind technique but in connection with clear biological concepts, may also reveal relationships that the eye would have missed. But what biometric procedure could ever reach the level of recognition needed for the eye's daily task of distinguishing human faces and their momentary moods?

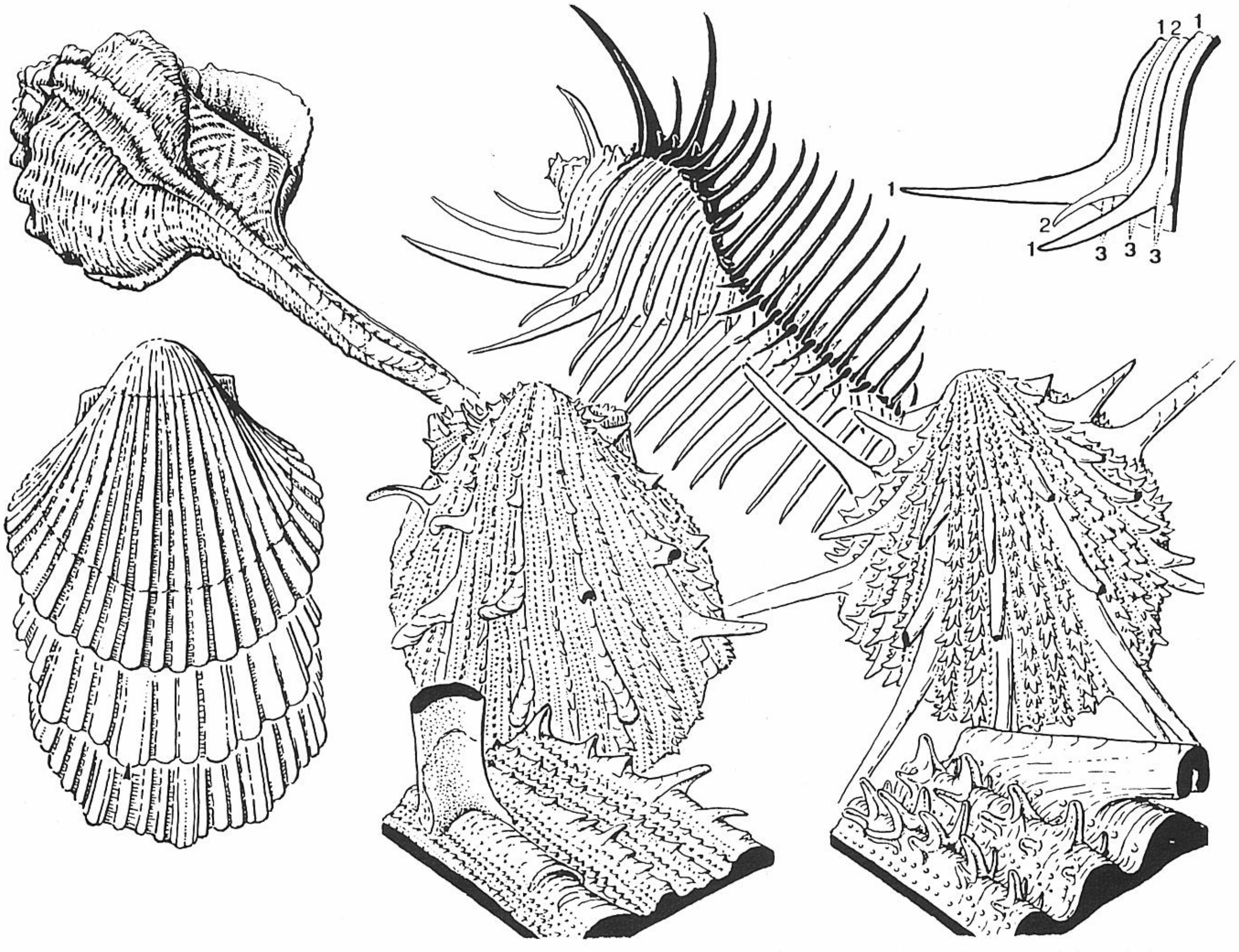

Figure 2. Mollusc ornamentations reflect the rhythmic change of cell states along the shell-generating mantle edge. In normal ribs, generating points maintain their relative positions. In pectinid bivalves (lower row), *Neithea* may retain the original intercalational hierarchy (three junior ribs between two senior ones), enslave one of the juniors by a senior rib, or produce associate riblets in addition. In most *Spondylus* species every rib order produces spines in its own appropriate size and rhythm. In the junior ribs of *Spondylus mirabilis,* however, smaller spines fire simultaneously with the larger ones to form tridents except for local disobedience. In muricid gastropods (upper row), spine formation is released by a single varix signal, to which ribs respond in the succession of their hierarchical order. This causes the angular spine positions that *Murex pecten* (right) uses for making a cage under the siphon. In *Haustor* the free inner lip, lacking the program for normal ribbing, uses a divaricate pattern to strengthen the temporary wall at every varix.

While regularities and variational modifications may already allow us to formulate hypotheses about underlying mechanisms, morphogenetic defects in pattern formation are even more revealing. They will be more common in mollusc shells exposed to predatorial attacks than in fingerprint patterns that have become established while the embryo was still in the womb. Nevertheless the case of echinoid tests growing into aberrant shapes in polluted waters (Dafni, 1986) should encourage the search for telling teratologies in modern and fossil examples.

In a third step we may search for analogies in the physical world and try mechanical and computer simulations. We should remember, however, that similar outcomes may refer only to the rules and not to the chemical or mechanical causations.

B. SYMMETRIES

Symmetry (radiality, polarity, bilaterality, segmentation) in metazoans reflects the sequence in which a hierarchically organized genome turns on the initial morphogenetic processes. *Drosophila* studies have revealed the details. On the other hand, Ediacaran organisms (Vendozoa; Seilacher, 1989) of the late Proterozoic show that large and morphologically differentiated organisms can form without entrenched hierarchy. In their plastic developmental system the first steps appear to have been highly variable between closely related species, resulting in radial, bilateral, bipolar or unipolar symmetries reminiscent of jelly-fish, seapens or annelids in metazoan-world terms. Vendozoa also lacked a morphological differentiation between dorsal and ventral sides. In contrast, the mode in which constant width of the "segments" was maintained during further growth is a more distinctive feature. While diverse forms in the Australian fauna introduce new quiltings by marginal addition, intercalation or dichotomous bifurcation, similarly diverse body plans from Newfoundland use almost exclusively a fractal mode to subdivide segments as they expand during growth. The unifying characteristic of all Vendozoa, however, is their construction as quilted pneus. Like in an air mattress (but filled with living fluid!), this hydrostatic construction allowed to maintain foliate shapes, maximize external surface and minimize the distance of any part of the internal fluid from the body wall without the use of mineralized skeletons.

C. PNEU MORPHOLOGIES

Hydrostatic "pneu" structures are ubiquitous not only in Vendozoa, but also in the morphologies of soft-bodied metazoans and internal organs. More interesting for paleontologists, most hard parts may also be seen as mineralized pneus. By converting the shapes of tensional lines or membranes into rigid material, organisms produce skeletons that are automatically optimized against compressional deformation —just as the architect Gaudí did, when he designed the breathtaking domes of the "Sagrada Familia" in Barcelona. This rule allows arthropod skeletons to form anew after each moulting. Since they do not have to grow between moulting phases, almost any skeletal shape and ornamentation is possible.

Echinoids:

Regular echinoid tests do grow, but still have pneu geometries. They are probably pressurized as tensional balloons during short periods of growth, as their Paleozoic ancestors with scale-like plates had to be all the time. In waters polluted by decalcifyers from washing powder, the necessary balance between hydrostatic pressure and internal or external tethering becomes upset. The result are teratological specimens whose shapes resemble gourds rather than melons (Dafni, 1986) —almost as spatangoid tests do in normal development.

The shapes of echinoid test plates are also pneu-controlled. Since trabecular calcite (stereom) is filled by a syncytium (stroma), every plate correponds to a single giant cell. So, as in a layer of soap bubbles, their close packing automatically produces the hexagonal shapes required for an optimal plate dome. In this case we need no teratologies to prove the model. The rule that smaller bubbles, or stroma cells, should indent the larger ones can be checked in most regular echinoids: small ambulacral plates produce serrated sutures on their large interambulacral neighbors.

Mollusc Shells:

The regular shapes of mollusc shells can be described and computer-simulated in terms of Euclidean geometry (Raup, 1966; Savazzi, 1990; Okamoto, 1988; Ackerly, 1989). They grow as straight cones or in logarithmic spirals by regular expansion of a given generating curve. In biological reality this curve corresponds to the free mantle edge, which is linked to the shell margin by a skin of periostracum. Since both structures are fluid-filled (by coelomic and extrapallial fluid, respectively), they can be considered as thin hydrostatic sausages. Thus their smooth curvature is as self-organized as in a blown-up inner tube or in the sausages hanging from the rack of a butcher's shop. Only the superimposed keels and ribs need a special morphogenetic explanation.

D. ORNAMENTATION IN MOLLUSC SHELLS

It is unknown what makes local cell groups in a molluscan mantle edge deviate from the smooth pneu curve to produce keels, ribs and spines in the growing shells. But even if we knew the "morphogenetic substances" involved, this would tell us little about the dynamic rules of their distribution through ontogenetic time. Nevertheless, such rules can be hypothetically modeled from observed patterns and defects.

The case of "radial" ribs normal to the growing margin is straightforward. Such ribs can be inserted into the computer simulation by simply tracing a given number of points through isometric spiral growth. Things become more difficult if rib growth is allometric. As the shell becomes larger, new normal ribs may be added either by dichotomous bifurcation or by intercalation. Bifurcation leads to different orders of ribs in a historic sense, but at any moment in ontogenetic time all rib loci would be of equal ranks. New ribs introduced by intercalation, however, are smaller than their senior neighbors. If growth is regular and a new rib is intercalated every time the space between older ones reaches a certain threshold, there will eventually be a hierarchy in which rib loci of descending ranks alternate regularly along the mantle margin.

It so happens that the bifurcating mode is virtually unknown in mollusc shells (while it characterizes vein patterns in fern leaves and septal pattern in heterocorallia). Intercalation, however, is common in gastropods and some bivalve families (as it is in scleractinian septa). Also, intercalational hierarchy has become an important template for producing spines of different size, distancing and angular position in both groups (Fig. 2).

A third method (also characteristic for rugose coral septa) is the introduction of new equidistant ribs in serial succession. This mode, however, is so incompatible with isometric spiral growth that the ribs run at an angle to both, growth tracks and growth lines. Although such "divaricate" patterns are difficult to accommodate in the simple computer model, they are not only very common in mollusc shells, but also appear as ribs, color or mineralization patterns (Seilacher, 1972).

E. ZEBRA PATTERNS

Another principle is most typically expressed in expanding skins. Leopards, tigers, zebras and our own fingerprints are familiar examples in the biological world (Fig. 3) and Bénard cells in physics. The latter

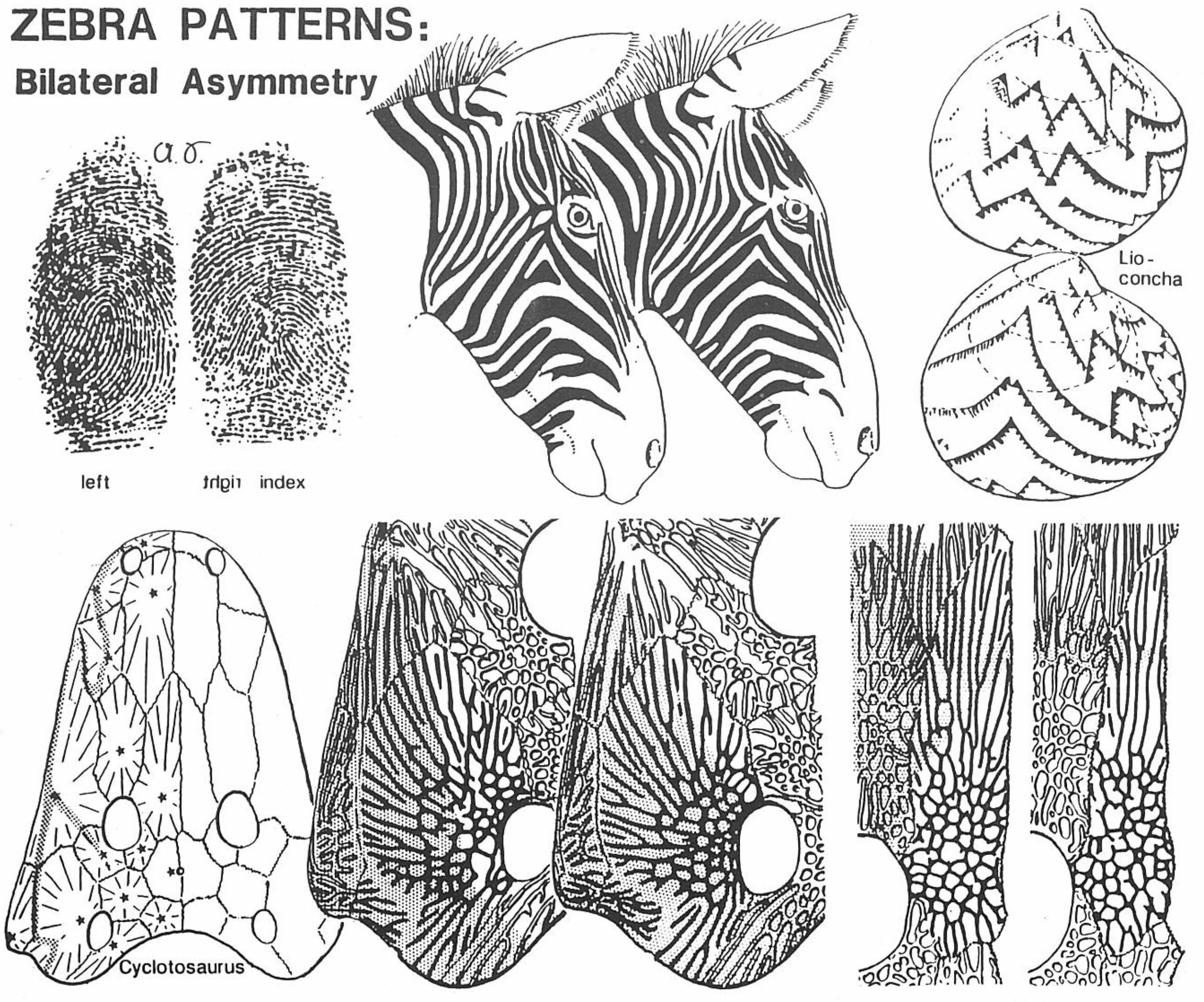

Figure 3. Zebra and other patterns related to self-organizing morphogenetic processes are never perfect mirror images on the two sides of bilateral organisms. This is also true for elements of the ammonite suture. The seeming exception (sculture of a Triassic stegocephalian skull) is a human artefact: stippled areas were restored by the preparator.

originate by the establishment of equal-sized convection cells in fluid sheets heated from below, but diffusion and the wrinkling of drying oil paint may produce similar patterns. What these processes have in common is the spontaneous establishment of a critical distance and the close packing of equidimensional realms in a surface. Fossilizable fingerprint patterns are found in the shells of Paleozoic ostracods *(Richterina),* on the outer side of some gastropod opercula *(Turbo)* and on the surface of agnathan fish skulls. In all these cases the sculptures were produced more or less simultaneously by skin coating the hard part from the inside (ostracods) or outside.

Divaricate patterns, in contrast, arise from marginal growth and record the dynamic migration of cell states along the mantle edge through accretional growth. In unconfined situations they begin with a point and spread towards the margin as chevrons or triangles. If crowded, however, they form regular sets of oblique ribs or color bands reminiscent of true zebra patterns. Still, the old triangular nature becomes visible where the mantle had locally lost the morphogenetic information by injury. Regeneration starts with chevrons (zig-zag anomalies: Seilacher, 1972) before the lines get again crowded into oblique sets —a sign that the original potentials have not been lost.

F. FRACTAL DENDROIDS

Dichotomous bifurcation is one of the means, by which fractal patterns can be created in nature and in the computer. If splitting occurs at a very low angle (as veins in gingko and fern leaves) it produces an array of almost parallel lines similar to intercalating ribs. If the angle becomes larger, more and more branches get stopped by near-collision with previous ones and the remaining branches become coiled into ever smaller spirals. As other fractals (Mandelbrot, 1982), this seemingly complex pattern is self-similar at various scales and originates by the continuous repetition of a simple program. The pelagic crinoid *Scyphocrinites* (U. Silurian) used this principle for the construction of its buoy (Haude, 1972). In one version of these "loboliths" the nested spirals of branching root cirri enlarge by growth of the constituent ossicles, allowing ever smaller spirals to evolve within the expanding spaces. In another form (plate loboliths), outer ends of the cirri transform into an array of larger and smaller hexagonal plates that looks like a minute version of a *Glyptodon* carapace. Both methods did allow the gas-filled lobolith to expand and provide the growing crinoid with additional buoyancy.

As another expanding structure, angiosperm leaves have veins following a similar branching pattern as the cirri in a lobolith. Still, spiral veins are seen only in primitive species. In more advanced groups an ever larger percentage of branches links with higher order ones to form a network of hierarchical meshes (Fig. 4).

As a third example we cite the dentitions of Mesozoic sharks (Hybodontida). In the slender teeth of *Hybodus,* ribs branch rarely and at a small angle, so that they run down the cusps almost parallel to each other. In the more obtuse *Acrodus,* branchings are more common and rib patterns resemble river systems. In the closely related, but flat-toothed, genus *Palaeobates,* ribs branch still more frequently and with wider angles and as a consequence fuse into a meshwork. Thus, the same morphogenetic mechanism serves, in combination with different tooth geometries, to generate patterns fitting the needs of carnivorous as well as durophagous species. That this mechanism nevertheless retains its autonomy is shown not only by teratologies (*Acrodus* teeth with twin cusps), but also by complete dentitions: teeth in one cross series never show identical rib patterns, although they originated sequentially from one and the same mold (Seilacher, 1973).

G. AMMONITE SUTURES

Let us return to molluscs. Among these, ammonite shells are the most fascinating because they combine Euclidean geometry (shell spiral), pneu geometry (anticlastic septal surfaces) and fractal geometry (suture lines) in a single structure. Since septa are built into the spiral shell secondarily, one might tend to consider them as independent entities, which they are not. Septal shapes in nautiloids vary with the shape of the whorl sections in the same way that a rubber balloon does when inflated in such a shell: keels in the outer shell induce saddles, flattened parts produce shallow lobes. To make the frilled ammonitic suture, this principle must be combined with the establishment of tie points for the attachement of mantle muscles in lobe positions. Drastic changes in whorl section during early ammonite ontogeny suggest that the tie points of the primary lobes are partly induced by shell geometry. Typical goniatites leave it at that, or rather fix the mantle septum at the primary lobes and blow out the saddles between them before they are also attached. Ammonitic suture lines are much more complicated. In fact, their frilling at ever smaller levels with self-similar repetitions has the characteristics of a fractal structure (Mandelbrot, 1982). Even fractal dimensions have been determined (Boyajian, 1990). But such statements are little more than descriptions and leave the mechanism open, by which the differentiation was achieved and the information carried on to the next septal position. The same is true for the viscous fingering model (García-Ruiz & Checa, 1990), although this analogy implies also the pneu-related roundishness of lobes and lobules, which remains a characteristic of ammonite sutures.

The proposed model (Seilacher, 1988) assumes that muscular tie points were not only introduced in fractal and hierarchic succession (primary ones by changing shell shapes, secondary ones by intercalation).

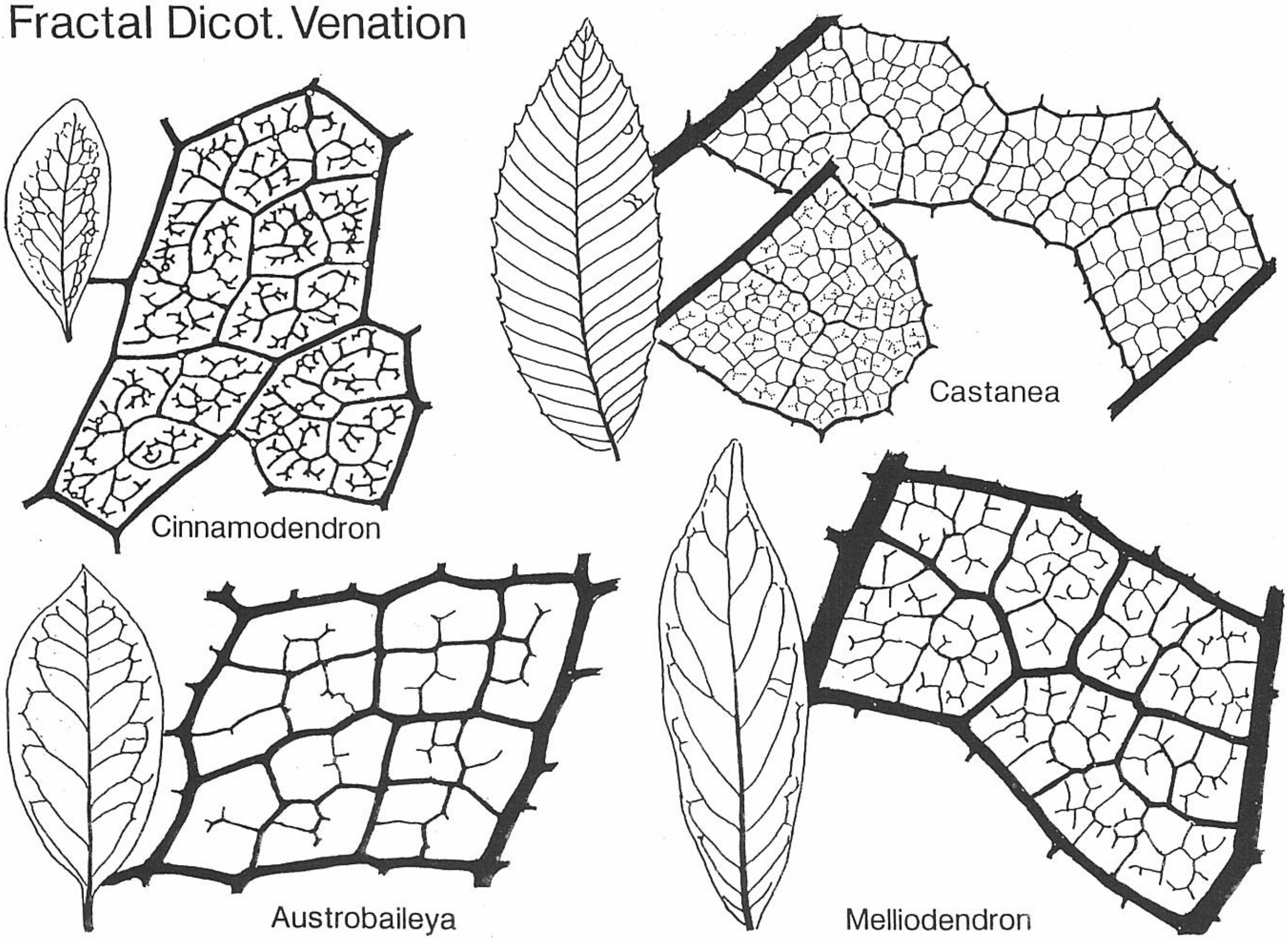

Figure 4. Dicotyledonous angiosperm leaf venation fills the expanding leaf area with nested systems of self-similar fractal dendroids. In the primitive genus *Cinnamodendron* the pattern appears complex, because only few branches manage to link with senior ones to form meshes (small circles), while the others keep bifurcating into ever smaller trees and spirals. In more advanced forms, linkage rate is much higher, although the principle of fractal differentiation remains the same (from preparations kindly supplied by Leo Hickey, Yale University).

They also got attached to the shell wall in their sequence of origin at every subsequent septal position. Thus it becomes understandable that in rib spaces (where the body sack must expand) lobe amplitudes increase, rather than smoothing out. The ordered sequential attachment of tie points also allowed a unique kinetic mechanism. Driven by osmotic pressure in the preseptal space (which also causes the sections between tie points to bulge in an apertural direction), the body sack could "walk" to the new septal position without ever giving up its tension by purchase to the shell wall. In the case that there was (in contrast to *Nautilus)* gas in the preseptal space, the lobe and saddle muscles could also have been used antagonistically to induce downward and upward movement in the mode of an active Cartesian diver.

H. EVOLUTIONARY CONSEQUENCES

The quasi-autonomous nature of morphogenetic mechanisms strongly changes our view of the evolutionary process:

1. New morphological traits can be expected to appear suddendly rather than being gradually built up from scrap.
2. They are likely to first show the full variability potential of the new fabricational mechanism and to become trimmed by selection towards an emergent functional paradigm at a following stage.
3. Being initially non-adaptive, the "adoption" of fabricational innovations lacks Lamarckian undertones, while their subsequent "taming" for specific functions is a strictly Darwinian process.

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