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Evolutionary basins of attraction and convergence in plants and animals

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Living organisms evolve, in part, according to the underlying properties of the amino acids and other compounds of which they are composed. Thus there are evolutionary basins of attraction that living organisms will tend to evolve toward. These processes are complex and probably beyond our current capabilities to fully envisage. But progress is being made toward an understanding of such principles by efforts to catalog protein folds and protein–protein interactions. Even plants and animals show convergent evolution, possibly driven by underlying evolutionary basins of attraction. Physical and chemical parameters and the properties of proteins present in the last common ancestor of these 2 taxa, including a putative connexin ancestor, may have played key roles here. Thus evolution is perhaps not as random as is sometimes depicted, but will follow predefined pathways. Here I address convergent evolution in plants and animals beginning at the molecular level and progressing to the organismic one.

Introduction

All lineages of living organisms are subject to evolutionary pressures that dictate that they are constantly evolving over time. From Weinreich et al. 2013:[1] "In 1932 Sewall Wright introduced the notion of the fitness landscape. By analogy with a physical landscape, whose gradient predicts a rolling marble's spatial trajectory, the contours of the fitness landscape are meant to predict an evolving population's genetic trajectory." A study on a computational model of protein folding and binding called "lattice proteins" discovered an important evolutionary principle related to the idea of the fitness landscape. "…the mutational landscape, the fitness landscape (binding process), and the genotype–phenotype map (folding process), together with the other scenario details, define a multi-dimensional set of evolutionary 'pathways' that the descendants of a given founder are likely to follow."[2] In addition, "Although these high-dimensional pathways are difficult for us to visualize, they are persistent across replicates of a given scenario. They describe basins of attraction that pull the lineages through the evolutionary process, to repeatable outcomes." Similarly, another study on equilibrium in games[3] states that "…the basic intuitions behind the calculations—that evolution with noise tends to favor limit sets with larger basins of attraction, and that the presence of intermediate steady states may facilitate evolution—each have predecessors in the literature. That a set with a large enough basin of attraction is selected has been noted in a number of places."

So what is a basin of attraction? An attractor is a set toward which a variable, moving according to the dictates of a dynamical system, evolves over time (**Fig. 1**). That is, points that get close enough to the attractor remain close even if slightly disturbed. For each such attractor, its basin of attraction is the set of initial conditions leading to long-time behavior that approaches that attractor. Attractors in 2 or 3 dimensions can be visualized (**Fig. 1**). Many attractors in biological evolution are extremely complex and therefore difficult to imagine.

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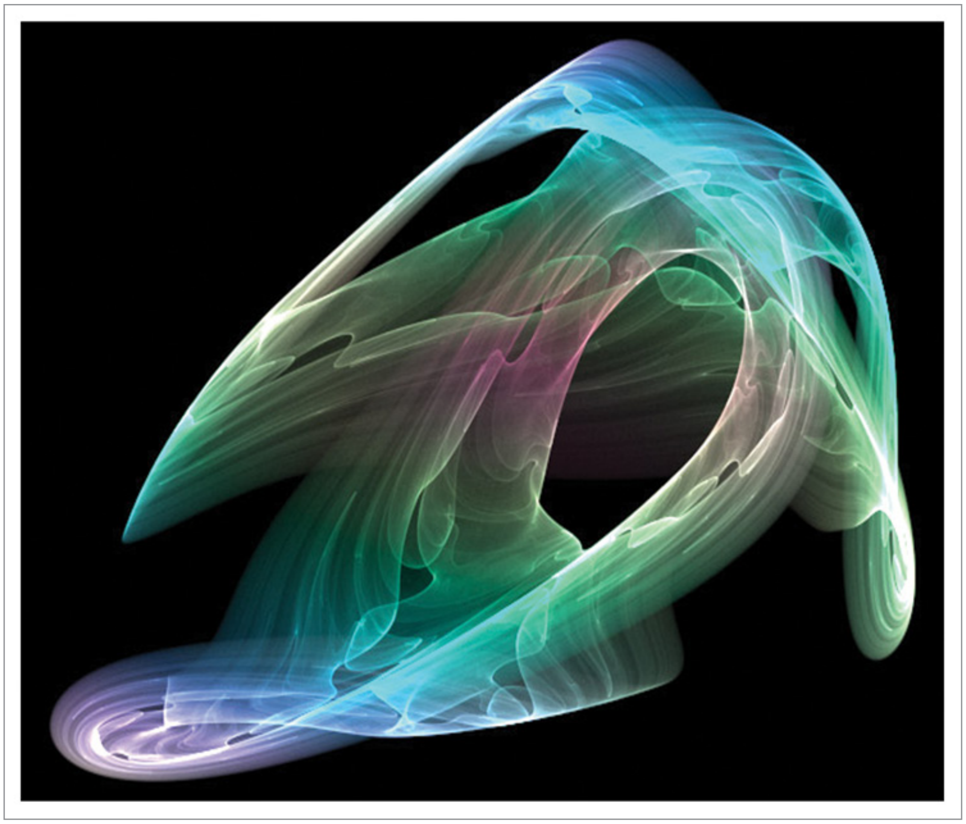

Figure 1. A Poisson attractor in 3 dimensions; even relatively simple attractors are complex. Evolutionary attractors are probably currently beyond our abilities to fully depict.

All living organisms are composed of water, other compounds and elements from both the a-biotic and biotic environment, DNA, RNA, amino acids, and other compounds generated through the action of proteins composed of amino acids (through photosynthesis, predation, saprofitic action, parasitism, symbiosis, mutualism, and diffusion). Proteins have an extremely large number of potential functions. Yet the range of their abilities is not infinite. A recent study predicts that 2957 different protein folds are required to cover all families in the Pfam protein database.[4] The number of new protein families being discovered in the Pfam database is gradually reaching saturation. Another study predicts that there are only about 4000 possible types of protein–protein interactions.[5]

As an organism evolves, its phenotype will be limited among other things by the bounds of protein function. Certain important protein functions will only be possible through a small, perhaps even unique, arrangement of amino acids. This means that there will be certain evolutionary outcomes that are more likely than others, or in other words, evolutionary basins of attraction. In addition to limits on the functions of proteins, there are only a certain number of ways it is physically possible to create a complex, multicellular organism. Here I explore how these evolutionary basins of attraction have caused convergence between plants and animals. The last common ancestor of these 2 eukaryotic lineages was unicellular, but there are many similarities in terms of multicellular organization, and other facets, between these 2 Kingdoms of organisms. These similarities stretch from the molecular level to the organismic one.

Protein preadaptation drives convergence

Some proteins present in the last common ancestor of plant and animal lineages appear to have preadaptation to certain functions in multicellular organisms. These proteins may then have "nucleated" certain structures over the course of evolutionary history in plants and animals. Invasive cells (invadopodia of transformed metazoan cells, neurites, pollen tubes and fibers) in both plants and animals depend upon evolutionarily conserved machinery of cellular polarization and oriented cell mobilisation, involving the actin cytoskeleton and the secretory pathway. Connexins are proteins that form gap junctions between cells in animals. Earlier antibody studies indicated that there may be a conserved connexin homolog at the heart of plasmodesmata, connecting organelles between plant cells.[7] Interestingly, performing BLAST protein homology searching between various animal connexins and the *Arabidopsis thaliana* proteome, cytochrome P450 proteins appear much more often than might be expected by chance alone. Thus this family of proteins may contain the elusive connexin homolog in plants. Indeed, a cytochrome P450 has already been shown to localize to plasmodesmata.[8] Armadillo/catenin repeat proteins in animals are involved in intercellular junction formation in animals.[9] In plants, an armadillo repeat protein links the microtubule cytoskeleton to the cell wall via cellulose synthases, suggesting that this family of proteins has an intrinsic ability to form such structures.[10]

Protein products can drive convergent evolution

In neurons, serotonin is synthesized from tryptophan in 2 steps involving tryptophan hydroxylase and aromatic amino acid decarboxylase. In plants, serotonin is synthesized in 2 steps by tryptophan decarboxylase converting tryptophan to tryptamine followed by the catalysis of tryptamine by tryptamine 5-hydroxylase to form serotonin.[11] Thus, here, there has been convergent evolution (to the synthesis of serotonin) but via 2 different biochemical pathways. This demonstrates that sometimes evolutionary basins of attraction depend upon not so much the proteins involved but the chemical products of those proteins. It appears that serotonin is highly useful as a signaling molecule. In animals it is a major player in neural signaling, and there is an increasing body of work showing that it plays an important role in plant intercellular communication as well, possibly acting as a natural auxin inhibitor.[12] Interestingly, serotonin is localized preferentially to vascular bundle companion cells and vascular parenchyma cells.[13] This is of interest since it appears possible that plant vascular bundles perform a role in long-distance signaling similar to that of neurons in animals.[14]

Other chemical pathways have evolved independently in plants and animals. Some universal infochemicals used as nutrient indicators by saprophagous, coprophagous, and necrophagous insects have evolved in plants. These compounds mimic those found in animal carrion and are used by plants to attract insects for the purpose of pollination.[15] It was proposed to simultaneously deter large herbivores.[16] Plants and animals have also independently evolved similar pathways to the synthesis of cyanogenic glucosides as defense compounds.[17]

Figure 2. Steel rebar ready to be embedded in cast concrete. Note ridges on steel to help binding to concrete.

Physical principles can drive convergent evolution

Rebar, short for reinforcing bar, is a common steel bar used as a tensioning device in reinforced concrete and masonry. Here I suggest that, as is so often the case, nature has "invented" rebar long before the human application of the practice, and indeed the use of rebar by living organisms has led to convergence in plant and animal lineages. During building, the bars are given ridges for better mechanical anchoring into concrete (**Fig. 2**) because concrete is strong under compression but relatively weak under tension. Steel is ideal for the reinforcement of concrete as both substances have similar coefficients of thermal expansion, meaning that reinforced concrete will not experience great stress as a result of changes in temperature. Concrete is a strain-softening substance while the steel reinforcement is strain-hardening.[18] Steel can be subject to rust, however, and therefore unidirectional glass fiber-reinforced thermoset resins are now being used in high-corrosion environments. These resins are available in many structural forms, including spirals.

Xylem in plants as rebar

Plants use xylem vessels to transport water and solutes from the root of the plant to the aerial structure of the plant. Xylem vessels are made of rigid cell wall material, largely cellulose, and undergo apoptosis during development, losing their cytoplasm so as to create empty tube-like structures. Xylem is important structurally as well, and indeed woody tissue is predominantly composed of xylem (**Fig. 3**). The *irregular xylem (irx)* mutants of *Arabidopsis thaliana* show collapsed xylem vessels as a result of reduced amounts of cellulose, lignin, or other cell wall components.[19] *irx* stems are also structurally weaker, and this leads to stunted plant inflorescences. While it appears that the collapse xylem vessels here may indicate that cellulose is important for compression resistance, and indeed wood is a strain-softening substance[20] similar to concrete,[21] there is evidence that cellulose in xylem is important in tension resistance as well.[22]

Angiosperms develop tension wood on the upper side of drooping branches. Tension wood is characterized by the development of a highly crystalline cellulose-enriched gelatinous layer next to the lumen of the tension wood fibers, along with a reduction in lignin (which is the principal compression-resistant component of plant cell walls) and hemicellulose.[23] The endoglucanase KORRIGAN, which is involved in cellulose deposition, and 3 xylem-specific cellulose synthases are all highly expressed in developing tension wood.[24] Thus

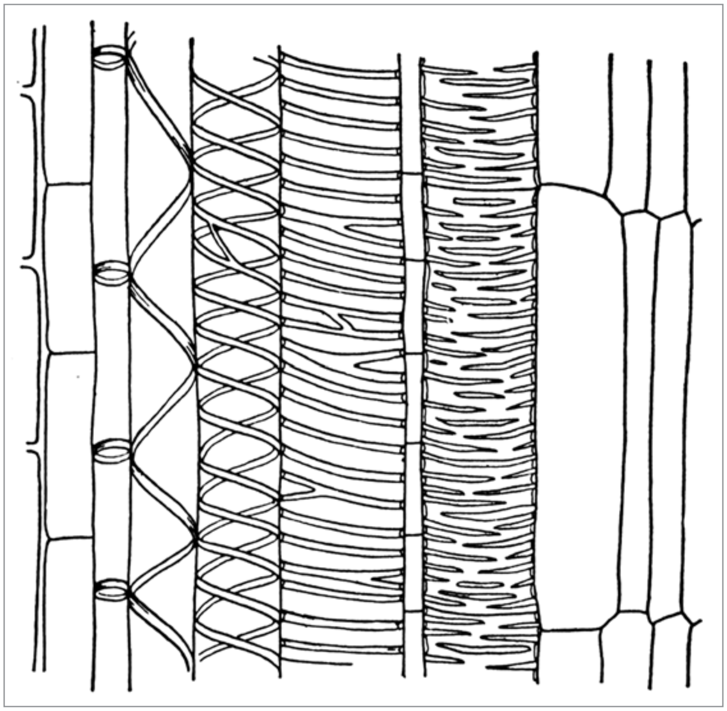

Figure 3. Image showing various cell wall forms in plants, including secondary cell wall forms of xylem vessels. Image downloaded from Florida Center for Instructional Technology website.

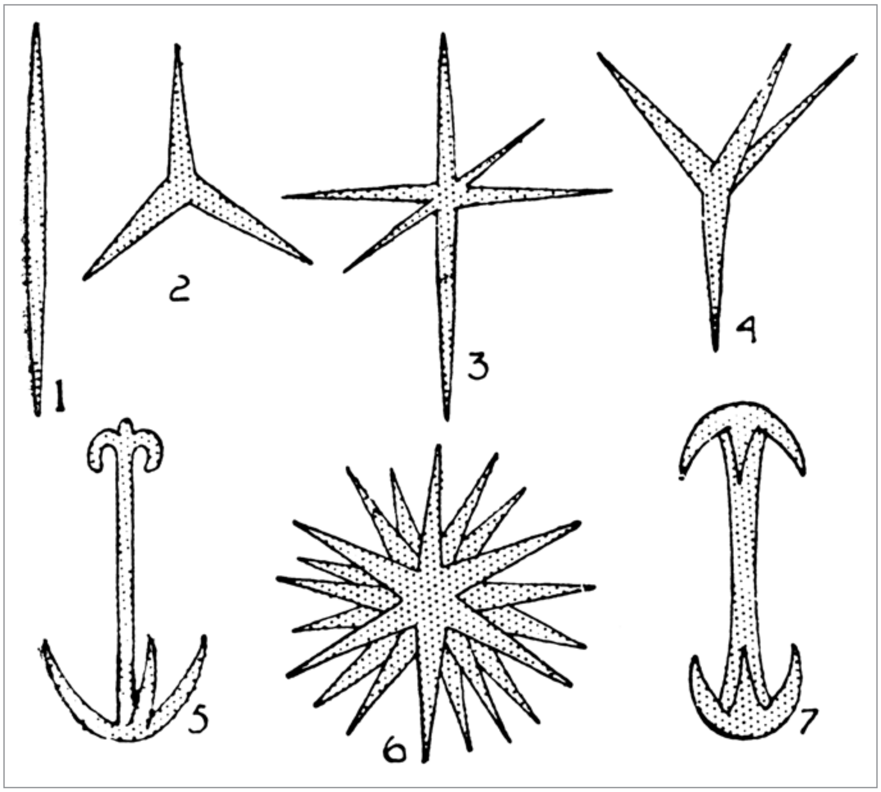

Figure 4. Sponge spicules of various forms. Image downloaded from Florida Center for Instructional Technology website.

cellulose-enriched xylem appears likely to act as rebar during wood development. Indeed the structure of xylem vessels is even reminiscent of steel rebar structure (**Fig. 3**). Some plants, including *Gnetum gnemon*, have extraxylary gelatinous tension fibers[25] that may function as cellular rebar.

Spicules in animals as rebar

Small pieces of calcareous or siliceous material are embedded in sponges as spicules, in cnidarians as sclerites, and as spicules in chitons, stalked barnacles, and ascidians. Sponge spicules are probably the best studied of this group. It is known that bio-silica is synthesized via the protein silicatein, which aggregates non-covalently to form larger filaments, a process that is stabilized by the silicatein-associated protein silintaphin-1. These structured clusters form the axial filament that is located in the center of the spicules, the axial canal.[26] Spicules can be quite long—the anchoring spicule of the sponge *Monoraphis* is up to a meter in length and several millimeters in diameter. When compared with a silica rod of the same size, the spicule is able to withstand a 4-fold higher stress before breaking due to its layered structure. Spicules with very high aspect ratios appear to act like rebar; stress is transferred by shearing from the pliable matrix to the stiff fibers, which thus bear in tension part of the load on the composite.[27] Indeed spicules come in a variety of shapes, some of which involve hooks at the ends of the spicules that may have a similar role to hooks or bends at the ends of steel rebar that lock it around the concrete (**Fig. 4**). The parallel phenomenon in plants is branched sclereids in the soft tissue of nymphaea leaves.

Murray's law

Two related "living fossil" plants, *Tmesipteris* and *Psilotum,* are found in Australia and other parts of the world. Due to its being more widely dispersed, most scientific work on this family of ancient plants, the Psilotaceae, has been performed on *Psilotum*. The xylem of *Psilotum nudum* does not provide structural support to the plant, unlike more modern plant lineages where disruption of xylem leads to stunted growth. The lack of mechanical support by the xylem of *Psilotum* has enabled an examination and confirmation of Murray's law for plant xylem vessels. Murray's law states that, as vessels branch, the sum of the conduit radii cubed at any point along the plant should decrease in direct proportion with volume flow rate to maximize hydraulic conductance per unit vascular investment.[28] Murray's law also governs the branching of blood vessels in animals.[29] Thus Murray's law has replaced earlier models of hydraulic conductance in a branched transport system including the pipe model and Leonardo's rule.[30] Here again physical principles have dictated convergent evolution between plant and animal lineages.

Conclusions

Evolution is a multi-faceted process. There are many variables to consider, and a full understanding of how it works is probably currently not possible. Convergence is one theme that appears time and time again. Even plants and animals, 2 very divergent lineages, show certain convergences. Within the taxa of plants or animals, there are even more instances of convergent evolution. These appear likely to be due to evolutionary basins of attraction that are in turn dependent upon the chemical and physical properties of the components of living organisms and other physical considerations. Thus evolution is not a random process but has led to certain outcomes that were, to a certain extent at least, preordained.

Disclosure of Potential Conflicts of Interest

No potential conflicts of interest were disclosed.

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