SPIRAL WAVES IN EXCITABLE MEDIA: A MODEL FOR DIVERSE ASPECTS OF ORGANISMAL DEVELOPMENT

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Conical skeletal elements of various morphologies are a feature common to numerous Lower and Middle Cambrian organisms of problematic affinity, not to mention their occurrence in multiple extant metazoan phyla. In some cases these display helicospiral morphology, sometimes with dextral and sinistral morphs that may have been paired structures in a bilaterally symmetrical body plan. Such paired elements, including spines of coeloscleritophorans, appear to show a spicular substructure with some suggestion of spatial organization comparable to that of phyllotactic systems in vascular plants. These recurring structural themes raise old questions regarding the significance and mode of development of spiral forms and patterns in many organisms, both unicellular and multicellular.

Most recent work on phyllotaxis has interpreted patterns of spiral organization as emergent geometrical properties of systems controlled by local reaction-diffusion interactions around the developing plant axis, without recourse to any explicitly spiral process. The term "generative spiral," for the pattern linking consecutively formed elements, has thus taken on a purely descriptive, rather than mechanistic, meaning. Likewise, helicospiral shells and comparable structures are generally assumed to reflect no truly spiral growth mechanism, but rather, the regular scaling and displacement of a fundamentally concentric, cone-within-cone, accretionary system. Explanations for the common appearance of such forms include the structural strength offered by adherent whorls (though many forms are evolute), and the simplicity of isometric growth (though departures from logarithmic spirals are common).

An alternative perspective was suggested initially by discovery of a higher order pattern in the phyllotactic systems of some conifers, wherein the handedness of the generative spiral reverses as each parent axis gives rise to daughters, through the full range of levels in the branching hierarchy. Although this may be explicable in conventional terms, it may also be interpreted as involving a spiral wave of activation passing rhythmically around the plant axis, at or within some critical distance of the apical meristem. Models for such phenomena are provided by several physical systems involving excitable media, the most well known of which is the Belousov-Zhabotinsky reaction, and by some biological systems, such as neural networks or aggregations of slime mold. At nearly the opposite end of the organismic realm, vertebrate teeth, most of which are subtly but fundamentally helicospiral in form, show features that also suggest rotating waves of activity. These include the common presence of an axial canal in the dentin underlying tooth cusps, which could represent the phase singularity of a rotating wave in the layer of odontoblasts responsible for dentin formation, and asymmetries in autoradiographic patterns associated with developing teeth. In such systems it may be generally true that the period of other physiological cycles that modulate secretory activity is not a simple multiple of the period of rotation of the spiral wave. This would result in a regular change in phase relationship, generating helicospiral form. Additional applications of this principle may illumine features as diverse as bovid horns and the handedness of supernumerary appendages in grafting experiments on insects and amphibians. Spiral waves in excitable media also have properties of symmetry and capacity for generating serial structure that make them intriguing candidates for involvement in even earlier stages of metazoan development.