DYNAMICAL SIMILARITY AND THE THEOREY OF BIOLOGICAL TRANSFORMATIONS

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The D'Arcy Thompson concept of biological transformations is developed in a form analogous to such physical concepts as the Law of Corresponding States in thermodynamics, and the Principles of Similitude found in engineering. We find that such concepts depend on a distinction between fundamental and derived quantities, in which the values assigned to the fundamental quantities set the natural scales for the derived ones. Among other things, we see that critical phenomena, such as phase transitions, arise as an immediate consequence of this distinction. In a biological context, we explore the implications of Thompson's hypothesis that closely related organisms are phenotypically similar, assuming that the organisms we see are the result of selection processes operating on phenotypes.

I. Introduction. In previous work (Rosen, 1962, 1967) we examined the relations between the D'Arcy Thompson Theory of Transformations (Thompson, 1917) and the idea of optimal design as formulated by Rashevsky (cf. Rashevsky, 1960). The object of this work was to attempt to provide some underlying mechanism which would convert D'Arcy Thompson's observation, that related organisms can be converted into one another through continuous transformations, into an actual theory of biological structure and function. In the present paper, we wish to provide a more extensive analysis of these ideas, and at the same time to place the Thompson work into a broader physical and mathematical context. We will begin with some simple and well-known non-biological examples, which will then be extended to biological cases.

II. Laws of Corresponding States. We shall begin our exploration of physical situations cognate to the Thompson Theory of Transformations with an example drawn from thermodynamics.

The point of departure for the application of thermodynamic concepts to
specific problems is the *equation of state* of a thermodynamic system. The equation of state is a functional relation among the state variables which characterize a thermodynamic system at equilibrium. A typical equation of state is the van der Waals equation, describing a particular kind of nonideal gas:

\[(p + a/v^2)(v - b) = rT\]

where \(p\), \(T\), \(v\) are the thermodynamic state variables (pressure, temperature and volume respectively), and the parameters \(a\), \(b\), \(r\) are determined by the particular "species" of gas under consideration. The thrust of this kind of description is the following: given a particular kind of gas satisfying this equation, then the specification of two of the state variables (say \(p\), \(T\)) allows the corresponding equilibrium value (or values) of \(v\) to be determined.

If we regard the parameters \(a\), \(b\), \(r\) as fixed, and solve the equation of state for the volume \(v\), then the equation of state becomes a cubic equation in \(v\), whose coefficients are determined by the values given to the other state variables \(p\), \(T\). For a given choice of values for \(p\) and \(T\), this equation will in general have one real root or three real roots. For one choice of values \(p_c\), \(T_c\), however, the equation will have as solution \(v = v_c\) only one value, which corresponds to three coincidental real roots. The resultant state \((v_c, p_c, T_c)\) corresponds to the *critical point* of the gas, and is, of course, related intimately to the gas–liquid phase transition.

The geometric interpretation of the critical point is as follows. Given any temperature \(T\), the equation of state becomes a function of \(p\) and \(v\) alone and can be plotted as a curve in the \((p, v)\) plane. Such a curve is called an isotherm. In general, the isotherms are of two types: they either possess no extreme points (maxima or minima), or they possess one maximum and one minimum. Separating the two types of isotherms is a critical isotherm (corresponding to \(T = T_c\)), which possesses a point of inflection. The co-ordinates \((v_c, p_c, T_c)\) of this point of inflection then give the critical point.

Thus, we can explicitly find the co-ordinates of the critical point from the equation of state. At the critical point, we have three conditions to be satisfied:

(a) since the critical point is an equilibrium point, the equation of state must be satisfied;

(b) since the critical point is an extreme point in an isotherm, we must have

\[\frac{\partial p}{\partial v} \bigg|_{T = T_c} = 0;\]

(c) since the critical point is a point of inflection, we must have

\[\frac{\partial^2 p}{\partial v^2} \bigg|_{T = T_c} = 0.\]