

Vol. 8, 1922

with a change in the distribution of matter among the several species composing the system, would probably play a subordinate rôle; in contrast with the condition of affairs familiar in ordinary physico-chemical systems. This is an obvious inference from the observation that the several species of organisms are distinguished much more by structural differences than by differences in chemical composition.

¹² Ostwald, W., Lehrbuch der allgemeinen Chemie, 1892, vol. 2, p. 37; Siebel, J. E Compend of Mechanical Refrigeration, 1915, p. 88. For a discussion of the validity and limitations of Ostwald's principle see Helm G., Die Energetik, 1898, pp. 248; Neumann, C., Leipziger Berichte, 1892, p. 184.

¹³ That living organisms may be capable of retarding the energy flux through the system of nature was suggested by the present writer in *Ann. Naturphil.*, 1910, p. 60.

¹⁴ Johnstone, J., The Mechanism of Life, 1921, p. 220.

NATURAL SELECTION AS A PHYSICAL PRINCIPLE*

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In a paper presented concurrently with this, the principle of natural selection, or of the survival of the fittest (persistence of stable forms), is employed as an instrument for drawing certain conclusions regarding the energetics of a system in evolution.

Aside from such interest as attaches to the conclusions reached, the method itself of the argument presents a feature that deserves special note. The principle of natural selection reveals itself as capable of yield-ing information which the first and second laws of thermodynamics are not competent to furnish.

The two fundamental laws of thermodynamics are, of course, insufficient to determine the course of events in a physical system. They tell us that certain things cannot happen, but they do not tell us what does happen.

In the freedom which is thus left, certain writers have seen the opportunity for the interference of life and conciousness in the history of a physical system. So W. Ostwald² observes that "the organism utilizes, in manyfold ways, the freedom of choice among reaction velocities, through the influence of catalytic substances, to satisfy advantageously its energy requirements." Sir Oliver Lodge also, has drawn attention to the guidance³ exercised by life and mind upon physical events, within the limits imposed by the requirements of available⁴ energy. H. Guilleminot⁵ sees the influence of life upon physical systems in the substitution of guidance by choice in place of fortuitous happenings, where Carnot's principle leaves the course of events indeterminate. As to this, it may be objected that the attribute of fortuitousness is not an objective quality of a given event. It is the expression of our subjective ignorance, our lack of complete information, or else our deliberate ignoring of some of the factors that actually do determine the course of events. Admitting, however, broadly, the directing influence of life upon the world's events, within the limits imposed by the Mayer-Joule and the Carnot-Clausius principles, it would be an error to suppose that the faculty of guidance which the established laws of thermodynamics thus leave open, is a peculiar prerogative of living organisms. If these laws do not fully define the course of events. this does not necessarily mean that this course, in nature, is actually indeterminate, and requires, or even allows, some extra-physical influence to decide happenings. It merely means that the laws, as formulated, take account of certain factors only, leaving others out of consideration; and that the data thus furnished are insufficient to yield an unambiguous answer to our enquiry regarding the course of events in a physical system. Whether life is present or not, something more than the first and second laws of thermodynamics is required to predict the course of And, whether life is present or not, something definite does happen, events. the course of events is determinate, though not in terms of the first and second laws alone. The "freedom" of which living organisms avail themselves under the laws of thermodynamics is not a freedom in fact, but a spurious freedom⁶ arising out of an incomplete statement of the physical laws applicable to the case. The strength of Carnot's principle is also its weakness: it holds true independently of the particular mechanism or configuration of the energy transformer (engine) to which it is applied; but, for that very reason it is also incompetent to yield essential information regarding the influence of mechanism upon the course of events. In the *ideal* case of a reversible heat engine the efficiency is independent of the mechanism. Real phenomena are irreversible; and, in particular, trigger action,⁷ which plays so important a rôle in life processes, is a typically irreversible process, the release of available energy from a "false" equilibrium. Here mechanism is all-important. To deal with problems presented in these cases requires new methods,8 requires the introduction, into the argument, of new principles. And a principle competent to extend our systematic knowledge in this field seems to be found in the principle of natural selection, the principle of the survival of the fittest, or, to speak in terms freed from biological implications, the principle of the persistence of stable forms.

For the battle array of organic evolution is presented to our view as an assembly of armies of energy transformers—accumulators (plants), and engines (animals); armies composed of multitudes of similar units, the individual organisms. The similarity of the units invites statistical treatment, the development of a statistical mechanics of which the units shall be, not simple *material particles* in ordinary reversible collision of the type familiar in the kinetic theory, collisions in which action and reaction were equal; the units in the new statistical mechanics will be *energy transformers* subject to irreversible collisions of peculiar type—collisions in which trigger action is a dominant feature:

When the beast of prey A sights its quarry B, the latter may be said to enter the field of influence of A, and, in that sense, to collide with A. The energy that enters the eye of A in these circumstances may be insignificant, but it is enough to work the relay, to release the energy for the fatal encounter. And because evolution works with armies built up of similar units, the seemingly erratic workings of the relay mechanism (in which action and reaction are not equal, and seem subject to no simple general law) are not, in effect, erratic, but range themselves according to law and order, for those species of units, those types of transformers, are picked out for survival, whose mechanism possesses certain definite properties. Thus the principle of natural selection makes its entry into dynamics.

Further elaboration of these concepts must be reserved for a future occasion.

In systems evolving toward a true equilibrium (such as thermally and mechanically isolated systems, or the isothermal systems of physical chemistry), the first and second laws of thermodynamics suffice to determinate at any rate the end state; this is, for example, independent of the amount of any purely catalytic substance that may be present. The first and the second law here themselves function as the laws of selection and evolution, as has been recognized by Perrin⁹ and others, and exemplified in some detail by the writer, for the case of a monomolecular reversible reaction.¹⁰

But systems receiving a steady supply of available energy (such as the earth illuminated by the sun), and evolving, not toward a true equilibrium, but (probably) toward a stationary state, the laws of thermodynamics are no longer sufficient to determine the end state; a catalyst, in general, does affect the final steady state. Here selection may operate not only among components taking part in transformations, but also upon catalysts, in particular upon auto-catalytic or auto-catakinetic constituents of the system. Such auto-catakinetic constituents are the living organisms,¹¹ and to them, therefore the principles here discussed, apply.

That the principle of selection is competent to yield information beyond the scope of the laws of thermodynamics has been very clearly set forth, independently, by H. Guilleminot.¹² The present writer has long realized that the principle is capable of such application; that it functions, as it were, as a third law of thermodynamics (or a fourth, if the third place be given to the Nernst principle). If he has not, before this date, explicitly stated the case, this is mainly because his writings have followed a definite, systematic plan, announced in his early publications.¹³ Viewing evolution as a change in the distribution of matter among the components of a physical system, the study of evolution naturally di-

vides itself into two fields. The one, which might be termed the stoichiometry of evolution, deals with mass relations: the relative amounts of the different species of matter present, and the changes in these amounts; the kinetics of evolution. The second field of study is the dynamics or energetics of evolution, the scope of which is sufficiently indicated by these terms. It appeared desirable to lay the foundation of the first, as the more elementary, of these fields, before proceeding to a systematic exposition of the second. This is the plan which has been closely followed by the writer in the past, and which it is hoped to develop in greater completeness in the future. Material held in reserve, and relating to the dynamics of evolution, will then be brought forward in its proper place. The present issue of this advance sheet is prompted by a recent reading of Guilleminot's book, which, through a series of mishaps, has only recently come to the writer's hand.

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¹ These PROCEEDINGS, 8 p. 147.

² Ostwald, W., Vorlesungen über Naturphilosophie, 1902, p. 328.

³ Sir Oliver Lodge, Life and Matter, 1906, p. 144.

⁴ Ibid., pp. 148, 149; Nature, 67, p. 595; 68, p. 31.

⁶ Guilleminot, H., La Matière et la Vie, 1919, p. 121, et passim.

⁶ This remark must be understood to apply only to that freedom which arises out of the incompleteness of the first and second law as determinants of the course of events. The writer does not here take sides, one way or another, in the controversies regarding free will, determinism, vitalism as distinguished from mechanistic conceptions, etc.

⁷ Compare Lotka, A. J., J. Washington Acad. Sci., 2, 1912, p.7 1; Guilleminot, H., loc. cit., p. 115; Johnstone, J., The Mechanism of Life, 1921, p. 49.

⁸ Lotka, A. J., Proc. Nat. Acad. Sci., 7, 1921, pp. 194, 196.

⁹ Perrin, J., Traité de Chimie, 1903, vol. 1, pp. 142–143; Chowlson, O. D., Lehrbuch der Physik., 1905, vol. 3, p. 499; Scientia, 3, 1910, p. 51; Lotka, A. J., Science Progress, 14, 1920, p. 406.

¹⁰ For recent substantiation of some of the details of the presentation there given see Baly, E. C. C., *Nature*, vol. 109, 1922, p. 344.

¹¹ D'Arcy Thompson (Growth and Form, 1917, p. 132) attributes the origination of this concept to Chodat, quoted by Monnier, A. (Publ. Inst. Bot. Univ. Genève, (7) III, 1905. There seem to be, however, some earlier indications of the same thought. The following bibliography, which makes no pretense of completeness, is culled from works ready at hand: Errera, L., Revue de l'Université de Bruxelles, 5, 1899–1900. May issue; Ostwald, W., Vorlesungen über Naturphilosophie, 1902, pp. 342, et seq.; Bastian, H. C., The Nature and Origin of Living Matter, 1905, p. 46, et seq.; Robertson, T. B., Arch. Entwickelungsmechanik Org., 25, 1908, p. 581, 25, p. 108; Ostwald, Wo., Die zeitlichen Eigenschaften der Entwickelungsvorgänge, 1908; Hatai, S., Anat. Rec., 5, 1911, p. 373; Enriques, Biol. Centralbl., 1909, p. 337; Lotka, A. J., Z. physik. Chem., 72, 1910, p. 511; 80, 1912, p. 159; J. Phys. Chem., 14, 1910, p. 274; Proc. Nat. Acad. Sci., 6, 1920, p. 275; Pearl, R., Amer. J. Hygiene, 1, 1921, p. 592.

¹² Guilleminot, H., loc. cit., p. 118, 154, et passim.

13 Lotka, A. J., Am. J. Sci., 24, 1907, p. 216; Ann. Naturphil., 1910, p. 74.