ARTICLES

EVOLUTION AND IRREVERSIBILITY

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The recent publication in Science Progress of Dr. Petronievics's article, "Sur la loi de l'évolution irréversible,"[1] seems to furnish an opportune occasion for a discussion of the relation between irreversibility as understood by the physicist, and evolution as conceived more particularly by the biologist.

Biology leaves us with a not very clearly defined idea of *progression* as one of the fundamental characteristics of those changes which are embraced by the term "evolution." Such phrases as "the passage from lower to higher forms," which are often employed to describe evolution, are vague, and undoubtedly contain an anthropomorphic element.[2] The fact seems to be that all we can predicate positively to-day is that evolution is a "unidirectional" change in time.

Now, the physicist is well acquainted with unidirectional changes. They are precisely those changes which he terms "irreversible." And, for certain cases at least, he is able to define in precise terms the direction of evolution. For example, in an isolated physical system evolution proceeds in such direction that the entropy of the system increases. More generally, if the state of a physical system is defined in terms of certain variables $X_1, X_2 \ldots X_n$ and certain parameters $P_1, P_2 \ldots P_m$, and if evolution is allowed to proceed (*i.e.*, if the X's are allowed to change by a spontaneous process) while keeping the parameters P constant, then certain definite and known functions of the variables X and of the parameters

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[1] January 1919, p. 406.

[2] "Evolution is thus almost synonymous with progress, though the latter term is usually confined to processes of development in the moral as distinguished from the physical world. Further, this idea, as Mr. Spencer remarks, has rather a subjective than an objective source, since it points to an *increased value* in existence, *as judged by our feelings*" (*Encyc. Brit.*, 9th edition, vol. viii, pp. 751-2).

P increase toward a maximum, while certain other such functions decrease toward a minimum.

When we pass on to biological systems evolving under the complex conditions presented to us in nature, we may, if we choose, apply the same language in a discussion of their history, and state empirically that their evolution is an irreversible process,[1] or make the guess that here also certain functions increase toward a maximum.[2] But no attempt seems to have been made to give explicitly the form of these functions, or even as much as to indicate just what are the

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[1] "The second law (of thermodynamics) is the law of evolution of the world accessible to our observation" (Chwolson, *Lehrbuch der Physik*, 1905, vol. iii, p. 499; *Scientia*, 1910, vol. iii, p. 51.

". . . the second law of the theory of energy is now generally regarded as essentially a statistical law. So viewed, the second law of energy becomes a principle stated wholly in terms of the theory of probability. It is the law that the physical world tends, in each of its parts, to pass from certain less probable to certain more probable configurations of its moving particles. As thus stated the second principle . . . becomes a law of evolution" (Josiah Royce, *Science*, 1914, vol. xxxix, p. 551).

"Un système isolé ne passe jamais deux fois par le même état.

"Le second principe affirme un ordre nécéssaire dans la succession de deux phénomènes, sans retour possible aux états déja traversés.

"C'est pourquoi j'ai cru expressif d'appeler ce principe un principe d'évolution.

"Il se trouve qu'en proposant ce nom je suis fidèle a la pensée de Clausius, car le mot ἐντροπή, d'où il a tiré entropie, signifie précisément évolution" (J. Perrin, *Traité de Chimie Physique*, 1903, vol. i, pp. 142-43).

Compare also:

"Il est hautement improbable qu'un système isolé passe deux fois par le même état; cela est d'autant plus improbable que la complication du système est plus grande, et pratiquement il serait insensé de se placer dans cette hypothèse d'un retour a l'état initial" (J. Perrin, *Traité de Chimie Physique*, 1903, vol. i, pp. 145-46).

The following is also of interest:

"The book of Nature is the book of Fate. She turns the gigantic pages—leaf after leaf, never re-turning one. . . . The face of the planet cools and dries, the races meliorate, and man is born. But when a race has lived its term, it comes no more again" (Emerson, *The Conduct of Life*).

The mere statement that a system "never twice passes through the same state" is, in itself, insufficient to distinguish between evolution as a "progress," or merely a "changeful sequence," to use the apt phrase of Prof. J. A. Thomson in *The Wonder of Life*, 1914. It is insufficient to define the direction of evolution. This direction is indicated by the more definite statement that the system passes from less probable to more probable states. A rigorous proof of this latter principle seems to be given only for certain special kinds of systems.

[2] "Un corps vivant qui reste vivant, suit toujours, quel que soit le dérangement qu'il a subi, la loi qui défini l'équilibre stable. Il est donc en état d'équilibre stable; la stabilité de cet équilibre résulte de ce qu'une certaine fonction de ces éléments est à un maximum" (Le Dantec, *La Stabilité de la Vie*, 1910, p. 25).

variables and the parameters appearing in them.[1] Until this is done the mere statement that such functions exist is of little value, except, perhaps, as pointing a certain direction for inquiry. Needless to say, the statement that such functions, relative to a system in the course of organic evolution, exist, lacks entirely the rigorous basis on which rest the corresponding propositions regarding the evolution of physical systems under certain clearly defined conditions.

It seems, therefore, worth noting that a process of organic evolution, when viewed or comprehended from a certain standpoint, falls naturally within a definite category or class comprising also that group of physical phenomena termed "change of state."[2] The fit is so complete that the same general method of analytical treatment can be applied, without distinction, to the entire category; and certain general conclusions relating equally to "change of state," as ordinarily understood, and to certain phenomena in an evolving organic system, follow in natural course.

This viewpoint is gained by regarding the evolution of the system under consideration as the redistribution of matter among the components of the evolving system.

In the case of an ordinary physico-chemical system, for example, the system may consist of the three components[3] H_2, O_2, H_2O, and in the course of the evolution of the system, matter redistributes itself among these components in accordance with a certain system of differential equations:

$$\left.\begin{aligned} \frac{dX_1}{dt} &= F_1(X_1,\ X_2,\ X_3\ ;\ p,\ T) \\ \frac{dX_2}{dt} &= F_2(X_1,\ X_2,\ X_3\ ;\ p,\ T) \\ \frac{dX_3}{dt} &= F_3(X_1,\ X_2,\ X_3\ ;\ p,\ T) \end{aligned}\right\} \qquad (1)$$

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[1] Similar remarks apply to various attempts to apply to biological systems the Principle of Le Chatelier. Inasmuch as this principle itself derives its validity from the second law of thermodynamics, its application can be regarded as established only for those systems and for those variables and parameters which we are competent to-day to treat by thermodynamical methods. The principle is quite meaningless unless the particular variables to which it is applied are clearly stated. Even then, and in the case of simple physical systems, the application of the principle is very liable to errors, of which the literature gives ample illustration. (See Ehrenfest, *Zeitschr. für Phys. Chem.*, 1911, vol. lxxvii, p. 735; Wolchonsky, *Jour. Russian Phys. Chem. Soc.*, 1912, vol. xliv, pp. 305, 310; Chwolson, *Lehrbuch der Phys.*, 1909, vol. iii, p. 547; Bancroft, *Jour. Amer. Chem. Soc.*, 1911, p. 92; Fournier d'Albe, *Contemporary Chemistry*, 1911, p. 38; Löwy, *Kosmos*, 1911, p. 331; Le Dantec, *La Stabilité de la Vie*, 1910, p. 25; Spencer, *First Principles*, chap. xxii, section 173, Burt's Edition, p. 433).

[2] This term is here used in a general sense, to include also change of state by chemical reaction.

[3] Not necessarily independent.

where X_1 = mass of H_2; X_2 = mass of O_2; X_3 = mass of H_2O; p = pressure; T = temperature; t = time.

Among reactions ordinarily considered, the form of the functions F is commonly given by the law of mass action.

In the case of organic evolution, we have a system comprising a number of different species of organisms, and also other components. We may denote the mass of these several species and other components, $S_1, S_2, \ldots S_n$ by $X_1, X_2 \ldots X_n$. The state of the system may be thought of as defined by statement of the values of these variables X; and, further, of certain parameters, $P_1, P_2 \ldots P_j$, which measure climatic conditions, extension-in-area, etc., of the system; lastly, of certain other parameters, $Q_1, Q_2 \ldots Q_k$, which define the character of each species, this character being, in general, variable with time as evolution proceeds.

It is reasonable to make the very broad supposition that the progress of redistribution of matter (evolution) in this system takes place in accordance with a system of differential equations:

$$\left.\begin{aligned}
\frac{dX_1}{dt} &= F_1(X_1, X_2, \ldots X_n;\ P_1, P_2, \ldots P_j;\ Q_1, Q_2, \ldots Q_k) \\
\frac{dX_2}{dt} &= F_2(X_1, X_2, \ldots X_n;\ P_1, P_2, \ldots P_j;\ Q_1, Q_2, \ldots Q_k) \\
&\cdots\cdots\cdots\cdots\cdots\cdots\cdots\cdots\cdots\cdots \\
\frac{dX_n}{dt} &= F_n(X_1, X_2, \ldots X_n;\ P_1, P_2, \ldots P_j;\ Q_1, Q_2, \ldots Q_k)
\end{aligned}\right\}(2)$$

which is merely a more general form of the system (1).

The rôle played in evolution by the changes in the parameters Q—*i.e.*, the changes in the character of the evolving species of organisms—is of such absorbing interest that in common conception this alone has almost come to be regarded as evolution.

In a systematic treatment of the subject from the point of view here set forth, however, it will be seen that this matter of the change of the parameters Q forms only one special subsidiary problem within the broader general problem. Furthermore, this subsidiary problem repeats, within its own borders, the general character of the broader problem.

This becomes apparent when we define the "character" of a species in a statistical way. Such definition takes the following form:

Let the total mass of the species S_i be X_i.

Let $p_1, p_2 \ldots p_r$ be parameters, measuring certain characteristics (*e.g.*, stature, mass, etc.) of individual units (organisms) of the species.

Let $c_i(\omega)$ be such a factor that

$$X_i \, c_i(\omega)\Delta\omega = X_i \, c_i(p_1, p_2, \ldots)\Delta p_1, \Delta p_2 \ldots \Delta p_r \qquad (3)$$

gives the mass of that portion of the species for which the parameters $p_1, p_2 \ldots p_r$ are comprised within the limits

$$\left.\begin{array}{l} p_1 \text{ and } p_1 + \Delta p_1 \\ p_2 \text{ and } p_2 + \Delta p_2 \\ \cdots\cdots\cdots\cdots \\ p_r \text{ and } p_r + \Delta p_r \end{array}\right\} \qquad (4)$$

The increments Δp may be infinitesimals if the conditions of the case commend such choice.

The character of the species being thus defined, it is evident that evolutionary change in character of the species is only one aspect of the redistribution of matter in the system comprising that species—it is that particular phase of the redistribution which occurs within the confines of the species itself. We may speak of this phase or part of organic evolution as intra-species or intra-group evolution.

In contradistinction with this we may speak of the phase of evolution to which the system of equations (2) refers as inter-species or inter-group evolution—*i.e.*, the redistribution of matter among the several species of matter of which the system is composed.

The relations which connect the several factors of intra-group evolution are evidently more complex than those which exist between the factors of inter-group evolution.

It is therefore expedient to consider the latter first.

We are thus led, primarily, to a consideration of the system of differential equations (2).

In physico-chemical dynamics it is customary to study processes taking place at constant pressure and temperature, or at constant volume and temperature.

We shall here introduce a similar restriction, and consider the case of inter-group evolution taking place at constant parameters P (*e.g.*, constant extension-in-area and constant climatic conditions).

Furthermore, a simple case which naturally invites first attention is that in which the changes in the parameters Q (in the character Q of the several species) take place very slowly as compared with the changes in the variables X—*i.e.*, as compared with the changes in the distribution of matter among the several species.

In this case we may, as a first approximation, regard the Q's also as constant.

For the purposes of our present discussion we may, then, write:

$$\left.\begin{aligned} \frac{dX_1}{dt} &= F_1(X_1,\ X_2,\ \ldots\ X_n) \\ \frac{dX_2}{dt} &= F_2(X_1,\ X_2,\ \ldots\ X_n) \\ &\cdots\cdots\cdots\cdots\cdots \\ \frac{dX_n}{dt} &= F_n(X_1,\ X_2,\ \ldots\ X_n) \end{aligned}\right\} \tag{5}$$

We define $C_1,\ C_2,\ \ldots\ C_n$ by the relation

$$\begin{aligned} F_1(C_1,\ C_2,\ \ldots\ C_n) = F_2(C_1,\ C_2,\ \ldots\ C_n) = \ldots = \\ F_n(C_1,\ C_2,\ \ldots\ C_n) = 0 \end{aligned} \tag{6}$$

and introduce new variables

$$x_i = X_i - C_i \tag{7}$$

so that

$$\frac{dx_i}{dt} = f_i(x_1,\ x_2,\ \ldots\ x_n) \tag{8}$$

We shall assume that the functions f are analytic, and write

$$\begin{aligned} \frac{dx_i}{dt} &= a_{i1}x_1 + a_{i2}x_2 + \ldots + a_{in}x_n \\ &+ a_{i11}x_1^2 + a_{i22}x_2^2 + \ldots \end{aligned} \tag{9}$$

Omitting the discussion of special cases,[1] a general solution of the system (9) is,

$$x_i = a_{i1}e^{\lambda_1 t} + a_{i2}e^{\lambda_2 t} + \ldots + a_{i11}e^{2\lambda_1 t} + a_{i12}e^{(\lambda_1+\lambda_2)t} + \ldots \tag{10}$$

where the exponential coefficients $\lambda_1,\ \lambda_2,\ \ldots\ \lambda_n$ are the n roots for λ of the equation

$$\Delta(\lambda) = \begin{vmatrix} a_{11}-\lambda & a_{12}\ \ldots & a_{1n} \\ a_{21} & a_{22}-\lambda\ \ldots & a_{2n} \\ \cdots & \cdots & \cdots \\ a_{n1} & a_{n2}\ \ldots & a_{nn}-\lambda \end{vmatrix} = 0 \tag{11}$$

and the coefficients a are determined in well-known manner.[2]

Marks of Irreversibility.—The question now arises, Where in our equations and in their solution do we find the earmarks of irreversibility?

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[1] Such as the case when the determinantal equation (11) has multiple roots. This offers no special difficulties, but is here omitted for the sake of brevity. See, for example, Picard, *Traité d'Analyse*, vol. iii, p. 30.

[2] See, for example, Webster's *Dynamics*, 1912, pp. 159, 161.

Considering, first of all, the system of equations (9) we see directly that the velocities $\frac{dx}{dt}$ vanish with the co-ordinates x.

Again, by differentiating (9) repeatedly, it is seen that the second and all the higher derivatives also vanish together with the first (and with the co-ordinates themselves).

This vanishing of the accelerations with the velocities is, of course, typical of an " inertia-free " or " completely damped " system.[1]

On the other hand, the solution (10) appears at first sight very similar in form to that obtained in the treatment of small oscillations according to Lagrange. Such small oscillations are not in general of the completely damped (inertia-free) type ; they may not be damped at all, in which case they represent a reversible process.

There is, however, one essential difference which distinguishes the solution (10) here obtained from the solution of the Lagrangian problem. In the latter, with a system requiring for its definition n co-ordinates, there appear in the solution $2n$ arbitrary constants ; on the other hand, in the case here considered, with n co-ordinates, there appear only n such constants in the solution. This fact is closely related to the fact that in a system possessing inertia it is, in general, necessary, in order to specify the state of the system, to give the values, not only of the co-ordinates, but of their first derivatives (velocities) also.

On the other hand, in an inertia-free or completely damped system, such as we have here been considering, after the co-ordinates are fixed, the velocities are no longer arbitrary, but are fully determined. This fact finds expression *ab initio* in equation (2) above, in which it is understood that the parameters P, Q do not include initial values of the first derivations of the X's.

Equilibrium defined by Minimum Condition.—In mechanics and thermodynamics the condition for equilibrium commonly takes the form that certain functions (potentials) of the variables defining the state of the system assume a minimum value.

As already remarked, the phraseology thus borrowed from mechanics and thermodynamics has been applied to biological systems, though no attempt has been made to give such expressions the analytical form without which they seem valueless or even meaningless.

As our reflections here have been conducted along analytical lines, the question arises whether they enable us to

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[1] See Buckingham, *Thermodynamics*, 1900, p. 33.

formulate the condition for equilibrium in precise terms and in form of a minimum or maximum condition.

We note, first of all, that the condition for equilibrium is given by (6) in the form

$$F_1 = F_2 = \ldots = F_n = 0 \qquad (6)$$

i.e., the equilibrium values of the n variables $X_1, X_2 \ldots X_n$ are defined by the vanishing of n given functions of these variables.

But evidently the same result can be achieved by stating that some arbitrary function $\Phi\ (x_1, x_2, \ldots x_n)$ has a minimum or a maximum when $x_1, x_2, \ldots x_n$ have their equilibrium values; for then we have, for these values,

$$\frac{d\Phi}{dx_1} = \frac{d\Phi}{dx_2} = \ldots = \frac{d\Phi}{dx_n} = 0 \qquad (12)$$

i.e., as before, the equilibrium values of the variables x are determined by the vanishing of n functions of these variables.

We can go a step further and select the function Φ so that it will have a maximum at the origin if, and only if, the equilibrium at the origin is stable. This will, for example, be the case if

$$\Phi = \mu_1 x_1^2 + \mu_2 x_2^2 + \ldots + \mu_n x_n^2 \qquad (13)$$

where $\mu_1, \mu_2, \ldots \mu_n$ are the real parts of the roots λ of the equation (11).

It can be seen by inspection[1] of the solution (10) that a necessary and sufficient condition for stability at the origin is that the real parts of all the roots λ shall be negative—*i.e.*, that the quadratic form Φ shall be definite and negative, so that Φ has a maximum at the origin.

As an illustration we may consider an example taken from Sir Ronald Ross's Quantitative Studies in Epidemiology[2] —namely, the equations representing the history (evolution) of a system comprising the three species: man—anopheles mosquito—malaria parasite.

Here Sir Ronald Ross develops the system of differential equations

$$\left.\begin{aligned} \frac{dz}{dt} &= k'z'(p - z) + qz = F_1(z, z') \\ \frac{dz'}{dt} &= kz(p' - z') + q'z' = F_2(z, z') \end{aligned}\right\} \qquad (14)$$

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[1] For a rigorous discussion of the conditions of Stability, see Poincaré, *Jour. Mathém.*, ser. 4, vol. ii, chap. xvii; also *Encyc. des Sci. Math.*, vol. ii, pt. 3, fasc. 1

[2] *Nature*, October 5, 1911, p. 466; February 8, 1912, p. 497.

Following the procedure set forth in dealing with the general case, we first put

$$F_1(z, z') = F_2(z, z') = 0 \tag{15}$$

One solution of (15) is

$$z = z' = 0 \tag{16}$$

It is not, however, this point of equilibrium in which we are interested, but the one given by the other solution of (15), namely

$$\left.\begin{aligned} z &= \frac{kk'pp' - qq'}{k(k'p' - q)} = C_1 \\ z' &= \frac{kk'pp' - qq'}{k'(kp - q')} = C_2 \end{aligned}\right\} \tag{17}$$

Accordingly we introduce as new variables

$$\begin{aligned} x_1 &= z - C_1 \\ x_2 &= z' - C_2 \end{aligned} \tag{18}$$

and obtain

$$\left.\begin{aligned} \frac{dx_1}{dt} &= (q - k'C_2)x_1 + k'(p - C_1)x_2 - k'x_1x_2 \\ \frac{dx_2}{dt} &= k(p' - C_2)x_1 + (q' - kC_1)x_2 - kx_1x_2 \end{aligned}\right\} \tag{19}$$

or, in the notation of our general discussion,

$$\left.\begin{aligned} \frac{dx_1}{dt} &= a_{11}x_1 + a_{12}x_2 + a_{112}x_1x_2 \\ \frac{dx_2}{dt} &= a_{21}x_1 + a_{22}x_2 + a_{212}x_1x_2 \end{aligned}\right\} \tag{20}$$

Assuming now, for the sake of illustration, that the constants in (19) are capable of assuming all kinds of values, we may distinguish the following cases :

1. Case in which the roots λ_1, λ_2, of (11) are real (and distinct).

The determinantal equation (11) here takes the form

$$\begin{vmatrix} a_{11} - \lambda & a_{12} \\ a_{21} & a_{22} - \lambda \end{vmatrix} = 0 \tag{21}$$

In the immediate neighbourhood of the origin the product terms in (20) are negligible.

By a well-known homogeneous linear transformation[1] we

$$\begin{aligned} \xi_1 &= a_1x_1 + a_2x_2 \\ \xi_2 &= \beta_1x_1 + \beta_2x_2 \end{aligned} \qquad (22)$$

can transform (20), omitting the product terms, into

$$\left.\begin{aligned} \frac{d\xi_1}{dt} &= \lambda_1\ _1 \\ \frac{d\xi_2}{dt} &= \lambda_2\xi_2 \end{aligned}\right\} \qquad (23)$$

where λ_1, λ_2 are the roots of (21).

From (23) it follows, firstly, that

$$\frac{d\xi_1}{d\xi_2} = \frac{\lambda_1}{\lambda_2} \cdot \frac{\xi_1}{\xi_2} \qquad (24)$$

$$\xi_2 = K\xi_1^{\frac{\lambda_2}{\lambda_1}} \qquad (25)$$

and, secondly, that

$$\left.\begin{aligned} \xi_1\frac{d\xi_1}{dt} &= \lambda_1\xi_1 \\ \xi_2\frac{d\xi_2}{dt} &= \lambda_2\xi_2^2 \end{aligned}\right\} \qquad (26)$$

Hence, by addition,

$$\frac{d}{dt}(\xi_1^2 + \xi_2^2) = \frac{dR^2}{dt} = 2(\lambda_1\xi_1^2 + \lambda_2\xi^2) \qquad (27)$$

where R is the radius vector of the point $\xi_1\xi_2$ in a diagram in which these two variables are plotted as rectangular coordinates. We thus obtain a graphic interpretation of the quadratic form $\lambda_1\xi_1^2 + \lambda_2\xi_2^2$. The topography[2] of the integral curves (25) near the origin is indicated in fig. 1 for $\lambda_1 < 0$, $\lambda_2 < 0$ (stable equilibrium); in fig. 2 for $\lambda_2 > 0$, $\lambda_2 > 0$ (unstable equilibrium); and in fig. 3 for $\lambda_1 > 0$, $\lambda_1 < 0$ (unstable equilibrium). The arrow heads indicate the direction of travel along the integral curves according to (27).

2. *Case of Complex Roots.*—Here we write

$$\begin{aligned} \lambda_1 &= \mu + iv \\ \lambda_2 &= \mu - iv \end{aligned} \qquad (28)$$

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[1] See, for example, Liebmann, *Lehrbuch der Differentialgleichungen*, pp. 99, 131.

[2] Compare Liebmann, *loc. cit.*; also von Dyk, *Akad. Wiss. Munich Sitzungsber.*, 1909, Abh. 15; *Munich Abhandlungen*, 1914, vol. xxvi, Abh. 10; also Sharpe *Ann. of Math.*, ser. 2, vol. ii, 1910, p. 97.

A transformation[1] somewhat similar to (22) then leads to

$$\left.\begin{aligned}\frac{d\xi_1}{dt} &= \mu\xi_1 + \nu\xi_2\\ \frac{d\xi_2}{dt} &= \mu\xi_1 - \nu\xi_2\end{aligned}\right\} \tag{29}$$

and we have, in this case,

$$\frac{d\xi_1}{d\xi_2} = \frac{\mu\xi_1 + \nu\xi_2}{-\nu\xi_1 + \mu\xi_2} \tag{30}$$

$$R = R_0\, e^{\frac{\mu}{\nu}\tan^{-1}\frac{\xi_1}{\xi_2}} \tag{31}$$

and

$$\frac{d}{dt}(\xi_1^2 + \xi_2^2) = \frac{dR^2}{dt} = 2\mu R^2 \tag{32}$$

$$R = R_0\, e^{\mu t} \tag{33}$$

The course of these integral curves is shown in figs. 4 and 5.

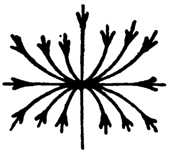

Fig. 1. Roots λ real and both < 0. Stability.

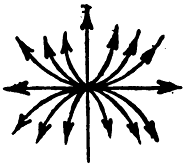

Fig. 2. Roots λ real and both > 0. Instability.

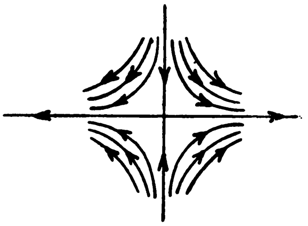

Fig. 3. Roots λ real and of opposite sign. Instability.

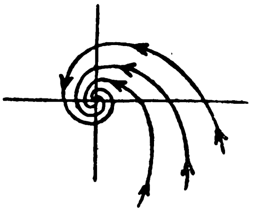

Fig. 4. Roots λ complex; $\mu < 0$. Stability.

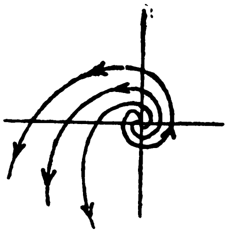

Fig. 5. Roots λ complex; $\mu > 0$. Instability.

Summary.—It has been pointed out by biologists that organic evolution is an irreversible process. Physicists also

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[1] See, for example, Liebmann, *Lehrbuch der Differentialgleichungen*, pp. 99, 131.

have spoken of the second law of thermodynamics broadly as the law of evolution.

In inorganic physical systems irreversible processes are attended with a decrease in certain functions of the variables defining the state of the system. Stable equilibrium is characterised by the fact that these functions assume a minimum value.

In the case of organic systems we have not, in general, any such definite criteria for irreversibility or for equilibrium.

In the present contribution a broad formulation of evolution, organic or otherwise, is presented in analytical form. From this it is shown that, for certain cases, functions of the variables X and the parameters P defining the state of the system, and of the coefficients a defining its characteristic properties, can be indicated, which have the property, in the neighbourhood of stable equilibrium, of diminishing in the (irreversible) process of the evolution of the system, and of assuming a minimum when stable equilibrium is established.

In these cases, therefore, it is possible to define in exact terms the *direction* of evolution, whereas the descriptions ordinarily given of this direction (passage from lower to higher, from simpler to more complex forms, etc.) are vague or inaccurate.

By the way of example, the principles thus established are applied to the system of equations given by Sir Ronald Ross to represent the history (evolution) of a system comprising a human population, mosquitoes, and malaria parasites.