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Energodynamic Theory of Biological Evolution

By Etkin V. A.

Togliatti State University

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ENERGODYNAMIC THEORY OF BIOLOGICAL EVOLUTION

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I. INTRODUCTION

Despite certain successes in the study of the processes of evolution of living and inanimate nature from the standpoint of the thermodynamics of irreversible processes [1-9], bioenergy [10-15] and synergetics [16-20], there is still an obvious contradiction between equilibrium and nonequilibrium thermodynamics and the nature of biological evolution. The principle of increasing entropy, interpreted as the essence of the second law of thermodynamics, imposes "thermal death" on the Universe as a whole, and on any of its autonomous regions – degradation [21]. The interpretation of evolution as a random process [22] or the result of the spontaneous emergence of "order" from "chaos" [19], and even more so as the absorption of some kind of "negentropy" [11], did not give satisfactory results. Moreover, the very concept of "self-organization" as spontaneous ordering of an isolated system [21], as well as attempts to "explain" antidissipative (thermomechanical, thermochemical, thermoelectric,

thermomagnetic, thermogalvanomagnetic) turned out to be in "blatant" contradiction with thermodynamics. threads, etc.) effects as manifestations of some kind of "synergy" [2,3].

A completely different view opens from the position of a more general and non-postulate thermodynamic theory of energy transfer and transformation processes in nonequilibrium systems [23], defended by the author in his doctoral dissertation [24] and then published in the form of a monograph "Thermokinetics" [24], recommended by the Ministry of Science and Education RF as a textbook for technical universities, and after its generalization to any form of energy in the monograph "Energodynamics" [25] - distributed by the Russian Foundation for Basic Research to university libraries. Unlike "pseudo-thermostatics" by W. Thomson [25] or "quasi-thermodynamics" by L. Onsager [26], this theory does not exclude from consideration any (irreversible or reversible) part of the phenomena being studied and covers the entire range of real processes - from quasi-static (reversible) to extremely irreversible (dissipative). This is achieved by finding the driving forces of real processes and their generalized rates directly on the basis of the law of conservation of energy in systems far from equilibrium, which opens up new possibilities for applying the method of nonequilibrium potentials to the study of biological systems and eliminates its contradiction with the laws of biological evolution.

II. METHODOLOGICAL FEATURES OF ENERGODYNAMICS

The fundamental difference between energodynamics and locally equilibrium thermodynamics of irreversible processes (IRP) and other field theories is the consideration of a nonequilibrium system as a whole, without breaking it up into an infinite number of elementary volumes dV , assumed to be homogeneous. This makes it possible to preserve the so-called system-forming connections that are inherent in the system, but absent in its individual parts. This is what distinguishes a living organism from a simple set of organs as macroscopic and even microscopic "subsystems" formed during such fragmentation. The realization of the hopelessness of attempts to restore the lost system-forming properties by finding "suitable integrals" was, according to A. Poincaré, "the biggest and most profound shock that physics has experienced since the time of I. Newton [28].

Author : Dr. Techn. Sc Togliatti State University (RF).

ORCID: 0000-0003-2815-1284. e-mail: etkinv3519@gmail.ru

Another methodological feature of energodynamics is considering the opposite direction of processes in various parts (regions, phases, components) of a nonequilibrium system. This circumstance makes nonequilibrium processes irreversible even when they occur quasi-statically (infinitely slow). The inconsistency of the concept of "quasi-stativity" of equilibrium thermodynamics of R. Clausius can be seen by presenting any extensive parameter of the system Θ_i (its mass M , the number of moles of k th substances N_k , entropy S , electric charge Θ_e , impulse P , its moment L , etc.) integral of its local $\rho_i = d\Theta_i/dV$ and average $\bar{\rho}_i = \Theta_i/V$ density $\Theta_i = \int \rho_i dV = \int \bar{\rho}_i dV$. It at once follows that

$$\int (\rho_i - \bar{\rho}_i) dV \equiv 0. \quad (1)$$

According to this identity, in the elements of the continuum where local equilibrium exists ($\rho_i - \bar{\rho}_i = 0$), no internal processes $d(\rho_i - \bar{\rho}_i)/dt \neq 0$ are possible. This provision emphasizes the need to consider spatial heterogeneity (internal disequilibrium) in any element of the system where any processes occur.

From identity (1) it also necessarily follows that in different parts (regions, phases or components), inhomogeneous systems of oppositely directed

processes (with different signs of speed $d(\rho_i - \bar{\rho}_i)/dt$) arise. This position is called in energodynamics the "principle of counterdirectional nonequilibrium processes" [24]. It is in tune with the dialectical law of "unity and struggle of opposites" and can serve as its mathematical expression.

Another starting point of energodynamics is the "principle of certainty of state" of nonequilibrium systems, according to which the number of independent arguments Θ_i of its internal energy U is equal to the number of independent processes occurring in it. This principle, proven in energodynamics "by contradiction," prevents "underdetermination" or "overdetermination" of a nonequilibrium system, i.e., tries to describe it with a missing or excessive number of parameters. An example of "underdetermination" is the local equilibrium hypothesis of I. Prigogine, according to which the volume elements of a system that is nonequilibrium as a whole are in local equilibrium (despite the occurrence of dissipative processes in them), so that their state can be described by the same number of variables as in equilibrium (despite the appearance of local "thermodynamic forces" X_i), and all equations of classical thermodynamics are applicable to them (despite their inevitable transition into inequalities).

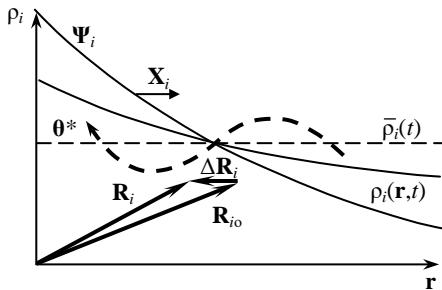


Figure 1: To the Formation of the Distribution Moment

Contrary to this hypothesis, energodynamics proves the need to introduce added parameters for the spatial heterogeneity of the systems under study. To find them, consider an arbitrary system with a non-uniform density $\rho_i(r) = \partial \Theta_i / \partial V$ of any extensive parameter Θ_i , considered as a quantitative measure of the i -th energy carrier (Fig. 1). As follows from the figure, when ρ_i deviates from the average value, a certain amount Θ_i^* of the energy carrier Θ_i is transferred from one part of the system to another in the direction showed by the dotted arrow. This causes a displacement of the center of its value from the first position $R_{i0} = \Theta_i^{-1} \int r dV = 0$, to the current $R_i = \Theta_i^{-1} \int \rho_i r dV$. In this case, a certain "distribution moment" Z_i arises:

$$Z_i = \Theta_i \Delta R_i = \int_V [\rho_i(r, t) - \bar{\rho}_i(t)] r dV. \quad (2)$$

with the shoulder $\Delta R_i = R_i - R_{i0}$, called the "displacement vector" in energodynamics [25].

Since in a homogeneous state $\Delta R_i = 0$, the state of the nonequilibrium system as a whole is characterized by twice the number of state variables Θ_i and ΔR_i , i.e. $U = \sum_i U_i(\Theta_i, R_i)$. In this case, its total differential can be represented as an identity [25]:

$$dU = \sum_i dU_i \equiv \sum_i \Psi_i d\Theta_i + \sum_i F_i dR_i, \quad (3a)$$

and the total derivative of the energy of the system with respect to time t is in the form

$$dU/dt \equiv \sum_i \Psi_i d\Theta_i/dt + \sum_i F_i \cdot v_i, \quad (3b)$$

where $\Psi_i \equiv (\partial U / \partial \Theta_i)_{R_i}$ – averaged value of potential Ψ_i (absolute temperature T and pressure p , chemical μ_k , electrical φ , gravitational ψ_g and other potentials); $F_i \equiv -(\partial U / \partial R_i)_{\Theta_i}$ – internal forces in their general

understanding as the antigradient of the i -th form of energy; $v_i = dR_i/dt$ – speed of the i -th transfer process.

The specificity of equation (3a) is that its terms no longer decide the heat or work of the i -th process, as would be the case for reversible processes. On the contrary, from the very beginning it is recognized that not only entropy S , but also other energy carriers Θ_i can change in the general case both due to external energy exchange and due to internal sources during internal spontaneous processes. In this case, the terms of the first sum in expression (3a) are under conditions of constancy ΔR_i , i.e., in the absence of redistribution processes. This means that local potentials ψ_i in such processes change to the same extent in all parts of the system (as in homogeneous systems). Due to this, the “global” (nonequilibrium) potentials Ψ_i buy the simple meaning of averaged values of local potentials ψ_i . This kind of change in state is reminiscent of uniform precipitation on an uneven surface. A special case of them are equilibrium (reversible) processes of heat and mass transfer of a system, the work of introducing k -th substances or charge into the system, its all-round compression, etc.

The second sum of identity (3a), on the contrary, owes its origin to the spatial heterogeneity of the systems under study. Its members characterize elementary work of a different kind than in thermodynamics, which is decided by the product of the force of the i -th kind F_i and the displacement dR_i of the object of its application (energy carrier Θ_i) caused by it. Since these forces are in conditions of constant parameters Θ_i , then $F_i = \Theta_i X_i$, where $X_i = -(\partial U / \partial Z_i)$. The work $dW_i = F_i dR_i = X_i dZ_i$ performed by the forces F_i or X_i consists of redistributing the energy carrier Θ_i throughout the volume of the system. Thus, energodynamics introduces into consideration a new class of transfer processes that are of a vector (directional, ordered) nature.

In the particular case of homogeneous systems ($\Delta R_i = 0$, $\Psi_i = \psi_i$) expression (3) goes into the combined equation of the 1st and 2nd principles of classical thermodynamics of open systems in the form of the generalized Gibbs relation [21], which is given the form in TIP:

$$dU = \sum_i \psi_i d\Theta_i, \quad (4)$$

where $i = 1, 2, n$ – the number of independent forms of energy of the system.

A unique feature of energodynamics, therefore, is that the main quantities with which TIP operates (thermodynamic forces X_i and flows $J_i = dZ_i/dt$ as generalized rates of transfer processes) are found directly from the thermodynamic identity (3b), thereby avoiding the most labor-intensive procedures for compiling an equation for the “production” of entropy.

III. FINDING THE DRIVING FORCES AND GENERALIZED RATES OF BIOLOGICAL PROCESSES

In the “quasithermodynamics” of L. Onsager [27], which deals with relaxation processes, the scalar thermodynamic forces X_i^* and “fluxes” J_i^* are found from the expression for the rate of entropy increase dS/dt in an adiabatically isolated system:

$$dS/dt = \sum_i X_i^* J_i^*, \quad (5)$$

where $X_i^* \equiv \partial S / \partial A_i$ is the deviation of some i -th parameter of the system A_i from its equilibrium value A_i^* ; $J_i^* \equiv dA_i / dt$ – “flows,” which actually have the meaning of the generalized rate of the i -th relaxation process.

However, in equilibrium thermodynamics the parameters A_i are obviously absent. Therefore, Onsager's theory remained a kind of formalism, unrelated to reality, until another future Nobel laureate I. Prigogine proposed moving to the study of so-called “stationary irreversible processes”, where the parameters X_i^* and J_i^* acquire a vector nature and are maintained unchanged with the help of “external coercion” i.e. performing work dW_i “against equilibrium” on the system. In this case, the concept of “flow” J_i acquires a very specific meaning as a parameter of the transfer process and could be found from disciplines operating with the concept of its speed, by isolating from their equations that part of the “production” of entropy dS/dt dS/dt , which is responsible for dissipation and in such processes is numerically equal to the work done on the system dW_i/dt . However, this required the compilation of cumbersome equations for the balance of energy, mass, charge, momentum, entropy, etc. in order to then isolate the irreversible part of the process. This most labor-intensive part of the TIP required the user not only to have extraordinary knowledge of the relevant fundamental disciplines, but also to apply a number of hypotheses, since these disciplines were deliberately limited to the consideration of conservative (non-dissipative) systems and did not contain dissipative terms. This was the main reason teaching TIP in higher education turned out to be unrealistic due to students being unprepared for this and going beyond the permissible duration of the course.

The situation is completely different in energodynamics, where the required forces X_i and flows J_i are already contained in its main identity (3b). In this case, the concept of force and generalized speed of the process buy a general physical meaning, due to which the inherent arbitrariness in their choice, due to the many ways of dividing the product $X_i J_i$ into factors, is eliminated. Thus, if the first sum (3a) includes the term TdS , which characterizes reversible heat transfer in classical thermodynamics, then the 2nd sum (3b) will have the term $X_s J_s$, where $X_s = -\nabla T$ is the

"thermomorphic" force, $J_s = Sv_s$ – entropy flow. Similarly, if the first sum (3a) includes the term pdV , which characterizes the reversible work of expansion, then in the 2nd sum (3) an additional term $X_v \cdot J_v$ will appear, characterizing the power of the process of compression of some and expansion of other parts of the system, for example the ventricle and atria ($X_v = -\nabla p$, J_v – volumetric flow). In the same way, if the first sum (3a) includes the term $M_k dN_k$, characterizing the diffusion of the k th substance across the boundaries of the system, then in the 2nd sum (3b) the term $X_k \cdot J_k$ will appear, characterizing the power of the separation process of this substance in the cell membrane or in the dialyzer ($X_k = -\nabla \mu_k$, $J_k = N_k v_k$ – flow of the k th substance). In an analogous way, driving forces can be found in so-called "polyvariant" systems that perform other types of work in addition to expansion work. Thus, if in the 1st sum (3a) we include the term $\varphi d\Theta_e$, which characterizes the reversible work of introducing an electric charge $\Theta X_e = -\nabla \mu_e$, $J_e = N_e v_e$ into a region with an average electric potential φ , then in the second sum (3) the term $X_e \cdot J_e$ will appear, characterizing the power of the process polarization (charge separation) in a cell membrane or in a galvanic cell ($X_e \equiv E = -\nabla \varphi$ – electric field strength, J_e – electric current).

It is easy to notice that the terms of the second sum (3a) can have different signs depending on whether the system does work, or work is done on the system. This is the fundamental difference between energodynamics and TIP, in which the terms $X_i \cdot J_i$ is always positive (as is the "entropy production" dS/dt). Meanwhile, in biosystems that consume free energy from the environment, $X_i \cdot J_i < 0$, which contradicts (5). This approach allows energodynamics to study real processes without excluding from consideration any of their components (reversible or irreversible).

A significant advantage of energodynamics over TIP is that it eliminates the need to draw up cumbersome equations for the balance of energy, mass, charge, momentum, entropy, etc. It is also important that energodynamics can reflect, at a quantitative and qualitative level, the emergence of new (acquired) properties. Indeed, the parameters Z_i are absent in equilibrium systems ($\Delta R_i = 0$) and their elements and arise only when they deviate from a homogeneous state. Thus, energodynamics is distinguished by considering not only the local nonequilibrium of the systems under study ($\nabla \psi_i \neq 0$), but also the ability to reflect the evolution of biosystems, which consists in the appearance of new properties (degrees of freedom) in them. It will be shown below that this also makes it possible to substantiate the dialectical unity of the processes of evolution and involution [30].

IV. CORRECTION OF THE EQUATIONS OF "PASSIVE TRANSPORT" IN BIOSYSTEMS

In "quasi-thermodynamics" by L. Onsager [27], it is postulated that each of the flows J_i linearly depends on all thermodynamic forces X_j ($j=1,2,n$) acting in the system. The corresponding equations are called "Onsager's phenomenological laws":

$$J_i = \sum_j L_{ij} X_j \quad (6)$$

Here L_{ij} are constant (independent of forces X_j) kinetic coefficients, called phenomenological and subject to the so-called "reciprocity relations" of Onsager $L_{ij} = L_{ji}$. These relationships reflect, in his opinion, the interconnection of J_i flows, which is the cause of the above-mentioned "side" effects of their "overlay."

The terms $J_{ij} = L_{ij} X_j$ of the flow $J_i = \sum_j J_j$ according to (6) have the same sign. This is natural for the case of purely dissipative processes when the total rate of approach of the system to equilibrium is the sum of the rates of individual relaxation processes. Meanwhile, a class of so-called "conjugate" processes is known, when some of them go ahead in the direction of equilibrium, while others, on the contrary, move it away from it. These are, for example, cyclic Belousov-Zhabotinsky reactions, called "chemical clocks" [31], "active transport" in biosystems (transfer of substances to the region of increased reaction affinity) [32], "upward diffusion" in metals and alloys [33], processes of concentration of matter in the Universe [30], etc. This means that at least part of the forces X_j and flows J_j have the opposite sign, i.e., when any i -th relaxation process occurs, the system moves away from equilibrium along other, j -th degrees of freedom. In other words, along with dissipative phenomena, processes of the opposite direction are seen in such systems. These include the phenomena of "self-organization" in biosystems, as well as the processes of structure formation in solutions and melts. Since it is possible to remove a system from a state of equilibrium only by performing work on it of an antidiisipative nature, we must admit that in biosystems, along with external energy exchange, internal work is performed that is not related to the production of entropy. Equations (6) do not take this specificity of systems performing useful work into account at all. This makes consumer goods inapplicable to biological systems.

In TIP, the interpretation of the effects of superposition of heterogeneous processes also turns out to be mistaken. Indeed, if the flows J_i in the TIP are found as derivatives with respect to time t from the independent parameters A_i , then they are also independent of each other and therefore cannot interact (they nevertheless overlap). This is especially obvious for stationary states, when some of the "overlapping" flows simply disappear, and yet the effects of

“overlapping” take on a maximum value. This means that the explanation of various (thermomechanical, thermoelectric, thermochemical, electromagnetic, etc. effects) in TIP because of the “superposition” or “entrainment” of heterogeneous flows, and not the summation of forces F_i and F_j , does not correspond to the essence affairs.

The transport equations appear in a completely different light from the perspective of energodynamics. It attracts equations of state or transfer from the outside as a kind of uniqueness conditions but does not build them into the foundations of the theory, as classical thermodynamics and thermodynamics do. This makes the mathematical apparatus of energodynamics independent of the form of these equations and cuts the contradiction between the TIP and mechanics. In it, for each independent process one can find a single (resulting) force F_i that generates the given process and disappears with its cessation [25]. The components of this force F_{ij} differ in their physical nature, but unlike X_i they have the same dimension [H]. If such (resulting) force is found, $L_{ji}X_i = 0$ and laws (6) take on the so-called “diagonal” form, like the equations of thermal conductivity, electrical conductivity, diffusion, etc., i.e., not having cross terms with $i \neq j$ [34]:

$$J_i = L_{ii}F_i = L_{ii}\sum_j F_{ij}. \quad (7)$$

In this case, the Onsager reciprocity relations are fulfilled trivially ($L_{ij} = L_{ji} = 0$) and become redundant, and with them the requirement of linearity of laws (6), necessary for the fulfillment of these relations, disappears. This means that the phenomenological coefficients L_{ii} in (7) can be arbitrary functions of the variables Θ_i and forces F_{ij} , and the laws (6) in the general case are nonlinear. As shown in [24], the laws of passive transport of k -substances take the form:

$$J_k = L_k X_k = -L_k \nabla \mu_k, \quad (8)$$

where L_k are the coefficients of osmotic diffusion of the k -th substance, depending on the fields of temperature, pressure, and concentration of all independent components of the system; $\nabla \mu_k$ is the gradient of chemical potential in the membrane. Meanwhile, in the laws of diffusion proposed by Onsager himself, the sum $\nabla \mu_k$ appears, as in (5) [27]. With the diagonal form of laws (7.8), their nonlinearity, due to the variability of the coefficients L_k , no longer prevents the detection of superposition effects. Let us demonstrate this using the example of a biological membrane that is permeable to the k th substance. Expanding the expression for the total differential of the chemical potential μ_k as a function of temperature, pressure, and concentrations of all j – independent components of the system ($j = 2, 3, K$), we have:

$$d\mu_k = (\partial \mu_k / \partial T) dT + (\partial \mu_k / \partial p) dp + \sum_j (\partial \mu_k / \partial c_j) dc_j. \quad (9)$$

This means that the transport equation (6) for discontinuous media in their integral form has the form:

$$J_k = -L_k [(\partial \mu_k / \partial T) \Delta T + (\partial \mu_k / \partial p) \Delta p + \sum_j (\partial \mu_k / \partial c_j) \Delta c_j], \quad (10)$$

where ΔT , Δp , Δc_j are differences in temperature, pressure, and concentration of j -th substances on the membrane. The terms of this expression represent the components of the resultant force $X_k = -\Delta \mu_k$, the first of which is responsible for the phenomenon of thermal diffusion (substance transfer due to temperature difference), the second – for the phenomenon of barodiffusion (substance transfer due to pressure difference), and the third – for the phenomenon of ordinary (concentration) diffusion. The mutual compensation of these components of the resulting force ($X_k = 0$) is the reason for the onset of a stationary state, which would be more correctly called the state of “partial equilibrium”. At the same time, the stationary effects themselves such as $\Delta T / \Delta p$, $\Delta T / \Delta c_j$ and $\Delta p / \Delta c_j$ are obtained in energodynamics because of the “superposition” of heterogeneous forces and not flows.

From (10) at $J_k = 0$, regardless of the value of L_k , the well-known expression for the stationary effect of the appearance of the so-called osmotic pressure Δp in a binary isothermal system (the first part is the solvent) directly follows:

$$(\Delta p / \Delta c_2)_{\text{set}} = -(\partial \mu_1 / \partial c_2) / (\partial \mu_1 / \partial p), \quad (11)$$

where Δc_2 is the stationary difference in the concentration of the dissolved substance on both sides of the biological membrane.

This made it possible to propose a method for studying superposition effects in nonlinear systems [23], which opens the possibility of studying the kinetics of processes in biological systems that are far from equilibrium.

V. SUBSTANTIATION OF THE RELATIONSHIP BETWEEN CHEMICAL REACTIONS AND METABOLIC PROCESSES

When applying TIP to chemical reactions, another contradiction of this theory was discovered, this time with the Curie principle, which sets up the conditions for the conservation of bonds under various transformations of the coordinate system in crystallography. About transfer and relaxation processes, this principle states that the generalized rate of any i -th process J_i in Onsager's laws (6) can depend only on thermodynamic forces X_j of the same (or even) tensor rank [1,2]. This means that chemical reactions described in TIP by scalar terms of the type $\sum_r A_r d\xi_r$ (where A_r is the standard chemical affinity of the r -th chemical reaction, ξ_r is the degree of its completeness) cannot interact with metabolic processes that have a vector nature. Meanwhile, it is known that metabolism



plays a decisive role in the vital processes of biosystems. To resolve this contradiction, I. Prigogine put forward the theory of "stationary coupling", in which the fact of the presence of active transport of substances through biological membranes due to the occurrence of chemical reactions on them was explained by the specificity of stationary processes with their inherent relationships between the costs of individual reagents. However, this did not solve the problem since the mentioned relationship between chemical reactions and metabolic processes was preserved in non-stationary processes. The solution to this problem is given by the basic identity of energodynamics in the form (3a) and (3b). If in the first sum (3a) the term $\sum_r A_r d\xi_r$ appears, describing the r-th scalar chemical reactions in homogeneous media, then in the second sum (3b) additional terms of a vector nature $\sum_r X_r J_r$ will appear, describing the same reactions, but carried out in a flow (in flow reactors, Van't Hoff boxes, cell membranes, etc.), where $X_r = -\nabla(A_r \xi_r)$, where $A_r \xi_r$ is the current (local) value of the chemical affinity of the r-th chemical reaction in a given section of the flow reactor; J_r is the flow of reagents participating in it. Indeed, for steady-state reactions, the term $\sum_r A_r d\xi_r$ can be represented as $\sum_r [\partial(A_r \xi_r)/\partial R_m] dR_m = -\sum_r F_r dR_m$, where $F_r = -\nabla(A_r \xi_r)$ is the local value of the driving force of the r-th flow chemical reaction; R_m is the coordinate of the "reaction front" in the flow reactor. In this case, the laws of active transport of substances in membranes take the form:

$$J_m = -L_m \sum_r \nabla(A_r \xi_r), \quad (12)$$

where $J_m = \sum_k N_k dR_m/dt$ is the flow of chemically reacting substances through the biological membrane. Thus, under conditions of spatial separation of reagents (as in a Van't Hoff box), chemical reactions buy a directional (vector) character, which decides their interaction with metabolic processes in full accordance with the Curie principle. In the absence of transfer of reagents in the field of intermolecular forces, chemical reactions inevitably buy a dissipative character, which is considered in the TIP by assigning the term $\sum_r A_r d\xi_r$ to heat sources. This removes one of the main contradictions between consumer goods and bioenergy [24].

VI. NON-ENTROPIC CRITERIA FOR THE EVOLUTION AND INVOLUTION OF BIOLOGICAL SYSTEMS

In classical thermodynamics and in thermodynamics there are no parameters or state functions that could be sufficiently general and strict criteria for the development (ontogenesis) and evolution (phylogeny) of biosystems. Entropy S is inapplicable for this purpose, since in biosystems exchanging energy and matter with the environment, it can change due to

heat or mass transfer in the absence of chemical reactions, or, on the contrary, remain unchanged if the system moves away from equilibrium or approaches it due to useful (reversible) work. In particular, the entropy of a biosystem can increase when more organized biomass is added to it, although in this case such an "extended" system only moves away from equilibrium.

As for the known "global" thermodynamic potentials such as the Helmholtz free energy F or Gibbs free energy G, they are defined only for closed homogeneous systems and are not applicable in the boundary conditions specified by matter flows [27]. Nor can its exergy (technical performance) [35] serve as a measure of the orderliness of a biosystem, since in extended systems it depends on environmental parameters, as well as on energy coming from outside in the process of performing work, and therefore is not a function of the state of such systems.

The so-called "production" of entropy dS/dt (the rate of its increase due to irreversibility) also does not meet these requirements, since this indicator has a minimum only for stationary states of linear systems, and then only near equilibrium [36].

Energodynamics again suggests a way out of the situation. The inhomogeneity parameters $Z_i = \Theta_i \Delta R_i$ and $X_i = -\partial U/\partial Z_i$ introduced in it, expressed by potential gradients $-\nabla \Psi_i$ averaged over the volume of the system V, are already such criteria. The advantage of such (non-entropy) criteria is that they are able to reflect the evolution of the system for each of its inherent degrees of freedom (mechanical, thermal, pressure, chemical, electrical, etc.), and are able to reflect not only its approach to equilibrium, but also removal from it:

$$dR_i, dZ_i, |dX_i| > 0 \text{ (эволюция)}, \quad (13)$$

$$dR_i, dZ_i, |dX_i| < 0 \text{ (инволюция)}, \quad (14)$$

These criteria for the evolution and involution (degradation) of systems are suitable not only for biological, but also for any other systems. They are simpler, more visual, and informative, since they allow us to monitor the behavior of each degree of freedom of systems separately, which entropy criteria cannot do. This also applies to evolution in various parts (regions, phases, and components) of the system, which makes it possible to detect the opposite direction of processes in them. Such criteria make it possible to distinguish the stationary states of nonequilibrium systems from the state of partial equilibrium, in which not only their differentials, but also these nonequilibrium parameters themselves vanish:

$$dR_i, dZ_i, d|X_i| = 0 \text{ (стационарный процесс)}, \quad (15)$$

$$R_i, Z_i, |X_i| = 0 \text{ (частичное равновесие)} \quad (16)$$

The ability to distinguish partial (incomplete) equilibrium from complete (characterized by the

cessation of all processes) allows one to distinguish the relaxation time of different subsystems of the body, which entropy criteria also cannot do. Finally, since in isolated systems all processes are spontaneous, the presence of non-entropic criteria makes the concept of self-organization meaningful, if we mean not the system, but its individual degrees of freedom. All this gives researchers a simple and extremely informative tool for analyzing evolutionary problems.

VII. UNITY OF THE LAWS OF ENERGY TRANSFORMATION IN TECHNICAL AND BIOLOGICAL SYSTEMS

One of the most important achievements of energodynamics is the establishment of the unity of the laws of energy conversion in thermal and non-thermal, cyclic, and non-cyclic, direct, and reverse machines. Let us now show that this unity extends to biological systems, including muscular movers. To this end, consider the expression $\sum_i X_i J_i = 0$, which follows from the energodynamic identity 3b in the steady process ($dU/dt = 0$, $d\Theta/dt = 0$) of energy conversion of the i -th form of energy into the j -th. It implies numerical equality and the opposite sign of the power of the process of transforming the i -th form of energy into the j -th:

$$X_i J_i = -X_j J_j \quad (17)$$

This means that previously independent flows and forces in energy conversion have a relationship $J_i/X_i = -J_j/X_j$, independent of their direction in space. At the same time, the laws of thermal conductivity, electrical conductivity, diffusion, etc. give way to more complex equations reminiscent of L. Onsager's laws of relaxation.

$$J_i = \sum_j L_{ij} X_j, \quad (18)$$

but differing from them in the antisymmetric nature of the matrix of its phenomenological coefficients L_{ij} . For the considered case of a two-stream system, they have the form:

$$J_i = L_{ij} X_i - L_{ji} X_j. \quad (19)$$

$$J_j = L_{ji} X_i - L_{ij} X_j. \quad (20)$$

This nature of the phenomenological laws of the energy transformation process becomes more understandable when considering, for example, a welding transformer, which converts the electrical energy of one voltage X_i into a lower one X_j while simultaneously increasing the current strength J_i to J_j . As is known, it clearly distinguishes between the "no-load" modes, in which the current in the primary circuit $J_i \rightarrow 0$, and the voltage in the secondary circuit X_j reaches its maximum value X_{j0} (open circuit voltage), and the "short circuit" mode, when $X_j \rightarrow 0$, and the current J_j is maximum and equal to the "short circuit current" J_{jk} . Moreover, as the overcome forces X_j increase

(approaching the "no-load" mode), the current in both the primary J_i and the secondary circuit J_j decreases. This is reflected by laws (19) and (20).

An analogue of such an energy converter in biological systems is a muscle element - a fibril, which can contract when a chemical reaction is started, i.e., converting chemical energy into mechanical energy. In it, the analogue of the primary energy carrier flow J_i is the flow of reagents J_r of a given chemical reaction, and the secondary flow J_j is the impulse of the contracted muscle. Each of these flows, in accordance with (19) and (20), depends on both forces, the first of which X_i in this case is the current value of the affinity of the chemical reaction $X_i = A_r \xi_r$, equal to the product of the standard affinity of this reaction A_r and the degree of its completeness ξ_r , and as X_j - the force of fibril contraction. In this case, the analogue of "idling" ($J_j = 0$) is the so-called "unloaded muscle contraction" mode, and the "short circuit" mode ($X_j = 0$) is the so-called "isometric muscle contraction" mode.

Expressing X_{j0} and J_{jk} through phenomenological coefficients L_{ij} (assuming their constancy), under conditions of constant forces X_i , laws (19) and (20) can be represented in a dimensionless form that does not contain phenomenological coefficients:

$$X_i/X_{j0} + J_j/J_{jk} = 1. \quad (21)$$

The applicability of these equations to biological systems is confirmed by the experimentally found Hill kinetic equations, which quite accurately describe the characteristics of muscles taken from various animal species [5]. The load characteristics of muscular movers constructed on their basis are shown in Figure 2.

Curves 1, 2, 3, 4 in this figure correspond to varying degrees of nonlinearity of Hill's kinetic equations. In linear systems, the dependence of X_i/X_{j0} on J_j/J_{jk} is expressed by a straight line intersecting the ordinate axes at $J_j/J_{jk} = 1$ and $X_i/X_{j0} = 1$ (curve 1). It is easy to notice that precisely this character follows from the kinetic laws (21). Thus, the work of the fibril as an element of any muscle is subject to the same laws as technical energy converters.

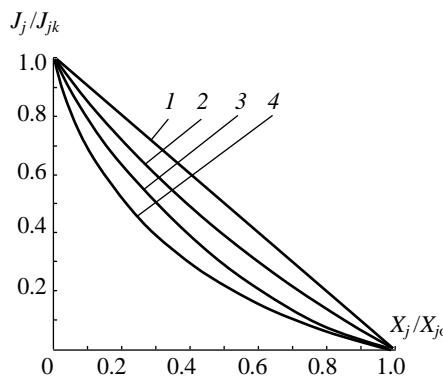


Figure 2: Load Characteristic of the Muscular Propeller

This unity makes it possible to use the theory of similarity of energy installations developed within the framework of energodynamics [37] to analyze biological energy converters. Based on equation (21), this theory introduces a number of dimensionless criteria for the similarity of linear energy-converting systems. One of them, the “constructiveness criterion” $\Phi = L_{ii}L_{jj}/L_{ij}L_{ji}$, is similar to the ratio of reactive and active resistances, known in radio engineering as the quality factor of the circuit, and, up to the temperature multiplier, coincides with the so-called “quality factor” Φ , introduced by A. Ioffe when analysis of thermoelectric generators (TEG) as their general characteristics. Its value ranges from zero to infinity ($0 < \Phi < \infty$), increasing with an increase in “reactive” resistances $R_{ij} = L_{ii}^{-1}$ (from the payload side) and a decrease in “active” resistances (from the side of dissipation forces) R_{ii} and R_{jj} . Like thermal resistances in the theory of heat transfer, these resistances depend on the properties of muscle tissue and their cross-section, composition, etc.

Another dimensionless criterion $B = J_j/J_{jk} = 1 - X_j/X_{jo}$, called “relative load”, is composed of boundary conditions specified by the value of forces X_j, X_{jo} or flows J_j, J_{jk} . It changes from zero in the “idle” mode (“unloaded muscle contraction”) to one in the “short circuit” mode ($X_j = 0$). As a determined criterion, this theory uses the “power” efficiency $\eta_N = N_j/N_i$, expressed by the ratio of the output power N_j and the input power N_i . This efficiency is numerically equal to the so-called “exergetic efficiency” and complements this concept by considering the kinetics of the energy conversion process through the transition to exergy flows. It considers all types of losses and therefore most fully reflects the perfection of the converter, i.e., the degree to which it realizes the capabilities that nature provides. Using these criteria, expression (21) can be given the form of a criterion equation for the energy conversion process:

$$\eta_N = (1 - B) / (1 + 1/B\Phi). \quad (22)$$

Criterion equation (22) allows us to construct a universal load characteristic that expresses the

dependence of this efficiency η_N on the power N_j and load B of the energy converter at varying degrees of its design perfection Φ (Figure 3) [37]. The solid lines on it reflect the dependence of the efficiency η_N on the load criterion B for various values of the quality factor factor Φ , and the dash-dotted line shows the dependence of the output power of the installation N_j on it. These characteristics reveal a circumstance unknown to classical thermodynamics - the efficiency η_N goes to zero twice: at idle ($B = 0$) and in the “short circuit” mode ($B = 1$). Another, also previously unknown, application is to demonstrate that the loads corresponding to maximum efficiency and maximum power diverge more noticeably the more advanced the energy converter is. In the absence of any energy losses (from friction, heat generation, all kinds of “leaks” of reagents, losses during no-load operation of the installation, etc., i.e., at $\Phi = \infty$), the power efficiency of the installation increases linearly with decreasing load, and at $B \rightarrow 0$ reaches, as one would expect, one. This case corresponds to an ideal Carnot machine, which has the highest thermodynamic efficiency, but has negligible power. This shows the existence of a best operating mode for each type of energy converter, including a muscular propulsion device. Universal characteristics facilitate the search for such a regime and allow the results of research on one of them to be transferred to others. Thus, a significant step is taken towards bringing the results of theoretical analysis of energy converters closer to reality.

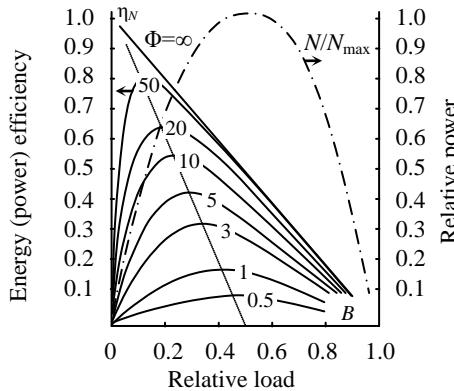


Figure 3: Universal Load Characteristics of Linear Energy Converters Systems

VIII. SURVIVAL AS THE BASIC LAW OF EVOLUTION OF BIOSYSTEMS

Among the numerous nontrivial consequences of energodynamics [38], associated with its introduction of nonequilibrium parameters X_i and R_i , is the possibility of studying the kinetics of relaxation processes in systems that simultaneously perform useful work. This allows us to raise the question of the life expectancy of living organisms and their reproductive period, which the “quasi-thermodynamics” of L. Onsager and TIP could not do. Meanwhile, this is precisely what decides the life expectancy and its reproductive period of bioorganisms. According to identity (3b), after isolating a nonequilibrium system ($\dot{U} \equiv dU/dt = 0$), processes of interconversion of energy occur in it until complete equilibrium occurs (all $J_i = 0$), subject to the condition

$$\sum_i X_i \cdot J_i = 0. \quad (23)$$

Let us now consider that a change in any parameter Z_i can be caused not only by the relaxation of a given degree of freedom, but also by the external $dW_i^e = F_i \cdot dr_i$ and internal $dW_i^u = X_i \cdot dZ_i$ work by the forces F_i and X_i . This circumstance can be expressed by equations like the entropy balance equations $dS = d_e S + d_u S$ proposed by I. Prigogine:

$$dZ_i = d_e Z_i + d_u Z_i + d_d Z_i, \quad (24)$$

where $d_e Z_i = dW_i^e / X_i$; $d_u Z_i = dW_i^u / X_i$; $d_d Z_i = dW_i^r / X_i < 0$ —components of the total change in the parameter Z_i caused by external W_i^e , internal W_i^u and dissipative work W_i^r , respectively.

So, the flow $J_i = dZ_i/dt$ as the generalized rate of any i -th transfer process includes external J_i^e , reversible internal J_i^u and dissipative internal J_i^r components:

$$J_i = d_e Z_i / dt + d_u Z_i / dt + d_d Z_i / dt = J_i^e + J_i^u + J_i^r. \quad (25)$$

In this case, condition (24) takes the form in isolated systems ($J_i^e = 0$):

$$\sum_i X_i \cdot (J_i^u + J_i^r) = 0. \quad (26)$$

It follows that if relaxation processes ($J_i^r \neq 0$) occur in the system, oppositely directed (anti-dissipative) processes of performing internal work “against equilibrium” will also occur in it. In energodynamics, this position is called the “principle of counterdirectivity” of nonequilibrium processes, which can be considered as a mathematical expression of the law of “unity and struggle of opposites” in dialectics [39].

In this case, this principle means that the approach to equilibrium of some (i -th) degrees of freedom of the system ($X_i \cdot J_i > 0$) is accompanied by the removal of other, j -th degrees of freedom ($X_j \cdot J_j < 0$) from it. This implies the unity of the processes of evolution and involution (degradation) of nonequilibrium systems. Unlike classical thermodynamics, which cannot say anything about the rate of approach of a biosystem to equilibrium, energodynamics allows us to raise the question of the time of approach of a system to a state of equilibrium, depending on the distance of the biosystem from the state of equilibrium. According to (3b), under comparable conditions, the rate of relaxation of the system prescribed by the second law of thermodynamics depends on the rate of reversible processes J_{iu} . In this case, one can compare the rate of approach to equilibrium of two arbitrary biological systems of varying complexity (with different numbers of degrees of freedom). If in an arbitrary system there are no reversible processes associated with the performance of internal work “against equilibrium” ($J_i^u = 0$), then the rate of its approach to equilibrium will be equal to

$$\dot{U}_r = - \sum_i X_i \cdot J_i^r. \quad (27)$$

In the presence of reversible work W_i^u , this speed is decided by expression (26). Comparing (23) and (26), considering the work of W_i^u , we find that their ratio is decided by the expression:

$$\dot{U} / \dot{U}_r = 1 + \sum_i X_i \cdot J_i^u / \sum_i X_i \cdot J_i^r. \quad (28)$$

This ratio can be either greater or less than one depending on the sign of the sum $\sum_i X_i \cdot J_i^u$, since $\sum_i X_i \cdot J_i^r$ is always positive. If $\sum_i X_i \cdot J_i^u < 0$, i.e., work is done in the system "against equilibrium," then the rate of approach of such a system to equilibrium decreases in comparison with a system where such processes are absent:

$$\dot{U} / \dot{U}_r = 1 - \sum_i X_i \cdot J_i^u / \sum_i X_i \cdot J_i, \quad (29)$$

Among the macroprocesses in which this kind of work is carried out is the so-called "active transport" of substances, which leads to the accumulation of reagents with a high Gibbs energy in the corresponding organs. These are the above-mentioned processes of "upward diffusion" in alloys, as well as the so-called "conjugate chemical reactions." Some of them, like the cyclic reactions of Belousov-Zhabotinsky ("chemical clock") or the process of circulation of matter in the Universe, can continue indefinitely. All processes of this kind arise only at a certain stage of their evolution. The lifespan of biosystems, as well as their reproductive period, depends on their intensity, which affects the evolution of the entire subsequent population of this type of bioorganism. When the work "against equilibrium" done by external forces $dW_j^e/dt = X_j \cdot J_j^e$ becomes equal to the work of a dissipative nature, the so-called "stationary state" of the nonequilibrium system will occur.

Here lies the key to understanding the general direction of the evolution of a biological system, understood as a transition from simple to complex. This direction of evolution is not imposed by a "higher mind" - it is a consequence of purely physical reasons, reflected in the energodynamic principle of "counterdirectivity" of nonequilibrium processes. These are any processes leading to the ordering of the system, its acquisition of new properties (increasing the number of degrees of freedom), complication of the structure, etc.

Since it is precisely this environment (including the field form of matter) that is responsible for the emergence of the biosystem and its further evolution, the advantage in extending the reproductive period is given to those systems in which mutations of hereditary characteristics lead to the complication of the system and the consolidation of new degrees of freedom and forms of interaction of the biosystem with this environment. This position can be briefly formulated in the form of the "principle of survival": "The more complex the biosystem and the more intense the evolutionary processes in it, the longer their life expectancy." This position is so general that it can be considered the basic law of biological evolution. It is easy to show that this law corresponds to the well-known "triad" of Darwin's doctrine of evolution - adaptability, variability, and heredity [40]. He also removes the "blatant contradiction between

thermodynamics and biological evolution" emphasized by I. Prigogine. At the same time, it also debunks the myth of "the emergence of order from chaos" [20], which contradicts classical thermodynamics, since maintaining "order" requires the expenditure of a certain external work, due to the absence of which the ordered energy of the system decreases. In other words, "order" in the system arises not from chaos, but due to a higher order in its environment. This fundamentally changes our worldview.

IX. CONCLUSION

1. The introduction of the missing parameters of spatial heterogeneity into thermodynamics reveals the occurrence in nonequilibrium systems of reversible processes of redistribution of energy carriers throughout the volume of the system and their opposite direction in different regions or degrees of freedom of the nonequilibrium system. This "opposite direction of processes" reflects at the physical level one of the main laws of dialectics, according to which the processes of evolution in some parts of a nonequilibrium system are invariably accompanied by processes of involution in others.
2. Description of the state of nonequilibrium systems requires the introduction of intensive X_i and extensive Z_i parameters of spatial heterogeneity, characterizing their deviation from equilibrium. This cuts the limitations of the thermodynamics of irreversible processes, which excluded their reversible part from consideration, which is why it also turned out to be unable to cut the contradiction between thermodynamics and evolution.
3. The introduction of nonequilibrium parameters X_i and Z_i allows us to return the concepts of force, speed, and power of real processes to thermodynamics, and obtain an energodynamic identity that remains valid for irreversible processes. It follows from this that the simultaneous occurrence in various parts (areas, phases, and components) of a non-equilibrium system of counter-directed processes of relaxation and the performance of work "against equilibrium" in the system, which reflects the dialectical unity and "struggle" of opposites.
4. The use of nonequilibrium parameters X_i and Z_i as criteria for the evolution and involution of biological systems makes it possible to reflect their approach to equilibrium and their distance from it both as a whole and for each inherent degree of freedom separately. Considering their vanishing in a state of equilibrium, this makes the mentioned criteria simpler and more informative than entropy.
5. Energodynamic identity allows us to develop a theory of similarity of energy machines, which allows

us to consider the dependence of the efficiency of technical and biological propulsion on the conditions and mode of their operation. The theory implies the unity of the laws of transformation of thermal and non-thermal forms of energy, including biological (muscular) and technical propulsion, which makes it possible to transfer the experience of studying one of them to others.

6. The occurrence of oppositely directed processes in biological systems slows down their approach to equilibrium and allows us to formulate the basic law of biological evolution as "the principle of their survival," which is based on the increase in the reproductive period of life and as they self-organize."
7. The reason for the "flagrant contradiction" of equilibrium thermodynamics to the laws of biological evolution is the absence of time as a physical parameter in its equations, which deprives it of the ability to consider the kinetics of real processes. It is precisely this that holds the key to understanding the relationship between reversible and irreversible processes occurring in them and deciding the duration of the reproductive period of biosystems.
8. The energodynamic theory of evolution confirms the main provisions of Darwin's theory of evolution, explaining them, however, by natural causes. This once again confirms the validity of the laws of materialist dialectics.

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