The growth and development of living organisms
from the thermodynamic point of view

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Abstract

The living organism is considered as an open system, whereas Prigogine’s approach to the thermodynamics of such systems is used. The approach allows one to formulate the law of individual growth and development (ontogenesis) of the living organism, whereas it has taken into account that the development and functioning of the system are occurring under the special internal program. The thermodynamic equation of growth is followed a method of estimation of the specific entropy of organism. The theory is compared with experimental data, whereas estimates of the specific entropy of some species were done; it shows a reduction of specific entropy in the evolutionary row: yeast - insects - reptiles - birds.

Keywords: Entropy of living organism, Energy exchange during growth, Thermodynamic equation of growth
1 Introduction

Many prominent investigators [1 - 4] approached the formulation of phenomenological (thermodynamic) theory of the development, growth and aging of a living organism (theory of ontogenesis). The theories were based on the analysis of quantities characterizing energy exchange between an organism and the surrounding. Measuring simultaneously both the incoming flux of energy and intensity of heat production, the investigators found [5, 6] that, under the growth, the former can surpass the later. The difference between the incoming flux of energy and intensity of heat production, dubbed as $\psi_u$-function [5, 6], has been qualified as a part of energy that is needed for the construction and growth of the organism [7]. This idea was central in our investigation, and we are going now to formulate the exact relation between $\psi_u$-function and the rate of mass growth of the living organism.

From the thermodynamic point of view, the living organism ought to be considered as an open thermodynamic system that exists in a non-equilibrium state [4, 8 - 10], and the desire to understand the general principles that govern the living organisms was one of the important motivations to investigate open systems. The living organism does not contain anything, apart of chemical compounds, and all processes that are occurring in the system are connected, in the large degree, with chemical transformations, so that there were some attempts to present simple models imitating the behaviour of the living organism. The brusselator, considered by Prigogine with collaborators [11], can be considered as one of the elementary models that reflects the essential features of the biological organism: an exchange of substances with the environment and existence of stable spatial internal structure within a limited volume. However, the living organism has extra peculiarities of the behaviour: unlike the brusselator, all processes are running under internal control, trying to keep the internal state of organism unchangeable, which is known as a phenomenon of homeostasis [12]. The control mechanism changes the speed of running of processes depending on the signals receiving from the outside. At the rise of outer temperature, for example, the control mechanism commands to increase perspiration, for the temperature of the organism not to be increased. This special congenital program also determines the development and growth of the organism.

Do all of this require some modification of thermodynamic laws at application to living systems in comparison with chemical systems of the brusselator type? In this paper, first of all, we are going to remind main results of Prigogene's formulation of thermodynamics of open systems (Section 2). In Section 3 we apply Prigogene's results to show how the control apparatus
can be introduced into the thermodynamic approach (Section 3.1); this gives a clue to the problem of the description of growth and development of the living organism. Then, we are formulating (Section 3.3) and testing (Section 3.4) the thermodynamic equation of growth of the living organism. The Discussion and Conclusions section contains a discussion of the resolution of the problem presented herein.

2 The Change of Entropy in Prigogine’s Formulation

The essential contribution to the thermodynamics of open systems was brought by Prigogine, when he and his collaborators investigated systems of chemically reacting substances. Stationary states of such systems exist due to exchange both particles and energy with the environment. In section 8 of the third chapter of his book [9], Prigogine has specified three contributions to the variation of entropy of an open system. The simple analysis [13, 14], reproduced in Appendix, demonstrates that the change of entropy $S$ of the system at the given temperature $T$ can be calculated according to the formula

$$ T dS = \Delta Q - \sum_j \Xi_j \Delta \xi_j + \sum_{\alpha} \eta_\alpha \Delta N_\alpha. $$

(1)

The first term on the right-hand side of the equation presents a stream of thermal energy into the system; it can be positive (the stream into the system) or negative (the stream out of the system). The last term depicts a stream of energy coming with the stream of particles of substances $\Delta N_\alpha$ that can be positive (the stream into the system) or negative (the stream out of the system), $\eta_\alpha$ is connected with chemical potential of substance labeled $\alpha$. The middle term on the right-hand side of equation (1) presents a change of the stored energy inside the system due to the existing of internal variables $\xi_i$, so called thermodynamic forces $\Xi_j$ are considered positive, so that this term gives a positive contribution into entropy at relaxation of internal variables. In the case of chemically reacting substances, which was investigated by Prigogine [9], the internal variables $\xi_i$ appear to be measures of incompleteness of chemical reactions, that are the measures of how much the considered system with chemical reactions is out of equilibrium; the thermodynamic forces $\Xi_j$ are affinities of corresponding reactions. The theory was generalized [13, 14] to consider any deviation from the equilibrium state as an internal variable, so that we can consider the set of internal variables $\xi_j$ in equation (1) to be comprised of the quantities determining not
only degrees of completeness of all chemical reactions occurring in the system, but also a structure of the system, gradients of temperature, difference of concentrations of substances and so on. Note that equation (1) presents the balance of energy and is not restricted to any approximations.

The sign of the middle term on the right-hand side of equation (1) is taken in such a way to ensure the positive production of entropy at the relaxation of internal variables $\xi_j$, but two processes are running simultaneously. Under some external influences (the fluxes of heat and substances) the system is passing to a new state, while internal variables could emerge and entropy of the system could change. Due to internal processes that cannot be controlled from the outside, the internal variables, as measures of non-equilibrium of the system, tend to disappear. For small deviations of internal variables $\xi_i$ from their equilibrium values $\xi_i^{(0)}$, the local law of disappearing can be written as relaxation equation for each internal variable

$$\frac{d\xi_i}{dt} = -\frac{1}{\tau_i} \left( \xi_i - \xi_i^{(0)} \right), \quad i = 1, 2, \ldots$$

where $\tau_i = \tau_i(T, x_1, x_2, \ldots, x_n)$ is a relaxation time of a corresponding internal variable that, being left on its own, permanently decreases and, eventually, comes close to equilibrium value $\xi_i^{(0)}$, which is conveniently considered to be equal to zero. In this situation, due to the recorded equation (2), the middle term on the right-hand side of equation (1), is positive and describes the dissipation of the stored energy. The dynamics of internal variables for arbitrary deviations from equilibrium was formulated in the paper [14].

Note that, in line with the notion of entropy of the open system $S$, one can introduce the notion of complexity, the latter has the same sense as notion of bound information [15] in application to complex systems. The complexity can be considered as a characteristic of the set of internal variables $\xi_i$: the internal variables themselves sometimes are called variables of complexity or variables of order. Though at the moment it is impossible to define how complexity is related to the number and connectedness of internal variables, one can assert that the greater the number of internal variables, their values and mutual connections, the greater the complexity. In virtue of equation (1), the change of complexity can be connected with the change of entropy of the system: increase or decrease in number and values of internal variables provokes decrease or increase in entropy.
3 Organism as an Open Thermodynamic System

We shall discuss the processes of growth and development of the living organism, considering it as an open thermodynamic system of undefined volume, but with the certain mass $M$ and temperature $T$. To describe a huge number of internal processes within the system, one needs a set of internal variables $\xi_j$, that, in case of the living organism, are emerged under the influence of the streams of substances and heat. On the basis of fundamental expression for variation of entropy of an open system (1), the equation for the growth rate of specific entropy $S/M$ of the organism can be written as

$$\frac{M}{S} \frac{d}{dt} \left( \frac{S}{M} \right) + \frac{1}{M} \frac{dM}{dt} = \frac{1}{TS} \left( \frac{\Delta Q}{\Delta t} - \sum_i \frac{\xi_i}{\Delta t} + \sum_{\alpha} \eta_{\alpha} \frac{\Delta N_{\alpha}}{\Delta t} \right).$$

It is marked with the symbol $\Delta$ that the corresponding quantities are objects of direct empirical observation.

The law of conservation of mass determines the equation of growth

$$\frac{dM}{dt} = \sum_{\alpha} m_{\alpha} \frac{\Delta N_{\alpha}}{\Delta t},$$

where $m_{\alpha}$ is mass of a particle of substance labeled $\alpha$. Unfortunately, this form of the growth equation is useless practically, so as there are a lot of the processes occurring in the living system, and it is extremely difficult to measure the substances coming in and out the organism [4].

The balance equations (3) and (4) give a basis for thermodynamic interpretation of the phenomena of existence, growth and ageing of a biological organism, but for this purpose, it is necessary to establish, first of all, correspondence of all symbols in these parities to the quantities concerning the living organism.

3.1 Three groups of internal variables

Let’s remind, that the internal variables that are present in the middle term of the right part of the equation (3) determine the deviation of the system from the state of equilibrium and, in this way, apart of the incompleteness of internal chemical reactions, describe the architectural and functional structure of the system. Considering the organism as an open system, we can note that there is permanent changing of internal variables, which emerge under fluxes of heat and substances and tend to disappear. The rate of disappearing is different for different internal variables; time of relaxation
of some of them are very small as compared with the lifespan of organism. The other internal variables exist during the total lifetime and even more. The difference of internal variables according to their rates of approach the equilibrium state determines their functional distinctions in the processes of the growth and development of the organism. For the further discussion, we are dividing the set of internal variables of the system into three groups, according to values of relaxation times; further on, the different functional roles of separate groups in the processes of development and growth are described.

First of all, it is possible to separate a group of internal variables, which originates from the complexity of the first cell that gives the beginning of the organism. The material carriers of complexity are the molecules of a deoxyribonucleic acid packed in the nuclei of the cells. The copies of internal variables (complexity) of the initial set are present in each cell and remain constant (at some idealization) up to the death of an organism. The number of copies of these variables increases at the proliferation of cells, and during the realization of the program of development. These variables comprise the foundation of a control mechanism that supervises all processes in the organism during its existence and growth. The organism is developing under the installed plan received by right of succession, whereas some internal variables are suppressed or expressed when the cells are multiplying. A role of internal variables of the first group is the conservation of hereditary instructions and the control over the construction of an organism.

The second group of internal variables describes the emerged structure of the organism in processes of morphogenesis and differentiation, when the interoperability of the parts of an organism is materializing. For example, conformations of the biomolecules having albuminous in the basis, change in such a manner that speed of reactions in which they participate, also sharply changes. The greater role is also playing a spatial arrangement of fibers and, in particular, enzymes [17]; it provides such processes that cannot occur in a random mixture of chemical reagents. The number and values of such internal variables increase at growth and development of the organism. The set of variables of the second groups determines some metastable structure (organs and tissues) of the living organism and have the times of relaxation comparable with the lifespan of the organism, so that they do not contribute into the current dissipation of energy (production of entropy).

1 Consideration of an hierarchy of relaxation processes is useful in many applications of non-equilibrium thermodynamics. For example, Gujrati [16] demonstrated recently that the division of internal variables according to their relaxation times is very helpful for description of the phenomena of solidification of glasses.
The set of internal variables of the third group emerges in the course of the above-described processes of multiplication of original complexity and construction of the structure of the organism. The processes are based on chemical transformations of substances, occur in non-equilibrium situations and are accompanied by excitation of internal variables and their fast relaxation. The set of internal variables of this group includes the variables locating gradients of temperature, differences in concentration of substances and degrees of completeness of all chemical reactions running in the organism. Internal variables of the third group accompany all existing processes anywhere they were. These internal variables have very small times of relaxation (in comparison with existence of the organism) and determine the basic contribution to the internal production of entropy. The dissipated energy is coming out in the form of heat.

Note that now we can record an expression for entropy of the organism as a function of the internal variables, whereas the expansion can be done over internal variables of the third group $\xi^{(3)}$

$$S(\xi^{(1)}, \xi^{(2)}, \xi^{(3)}) = S_0(\xi^{(1)}, \xi^{(2)}) - \frac{1}{2T}S_{ij}(\xi^{(2)})\xi^{(3)}_{i}\xi^{(3)}_{j}.$$ 

The quantity $S_0$ is entropy of a dead body (a corpse), the quantity is a decreasing function of variables of the first group $\xi^{(1)}$ (carriers of instructions for construction and functioning of an organism) and the second group $\xi^{(2)}$ (the description of metastable structures of the organism). The last term on the right hand side of the equation presents all processes running in the live organism; the quantities $S_{ij}$ are positive and essentially depend on internal variables of the second group, which define metastable structure (a set of structures) of the system and cannot be considered as small quantities.

The difference in the relaxation times of internal variables allows us to distinguish different functional roles of internal variables in the processes of development and growth. The distribution of the all internal variables over three groups can be helpful for designing of the functional scheme of the living organism.

3.2 Exchange of energy between the organism and environment

There are methods of assessments of incoming and outgoing fluxes of energy for the organism of an animal [4]; these fluxes are presented in the right part of the equation (3) by the first and the last terms. The greatest amount of energy is delivered into organisms with food in the form of energy of chemical links of organic molecules [4, 18]. The speed of synthesis of adenosine
triphosphate (ATP) gives us an estimate of the coming-with-food energy (in a unit of time). The synthesis can be realized in the two basic processes: the oxidizing phosphorylation and glycolysis. One can assume that the energy received in the process of glycolysis, can be neglected in comparison with the process of oxidizing phosphorylation [4], and one can judge about the speed of synthesis ATP indirectly, namely on the rate of oxygen consumption or the rate of allocation of carbonic gas. It is shown, that quantity of the consumed oxygen is proportional to the energy coming into the organism, whereas the factor of proportionality (so-called oxi-caloric coefficient) is approximately equal to 4.821 cal/ml O$_2$ [19]. The estimating of incoming energy by the speed of consumption of oxygen has received the name the method of indirect calorimetry.

The energy of molecules of ATP is used basically for the synthesis of molecules, which are included in the organism, also as for other processes requiring expenses of energy (muscle contraction, migration of cells, conduction of nervous impulses, etc.). Regarding the above-described classification of internal variables, the result of the release of energy of molecules of ATP is the emergence of internal variables of the second group, which is accompanied by excitation of internal variables of the third group.

The flux of heat energy from the living system $\Delta Q$ is measured by the method of direct calorimetry, that is by direct measurement of the speed of heat production of the organism by means of a calorimeter. The amount of thermal energy coincides with the dissipation of energy that appears at the relaxation of internal variables of the third group with small times of relaxation. The amount of the heat flux is evidence of the presence of quickly relaxing internal variables.

In steady state, when there are no changes of thermodynamic functions, incoming and outgoing flows of energy, according to equation (1), are equal. When an organism grows, the incoming stream of energy provokes the emergence of internal variables of the second and third group. The relaxation of variables of the third group defines dissipation of energy that in thermal form is deleted completely from the organism. Remind that the internal variables of the first and second groups do not contribute to the dissipation due to their huge relaxation times. Thus, the difference between the incoming and outgoing flows, if exists, gives rise to the emergence of structural variables of the second group, providing the construction of organs and tissues of the organism.

Entropy $S$ of the whole organism, due to the mass growth, increases; simultaneously increases in the number of internal variables and their mutual connections that is, one can say, increases in structural complexity of
the organism. The better, than the total entropy $S$, characteristic of the living organism is the specific entropy $S/M$: under the balance of incoming and outgoing energy, specific entropy $S/M$, as it follows from equation (3), can only decrease. In the situations of growth, the complexity of organism increases, and, so as the greater the complexity, the less entropy, one can assume that the specific entropy does not increase, and it gives

$$\frac{M}{S} \frac{d}{dt} \left( \frac{S}{M} \right) = -\sigma, \quad \sigma \geq 0. \quad (5)$$

At the moment we cannot say that the quantity $\sigma$ is constant, but later (in Section 3.4), its value will be estimated and appears to be about zero.

The permanent exchange of substances and energy between the organism and environment, which is a necessity for the creation of structures and maintenance of functioning, is controlled by the program (the internal instructions) stored with internal variables of the first group.

### 3.3 Equations of growth

From the previous reasoning, it follows that the growth rate of mass of the organism is essentially determined by a difference between quantities of incoming energy and outgoing heat. Equation (3) shows the linear dependence of the specific growth rate of mass on the difference, which had attracted special attention and attained the name of $\Psi_u$-function [5]. The specific psi-function is defined as

$$\psi_u = \frac{1}{M} \left( \frac{\Delta Q}{\Delta t} - \sum_i \Xi_i \frac{d\xi_i}{dt} + \sum_{\alpha} \eta_{\alpha} \frac{\Delta N_{\alpha}}{\Delta t} \right). \quad (6)$$

Now one can reformulate relation (3), using definitions (5) and (6), so that the equation of growth can be recorded in the form

$$\frac{1}{M} \frac{dM}{dt} = \sigma + \kappa \psi_u, \quad (7)$$

where $\kappa = M/TS$. According to the above equation, the origin of growth is the difference between quantities of incoming and outgoing flows of energy. The growth occurs until the organism will not reach the final steady state defined both by the genetic program, and conditions of the inhabitancy. The majority of poikilothermal animals (mammals and birds) and some of the poikilothermal ones reach the stable mass [20].
In the stationary case the organism should be considered as a system, in which all processes appear balanced:

$$\frac{\Delta Q}{\Delta t} - \sum_i \Xi_i \frac{d\xi_i}{dt} + \sum_\alpha \eta_\alpha \frac{\Delta N_\alpha}{\Delta t} = 0.$$  \hfill (8)

The adult organism, thus, can be considered as the certain constant structure that is being in the non-equilibrium stable state described constant thermodynamic functions.

The time dependence of the mass growth for all types of animals can be approximated by a simple equation [21]:

$$\frac{dM^{1/u}}{dt} = V_0 c^t, \quad 0 < c < 1,$$

where \(V_0\) is the speed of the growth in initial point in time \(t = 0\); \(c\) is a parameter determining the rate of growth; \(u\) is a correction factor that is taking into account interfaced processes (morphogenesis, differentiation, etc.).

The special case of equation (9) - the equation of Bertalanffy [22] – can be recorded in the form

$$\frac{1}{M} \frac{dM}{dt} = \frac{u \ln c}{c^{t-t_0} - 1},$$

where \(t_0\) is a conditional time, at which assumingly \(M = 0\), \(c\) is a factor determining the rate of growth, \(u\) is a factor connected with the influence of morphogenetic processes during the growth.

3.4 Testing of the thermodynamic equation of growth

To estimate correspondence of equation (7) to reality, we address to results of direct observation of growth of animals in the situations, when one can control the fluxes of energy between the organism and environment [4, 5, 23 - 28]. The fluxes of heat from the organism were measured by the method of direct calorimetry. The fluxes of chemical energy in the organism were estimated by the method of indirect calorimetry according to the rate of oxygen consumption. We can draw certain conclusions from the results.

It has appeared, that during an essential period of ontogenesis of organisms, the values of incoming and outgoing energy fluxes practically coincide,
Figure 1 The dependence of specific growth rate on $\psi_u$-function

Species: a - yeast *Saccharomyces cerevisiae* (according to Schaarschmidt et al. [24];
b - larvae of crickets *Acheta domestica*;
c - embryos of lizards *Lacerta agilis*;
d - chicken embryos *Gallus domesticus* (according to Kleymenov [28]). The dependences are approximated by straight lines, according to equation (7).
Table of Estimates of Specific Entropy

| Type (class)                      | $\kappa$, g/mW · day | $\sigma$, day$^{-1}$ | $r^2$ | $S/M$, J/g · K |
|----------------------------------|-----------------------|----------------------|-------|-----------------|
| Saccharomyces cerevisiae (Saccharomycetes)$^1$ | (4.73 ± 0.43) $\cdot 10^{-7}$ | (5.70 ± 2.98) $\cdot 10^{-6}$ | 0.92 ± 0.08 | 365 $\cdot 10^6$ |
| Acheta domestica (Insecta), larvae$^2$ | 0.042 ± 0.009          | 0.011 ± 0.014        | 0.76 ± 0.16 | 4400            |
| Lacerta agilis (Reptilia), embryos$^2$       | 0.062 ± 0.016          | 0.015 ± 0.046        | 0.87 ± 0.22 | 3350            |
| Gallus domesticus (Aves), embryos$^2$       | 0.166 ± 0.046          | 0.123 ± 0.098        | 0.98 ± 0.07 | 300             |

Sources of data: 1 – Schaarschmidt et al. [24]; 2 - Kleymenov [28].

and such a situation has received the name of the current steady state of the organism [4, 7, 18]. However, there is mass growth in such situations, and, according to equation (7), the difference between incoming and outgoing flows of energy must exist. One can assume that the growth occurs so slowly, that the difference appears to be so small, that, apparently, cannot be detected with the used methods. Apart of it, when the method of indirect calorimetry is used for the assessment of incoming stream of energy, the contribution of processes of glycolysis, which are also processes of synthesis of ATP, are neglected in comparison with the process of oxidizing phosphorylation. However, the contribution of the processes of glycolysis can appear comparatively essential in this phase of growth.

The authentic distinction between data of the indirect (according to the rate of oxygen consumption) and the direct (according to the rate of heat production) calorimetry in situations of the constant environment is observed in cases of the initialization of such processes, as differentiation, morphogenesis etc [28]. At early stages of the growth in ontogenesis, the distinction of results of the direct and indirect calorimetry is great enough to address to an assessment of the adequacy of equation (7).
Figure 2 The time dependence of $\psi_u$
Species: a - yeast *Saccharomyces cerevisiae* (according to Schaarschmidt et al. [24]); b - larvae of crickets *Acheta domestica*; c - embryos of lizards *Lacerta agilis*; d - chicken embryos *Gallus domesticus* (according to Kleymenov [28]). The dependences are approximated by curve lines, according to equation (11).
The specific growth rates, as functions of $\psi_u$, according to experimental data [24, 28] are shown on Fig. 1. The values of coefficients of correlation and parameters of equation (7) are collected in Table. Though the variability of data is great, the coefficient of correlation between the $\psi_u$ and specific growth rate differ reliably from zero ($p < 0.01$). Note that the quantity $\sigma$ is not significantly different from zero considering the error bars. Thus, specific entropy can be considered as a constant during a significant time interval, and the calculated values of the coefficient $\kappa$ allow to estimate specific entropy $S/M = 1/\kappa T$ (see the Table). It is seen that specific entropy decreases in the evolutionary raw: yeast $\rightarrow$ insects $\rightarrow$ reptiles $\rightarrow$ birds. These results show a reduction of entropy or, in other words, an increase of a degree of complexity of living systems during evolution.

A positive correlation between the specific growth rate and $\psi_u$ also has been noted for representatives of different taxons: bacteria *Serratta marinorubra, S. mercescens* [27], yeast *Saccharomyces cerevisiae* [24], larvae of mealworm beetle *Tenebrio molitor* [25], larvae of house crickets *Acheta domestica*, embryos of sand lizard *Lacerta agilis*, chicken embryos *Gallus domesticus* [28], larvae of juvenile fishes *Xiphophorus Helleri* [23], larvae of axolotl *Ambystoma mexicanum* [26], ovogenesis of clawed frogs *Xenopus Laevis* [5]. It is important to have a look at the time dependence of the quantity $\psi_u$ at the growth of the organisms: it gives an additional way of assessment of adequacy of the equation (7). Comparing equation (10) with the equation (7), we receive:

$$\psi_u = \frac{a}{1 - e^{d-t_0}} - b,$$

(11)

where $a = -u \ln c/\kappa; b = \sigma/\kappa$. On the plots of Fig. 2, the experimental values of psi-function, corresponding to values in Fig. 1, are shown with empty circles. The solid curves are calculated, according to equation (11), at individual values of quantities $a$, $b$ and $c$. This comparison confirms the existence of the universal law of growth in the form (10).

4 The Discussion and Conclusions

The thermodynamic approach for the open systems, developed by Prigogine [9] and his followers, gives a general foundation for description of dynamics of processes running in living systems. The internal variables, the number of which is huge, describe the deviations of the biological organism, as a thermodynamic system, from equilibrium and appears to be the most essential elements of description. However, we cannot even inventory all internal
variables, and are still very distant from the detailed description of the living organism. We have found that, though the biological organism exists as integral system and all internal variables are anyhow connected with each other, it is useful to allocate some groups of the internal variables according to the relaxation times. The mechanisms of heredity and control, which is the main thing that distinguish the biological organism from a system of coupled chemical reactions, is assumed to be ascribed to a special group (the first group in our classification) of internal variables. The internal variables with relaxation times comparable with the lifespan of organism (the second group) describe the metastable structure that is a real implementation of living organism. The variables of the third group are participating in thermodynamic processes that are obeying the linear laws of the non-equilibrium thermodynamics.

The clarification of functional roles of the internal variables allows us to formulate the thermodynamic equation of growth of organisms that corresponds not only to the results of experimental observations but also to basic phenomenological equations of growth. It is remarkable that application of the derived equation of growth to experimental data allows one to estimate the value of specific entropy of living organisms.

The specific entropy appears to be the most important thermodynamic characteristic of the living organism. In some examples, it was shown that specific entropy remains constant during the growth and development of the organism. It is possible that this property is valid only for many-cell bodies, when the growth is connected with the multiplication of the high complexity of the original cell. So as the specific entropy does not change substantially during the lifespan, it appears to be an individual characteristic of the organism. The assessments of specific entropy for larvae of crickets, embryos of the sand lizard and chicken embryos confirm that there is decrease of specific entropy and, consequently, an increase of a degree of complexity of the living systems during progressive macroevolution.

Appendix: Entropy of the open thermodynamic system

The concept of entropy, as a measure of the degraded energy, has arisen at the description of the ideal equilibrium situations. Variation of entropy $S$ under reversible process of a heat transaction to system in the amount $\Delta Q$ is defined as

$$\Delta S = \frac{\Delta Q}{T},$$

(A.1)
This circumstance allows to interpret entropy of the systems in equilibrium situations as a measure of thermal, completely degraded energy under some restrictions by a set of constitutive parameters (volume $V$ in the simplest case) that are defined the thermodynamic system. At the extension of concept of entropy for non-equilibrium states of the system, it is natural to demand, that interpretation of entropy as a measure of thermal, completely degraded energy is being kept. The ignoring of this requirement has brought to existence of a set of 'non-equilibrium entropies' and appears to be a source of some misinterpretation.

We shall demonstrate the realization of such an approach, following the works [13, 14], for general case of open system, which is assumed performs no work. Then, the expression for variation of total internal energy $U$ (the first law of thermodynamics) is recorded in the form of

$$\Delta U = \Delta Q + \sum_{\alpha} (\eta_{\alpha} + \mu_{\alpha}) \Delta N_{\alpha}, \quad (A.2)$$

where $\Delta Q$ is a flux of heat into the system, $\Delta N_{\alpha}$ is a change of substance of a kind $\alpha$ within the system. The enthalpy of unity of the substance of kind $\alpha$ is presented as a sum of two quantities, $\eta_{\alpha} + \mu_{\alpha}$, one of them $\mu_{\alpha}$ is chemical potential of the substance.

The parity (A.2) is valid both for equilibrium, and for non-equilibrium situations, however, if, in equilibrium states, internal energy $U$ represents completely degraded energy, in a non-equilibrium situation only some part of the total internal energy $U$, which we shall designate as $E$, is in the form of thermal energy. Other part of energy is connected with the restrictions caused by constant constitutive parameters (volume $V$ in the simplest case) and relaxating internal parameters $\xi$. The latter are introduced to describe deviations of the thermodynamic system from the equilibrium state. The total internal energy of the system changes due to the change of the composition of the system and work on variations of the internal parameters $\xi$, so that it can be recorded as

$$\Delta U = \Delta E + \sum_j \Xi_j \Delta \xi_j + \sum_{\alpha} \mu_{\alpha} \Delta N_{\alpha}. \quad (A.3)$$

The part of total internal energy is in the thermal form, and a part in the form that is ready to turn in thermal energy.

There are various ways of definition of entropy for the open thermodynamic system in view of all of non-equilibrium processes. In the simplest

\[\text{Thanks to W. Muschik, who pointed at the existence of this contribution.}\]
version, one keeps definition (A.1), which, apparently, is wrong, because since times of Clausius is known that in non-equilibrium processes for the closed system

$$\Delta S \geq \frac{\Delta Q}{T} \quad (A.4)$$

In view of it, the definition of non-equilibrium entropy for the closed system should contain additional positive terms

$$\Delta S = \frac{\Delta Q}{T} + \ldots$$

To define entropy as a measure of thermal energy, we shall return to the law of conservation and transformation of energy for the system, which can be recorded, according to parities (A.2) and (A.3) in the form of

$$\Delta E = \Delta Q - \sum_i \Xi_i \Delta \xi_i + \sum_\alpha \eta_\alpha \Delta N_\alpha. \quad (A.5)$$

Further, adhering to interpretation of entropy as a measure of energy in the form of heat, we follow an equation (A.1) and, neglecting the work of the system, record

$$\Delta S = \frac{\Delta E}{T}. \quad (A.6)$$

Here temperature $T$ is also defined as absolute temperature for the thermal part of the system that has thermal energy $E$. Of course, the real temperature of the system in a non-equilibrium state could differ from this temperature $T$, but the difference can be considered as an internal variable and included in the list of $\xi$ (inexplicitly).

In such a way, equation (A.5) and (A.6) determines the differential of entropy

$$dS = \frac{1}{T} \left( \Delta Q - \sum_i \Xi_i \Delta \xi_i + \sum_\alpha \eta_\alpha \Delta N_\alpha \right). \quad (A.7)$$

Equation (A.7) is the only definition of entropy of the open system, which is consistent with the understanding this quantity as a measure of the degraded energy and empirical evidences.
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