

Summary of primary and secondary constrictions and the percentage of the largest chromosome

Species <i>Rhinoderma rufum</i>	Chromosomes												
	1	2	3	4	5	6	7	8	9	10	11	12	13
<i>r</i> ^a	1.5	1.8	3.2	2.0	2.0	1.2	1.2	∞	1.5	1.6	1.0	1.0	∞
type	<i>m</i>	<i>sm</i>	<i>st</i>	<i>sm</i>	<i>sm</i>	<i>m</i>	<i>m</i>	<i>t</i>	<i>m</i>	<i>m</i>	<i>m</i>	<i>m</i>	<i>t</i>
%	100	69.3	65.3	63.0	59.6	27.2	26.7	26.4	24.4	22.7	20.4	19.3	17.6
C							<i>sm</i>	<i>sm</i>					
<i>R. darwini</i>													
<i>r</i>	1.5	1.6	2.7	2.6	2.2	2.3	1.3	1.4	1.6	1.7	1.7	∞	∞
type	<i>m</i>	<i>m</i>	<i>sm</i>	<i>sm</i>	<i>sm</i>	<i>sm</i>	<i>m</i>	<i>m</i>	<i>m</i>	<i>m</i>	<i>m</i>	<i>t</i>	<i>t</i>
%	100	79.8	65.6	61.2	60.9	36.6	28.4	27.5	26.3	23.6	21.5	19.2	18.0
C							<i>sm</i>			<i>sm</i>			

^a*r* is the ratio of the short arm divided into the long arm. For a ratio of 1.0 to 1.7 the chromosome type is metacentric (*m*; 1.7 to 3.0 is sub-metacentric (*sm*); 3.0 to 7.0 is subtelocentric (*st*); 7.0 and above is telocentric (*t*). The positions of the secondary constrictions (C) are based on similar ratios. The chromosome lengths are expressed as a percentage of the longest chromosome in the karyotype.

chromosomes, all bi-armed (NF 52)¹², is postulated as basic for the 'higher' Anura (here, only the Acosmanura¹³ are considered 'higher' Anura). This formula appeared for the first time among the species of Pelobatidae (*Leptobrachium*¹², *Megophrys*¹², *Pelobates*^{12,14}, and *Scaphiopus*^{15,16}) family to which the bufonoids (Bufonoidea) frogs are probably related¹⁷. Morescalchi¹⁸ attempted this hypothesis on a karyological basis. The leptodactyloid frogs constitute one of the most extensive (Neotropical Region, Southern South Africa and Australo-Papuan Region) and interesting group of families (Leptodactylidae and Miobatrachidae) of the 'higher' Anura, which the other bufonoid families probably lack. According to REIG¹⁹, the primitive chromosomal number for this group is 26 and I think that the NF should be 52, as Morescalchi¹² postulated as basic for the 'higher' Anura. This primitive formula (2*n* = 26 and NF 52) was maintained in the ancestral stock of leptodactylids, which are represented in South America by the subfamily Telmatobinae⁷. According to our results, it could be alleged that since *Rhinoderma* and many Telmatobinae species share a very similar primitive chromosomal formula (2*n* = 26), they should be closely related. However, this conclusion would be based on a false interpretation of the chromosomal evidence for phylogenetic inference, since the possession of 26 chromosomes is probably a primitive character for the Bufonoidea. According to HENNING²⁰, the sharing of a primitive character state (symplesiomorphy) does not indicate close phylogenetic relationships; instead this must be inferred from the common possessions of derived character states (synapomorphy). Therefore the chromosomal data do not afford new relevant evidence that permit us to settle the conflicting views of relationships and familiar status of *Rhinoderma*

among the families of Bufonoidea. The results here obtained reinforce the previously known picture of the wide-spread occurrence of the formula 2*n* = 26 among the members of Bufonoidea. Robertsonian mechanisms (centric fissions and fusions) have been generally postulated for chromosomal evolution in Anura²¹. Reduction or increment of chromosomal number are characteristic of these karyological changes, while the fundamental number remains constant. However, *Rhinoderma* species maintain the same primitive formula (2*n* = 26), like their leptodactyloid ancestors, but the NF is changed from 52 to 48. The constancy of the chromosomal formula and the change in the NF suggest that the Robertsonian mechanisms have no influence on the karyological evolution of *Rhinoderma* species. The presence of 2 acrocentric chromosome pairs in *Rhinoderma*'s karyotype and conservation of the chromosomal formula (2*n* = 26) suggest that pericentric inversions or other types of translocations could be related to these karyological evolutions.

¹³ P. H. STARRET, in *Evolutionary Biology of the Anurans* (Ed. J. L. VIAL; Univ. Missouri Press, Columbia 1973), p. 251.
¹⁴ A. MORESCALCHI, R. Acad. Sci. fis. mat., Napoli 31, 326 (1964).
¹⁵ A. O. WASSERMAN and J. P. BOGART, Copeia 2, 303 (1968).
¹⁶ A. MORESCALCHI, Experientia 24, 964 (1968).
¹⁷ J. D. LYNCH, Misc. Publs Mus. nat. Hist. Univ. Kansas 53, 1 (1971).
¹⁸ A. MORESCALCHI, Experientia 23, 1071 (1967).
¹⁹ O. A. REIG, in *Evolution in the Genus Bufo* (Ed. W. F. BLAIR; University of Texas Press, Austin and London 1972), p. 34.
²⁰ W. HENNING, *Elementos de una sistemática filogenética* (Editorial Universitaria, Buenos Aires 1968).
²¹ M. L. BEÇAK, Caryologia 21, 191 (1968).

Thermodynamic Aspects of Development for *Tenebrio molitor* L.

K.-D. LOEHR, P. SAYYADI and I. LAMPRECHT
Zentralinstitut für Biochemie und Biophysik der Freien Universität Berlin, Habelschwerdter Allee 30, D-1 Berlin 33
(German Federal Republic, BRD), 16 February 1976.

Summary. Predictions of the thermodynamics of irreversible processes are tested for the development and aging of an insect. Specific heat production and specific respiration rate decrease towards a steady state with deviations for the time of hatching of the imago.
It has long been known that classical thermodynamics does not apply to living matter. The concept of the evolution towards minimum free energy and maximum entropy is bound to closed systems, while organisms per se are open systems exchanging energy and entropy with their surroundings. The attempt to prove the theory of linear irreversible processes in this field could only be a zero order approach, since animals are normally far from equilibrium, and the linear relationships between flows and forces are only valid near equilibrium¹⁻³. Therefore,

it is more favourable to apply the thermodynamics of non-linear irreversible processes to the phenomenon of developing systems.

According to ZOTIN⁴, the specific dissipation function which describes the entropy production per weight must be divided into two terms, the external dissipation function ψ_a and the bound dissipation function ψ_u

$$\psi = \psi_a + \psi_u = \frac{T}{m} \left(-\frac{d_i S_a}{dt} + -\frac{d_i S_u}{dt} \right) = \frac{T}{m} - \frac{d_i S}{dt}$$

where T is the absolute temperature, m the mass of the organism, and $d_i S/dt$ rate of entropy production in the system. One part ($d_i S_a/dt$) is released to the surroundings; the other ($d_i S_u/dt$) is used in the system.

It was shown¹ that, for linear relationships, ψ decreases with time to a steady state of minimum entropy production and dissipation. Thus, near equilibrium ψ_a equals ψ and ψ_u becomes zero.

The total specific dissipation function ψ is defined by the respirative metabolism of the animal, which might be determined by manometric methods, while the external dissipation function is given by the heat production of the system measured calorimetrically.

The manometric data (μ l oxygen consumed per sec) are transformed into caloric figures by the well known relation that the enthalpy of respiration of 1 mole glucose, is 673 kcal \cong 2820 kJ which calculates to 5.0 cal or 21 J per μ l oxygen consumed. The difference between the manometric and the calorimetric figures is the bound dissipation function ψ_u . According to the theory, this difference should be maximum for the juvenile organism and decrease to zero during development and aging.

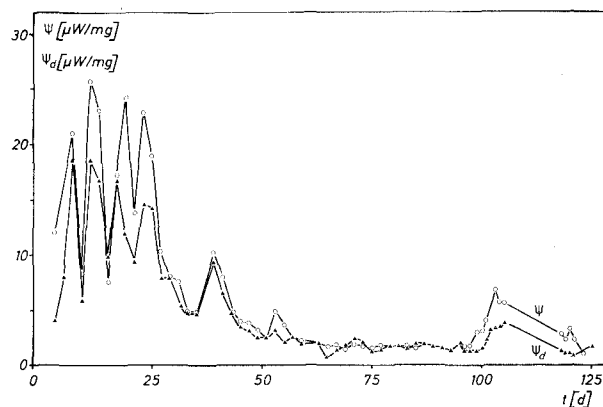


Fig. 1. The dissipation functions ψ and ψ_a during the development of *T. molitor* L.

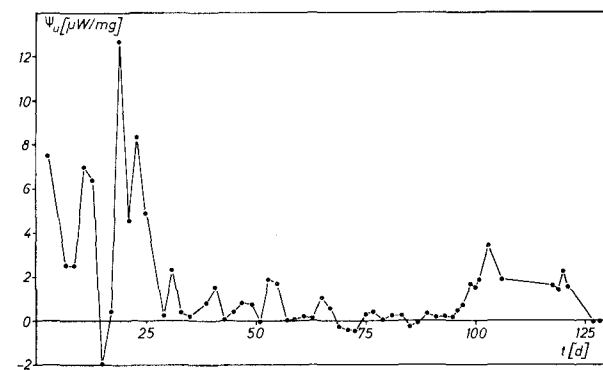


Fig. 2. The dissipation function ψ_u during the development of *T. molitor* L.

The experiments were performed at 25°C with the meal worm *Tenebrio molitor* L., which has a) a life-span of less than half a year, b) an appropriate size for the manometric and calorimetric experiments, and c) passes through different larval states. It was bred as described in the literature^{5,6}. The respiration rate was determined by means of a Warburg apparatus, the heat production with a Calvet microcalorimeter (Setaram/Lyon). Both experiments and the weighing of the animals were done consecutively, within a few hours, and with the same individuals. To adapt to the sensitivity of the instruments and the size of the animals, the initial number of individuals – 23 – was reduced to 1 in the course of the whole experiment. Between day 5 and 50 the growth followed an exponential law with a mass doubling time of 5.7 days. After the last larval molt (day 76) the weight dropped until the imago hatched. By referring all specific values to the wet weight instead of the dry weight, it was possible to avoid killing the animals and to perform all experiments with the same individuals.

Figure 1 shows strong fluctuations in the two specific metabolic data ψ and ψ_a of the juvenile animals. That they are not due to instrumental artifacts may be argued from the good correlation between ψ and ψ_a and from the fact that they disappeared later in the experiment. For the moment, no connection is seen to molting or other activities. Approximately after 4 weeks the larval are 'ready' in a thermodynamical sense, and the specific rates decline to a fairly constant value during the pupal state. But with the emergence of the imago (day 100), a thermodynamically 'new' animal is born leading to a temporal deviation from the steady state and approaching a new one later on.

The ψ_u -function, as the difference between the two metabolic rates, shows the predicted behaviour of approaching zero during the development (Figure 2). As ψ_u is obtained as a small difference between two larger quantities, the negative values are deviations without any meaning. The increase in ψ_u at the moment of hatching is in good agreement with the theory.

The experiments reported here confirmed by similar ones with the cockroach, *Blattella germanica*, which shows an equivalent behaviour. The results of these experiments will be discussed in greater detail elsewhere. They demonstrate that the thermodynamics of the non-linear irreversible processes is well suited to describe the development and aging of these insects, as found for other organisms earlier^{4,7}.

¹ I. PRIGOGINE, *Introduction to Thermodynamics of Irreversible Processes* (Thornes, Chicago 1955).

² P. GLANSDORFF and I. PRIGOGINE, *Thermodynamic Theory of Structure, Stability and Fluctuations* (Wiley-Interscience, London 1971).

³ G. NICOLIS, *Adv. Chem. Phys.* 19, 209 (1971).

⁴ A. I. ZOTIN, *Thermodynamic Aspects of Developmental Biology* (Karger, Basel 1972).

⁵ F. STELLWAAG-KITTLER, *Biol. Zbl.* 73, 12 (1954).

⁶ SISTERS K. M. TRACEY, *Ann. ent. Soc. Am.* 51, 429 (1958).

⁷ B. SCHAARSCHMIDT, A. I. ZOTIN, R. BRETEL and I. LAMPRECHT, *Arch. Microbiol.* 105, 13 (1975).