SIMULATION AND OPTIMIZATION OF EVOLUTION IN BIOSYSTEMS BY INFORMATION-THEORETIC ENTROPY

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ABSTRACT

Evolution of animals with multiple organs or limbs is considered. We report computer-aided modeling and simulation of evolution in biological systems with living organisms as the effect of extremum properties of classical statistical entropy of Gibbs-Boltzmann type or its associates, e.g. Tsallis *q*-entropy. A variational problem searches for the maximum entropy subject to the geometric constraint of constant thermodynamic distance in a non-Euclidean space of independent probabilities p_i , plus possibly other constraints. Tensor form of dynamics is obtained. Some processes may terminate rapidly due to instabilities. A gradient dynamics can be predicted from variational principles for shortest paths and suitable transversality conditions.

Keywords: evolution, entropy, gradient dynamics.

1. INTRODUCTION

Systems capable of increasing their size and/or number of states (growing systems) can exhibit critical behavior when their size increases beyond a certain value. In effect, some developmental processes, i.e. biological evolution, may progress in a relatively undisturbed way, whereas others may terminate rapidly due to strong instabilities. То describe such phenomena quantitatively, we present here an extremum principle for entropy S of a physical or a biological system with variable number of states, thus making it possible to investigate processes of biological development and evolution. The extremum principle is of the variational nature and may be formulated as the problem of maximum S subject to the geometric constraint of the constant thermodynamic distance in a (generally non-Euclidean) space of independent probabilities p_i , plus possibly other constraints. The dynamics found are presented in the tensor form. An essential result implies that various dynamics, in particular those of growth processes (characterized by the increase in number of states), are governed by the gradient of the entropy in a Riemannian space.

2. ROLE OF COMPLEXITY AND ENTROPY

In the thermodynamic theory of evolution extrema of complexity Γ with respect to entropy S provide important information. There is a multitude of complexity measures in the literature, all capturing

some aspects of what we mean when we say a process is complex. According to Saunders and Ho (1976, 1981) the complexity growth is the most probable effect in evolving systems. Complexity Γ is a function of disorder D and order Ω , which, in turn, are functions of the information-theoretic entropy S and number of possible states *n*. When speaking about the complexity and related entropy one issue is particularly important: a nonequililibrium entropy has to be necessarily applied because the difference between the maximum entropy and the actual system's entropy governs the organization in a complex system. Schrödinger (1967) has defined the disorder D and order Ω as expotential functions of non-dimensional quantities S and -Srespectively, in units of $k_{\rm B}$. Yet, as pointed out by Landsberg (1984) these notions are inappropriate for growing systems. For such systems, Landsberg's definitions of disorder D and order Ω apply

$$D \equiv S / S_{\text{max}} \tag{1}$$

$$\Omega \equiv 1 - D = 1 - S / S_{\text{max}} \,. \tag{2}$$

As S_{max} depends on the number of states, n, in Landsberg's definition both disorder D and order Ω are functions of the information entropy S and number of states, n, i.e. D = D(S, n) and $\Omega = \Omega(S, n)$. One especially simple form is the complexity

$$\Gamma_n(S) \equiv 4D\Omega = 4(S/S_{\max(n)})(1 - S/S_{\max(n)})$$
 (3)

The coefficient 4 in Eq. (3) is introduced to normalize the quantity Γ_n . The subscript *n* refers to a complexity sequence in a system with growing number of states, *n*. The solution to the following equation

$$d\Gamma_n(S)/dS = 0 \tag{4}$$

allows one to determine the extremum value of the information-theoretic entropy, \hat{S} , which maximizes complexity Γ_n (Szwast, Sieniutycz and Shiner 2002). The maximum attained by the function $\Gamma_n = \Gamma(S, n)$ equals the unity. This maximum appears for D = 0.5.

Hence the complexity-maximizing *S* equals to one half of the maximum entropy (the total randomness)

$$\hat{S} = \frac{1}{2} S_{\max}(n) \tag{5}$$

Evolution occurs on submanifolds that are surfaces of constant entropy (Szwast, Sieniutycz and Shiner 2002). Here the generalized *q*-entropy or Tsallis entropy *S* is used in probabilities $\mathbf{p} = p_0, p_1, \dots, p_n$

$$S = (q-1)^{-1} \left(1 - \sum_{k=1}^{n} p_k^q \right), \tag{6}$$

where p_k is the probability of finding an element in the state *i* among *n* states possible and $\Sigma p_k=1$. Equation (6) refers to Tsallis statistics (Kaniadakis, Lissia, Rapisarda, 2002) which generalizes the Boltzmann-Gibbs statistics by introducing an additional parameter *q*, that is called non-extensivity parameter. The additive Boltzmann entropy is regained from (6) in the limit of *q*=1. Performing maximization of *S* one can easily show that for a sole constraint $\Sigma p_k=1$ maximum of entropy occurs for the total randomness. All probabilities satisfy then the equality $p_i=p_k=n^{-1}$ and the maximum entropy is

$$S_{\max} = (q-1)^{-1} \left(1 - n^{1-q} \right).$$
 (7)

In the classical case $(q \rightarrow 1)$ this formula yields a well-known result, $S_{\text{max}} = \ln(n)$.

Yet, in an example considered, a multi-organ animal is a system with 2n+1 probabilities that describe *n* pair of legs plus the remaining part of the body, hence

$$S_{\max} = (q-1)^{-1} \left(1 - (2n+1)^{1-q} \right).$$
(8)

In the classical case $(q \rightarrow 1)$ this formula yields, $S_{max} = \ln(2n+1)$. The complexity-maximizing entropy \hat{S}_n equals to one half of these quantities. In the classical case of q=1 one obtains

$$\hat{S}_n = (1/2)\ln(1+2n)$$
. (9)

Generally, the complexity-maximizing entropy is

$$\hat{S}_n = \frac{1}{2} S_{\max} = \frac{1}{2} (q-1)^{-1} \left[1 - (2n+1)^{1-q} \right], \quad (10)$$

where \hat{S}_n of Eq. (9) follows in the classical case of q=1. To work with independent p_i we eliminate the last probability from entropy (6) and normalization condition $\Sigma p_i=1$. We then obtain a *tilde entropy function*

$$S = \tilde{S} \ (p_0, \ p_1, \dots p_{n-1}) \tag{11}$$

and, from Eq. (3), a related complexity

$$\tilde{\Gamma}_n = F_n \left[\tilde{S}(p_0, p_1, \dots p_{n-1}) \right].$$
(12)

Using independent probabilities we work with the tilde entropy. For the evolutions satisfying the maximum complexity (Saunders and Ho 1976), the entropy $\tilde{S}(\mathbf{p})$ equals to the complexity-maximizing entropy \hat{S} . This is consistent with the statement of Saunders and Ho (1976) "The only completely reversible changes are those which are isocomplex". For $\hat{S} = \tilde{S}(p_0, p_1...p_{n-1})$, a subset of probabilities $\mathbf{p} = (p_0.p_1...p_{n-1})$ is found describing the evolution submanifolds by an equality

$$\tilde{S}(p_0, p_1, \dots, p_{n-1}) = \hat{S}_n$$
 (13)

and assuring the value of $\hat{S}_n = (1/2)S_{\max}(n)$. Within this manifold, a reversible modification of states is possible. In other words, in the evolution examples, the solutions to equality $\tilde{S}(p_0, p_1, .., p_{n-1}) = (1/2)S_{\max}(n)$ refer to the *submanifolds of evolution*, or surfaces on which modifications (mutations) of organs may occur.

3. EVOLUTIONS OF MULTIPLE ORGANS WITHOUT MUTATIONS

Following earlier works (Saunders and Ho 1976, 1981; Szwast, Sieniutycz and Shiner 2002; Szwast 1997) we analyse here the *evolution of a multiple-organ or a multi-limb organism*, e.g. trilobite, an animal with many pair of legs. Although trilobites died out millions years ago, their anatomical structure is known due to the excavations. For our purposes it is sufficient to distinguish one pair of legs, of probability $2p_i \equiv 2p_1$ from the remaining parts of the organism. The remaining part has probability p_0 . For a multi-organ animal with *n* pairs of legs, the following holds

$$S = (q-1)^{-1} \left(1 - p_0^q - 2np_1^q \right)$$
(14)

and, in the classical case,

$$S = -p_0 \ln p_0 - 2np_1 \ln p_1.$$
(15)

They both hold subject to the condition of $\Sigma p_i=1$, or

$$p_1 = (1 - p_0) / 2n \tag{16}$$

Whence the entropy in terms of single independent p_0

$$\widetilde{S}(p_0) = (q-1)^{-1} \left(1 - p_0^q - (2n)^{1-q} (1-p_0)^q \right)$$
(17)

and its classical limit of q=1

$$\widetilde{S}(p_0) = -p_0 \ln p_0 - (1 - p_0) \ln[(1 - p_0)/2n].$$
(18)

Each of these entropies must be equal to its complexity-maximizing counterpart as described by Eq. (10) and its classical limit (9). By comparing Eq. (10) and (17), for an arbitrary q, we obtain equations for independent probabilities in terms of n and sole p_0

$$(q-1)^{-1} \left(1 - p_0^q - (2n)^{1-q} (1-p_0)^q \right)$$

= $\frac{1}{2} (q-1)^{-1} \left[1 - (2n+1)^{1-q} \right]$ (19)

In the case of classical entropy

$$- p_0 \ln p_0 - (1 - p_0) \ln[(1 - p_0)/2n]$$

= (1/2) ln(1 + 2n) (20)

From these equations probabilities p_0 and (then) p_1 can be calculated in terms of *n*. Graphs of these results for q=1 are presented in the literature (Szwast, Sieniutycz and Shiner 2002; Szwast 1997), where appropriate results are restricted to points describing the evolution without modifications or specializations.

4. ORGANISMS WITH MUTATIONS OR SPECIALIZATIONS OF ORGANS OR LIMBS

Here we analyze the evolution of a multiple-organ animal with mutations or specializations. An example relevant to this case follows the scheme including the stage trilobite \Rightarrow crab. With entropies *S* expressed in terms of independent probabilities p_i (functions \tilde{S} ($p_0,...,p_{n-1}$) one may consider effects of reversible modifications (mutations) of multiple organs (e.g. pair of legs), for a fixed value of \hat{S}_n . In the considered example, after modification of a pair of legs to claws a crab emerges from a trilobite. Considering the anatomical structure of the crab, one pair of claws is distinguished with probability $2p_2$. When the modification occurs without change in number of pairs of legs and claws, the following equality holds

$$2p_2 + 2(n-1)p_1 + p_0 = 1.$$
⁽²¹⁾

For an organism with one pair of organs modified (specialized) on the reversibility surface, Eq. (13) and (21) are applied in the space of independent probabilities to describe the equality of the generalized entropy \tilde{S} and the complexity-maximizing \hat{S}_n . After comparing the two entropy expressions we obtain

$$(q-1)^{-1} \left(1 - p_0^q - 2(n-1)p_1^q - 2p_2^q(p_0, p_1) \right)$$

= $\frac{1}{2} (q-1)^{-1} \left[1 - (2n+1)^{1-q} \right]$ (22)

in the generalized case, and

$$-p_0 \ln p_0 - 2(n-1)p_1 \ln p_1$$

$$-2p_2(p_0, p_1) \ln p_2(p_0, p_1) = \frac{1}{2}\ln(1+2n)$$
(23)

in the classical case. The probability function $p_2(p_1, p_0)$ used in these equations has the form

$$p_2 = \frac{1}{2} \left(1 - p_0 - 2(n-1)p_1 \right) \tag{24}$$

that follows from the condition $\Sigma p_i=1$ represented by Eq. (21). Note that $2p_2$ is the probability attributed to the modified organ or limb. The complexitymaximizing entropies ($\hat{S}_n = S_{\max/2}$) are those used earlier, Eq (10). The evolution submanifolds are now the family of lines $p_0(p_1, n)$. They describe organisms possessing *n*-1 of identical organs (pairs of legs) and one organ being modified, specialized, or subjected mutations. A special subset of data refers to organisms without specialization (Sec.3).

In the evolution literature Williston's law is frequently quoted (Saunders and Ho 1976, 1981; Szwast, Sieniutycz and Shiner 2002), which subsumes the results of observation and comparative analysis. This law states that if an organism possesses many of the same or similar elements, a tendency appears to reduce the number of these elements along with the simultaneous modification (specialization) of these elements which are saved by the organism. In the example considered here, the evolution submanifolds describe organisms possessing n-1 of identical organs (pairs of legs) and one organ being modified, specialized, or subjected mutation. Spontaneous increase of complexity is here a basic feature of evolution. For biological systems a reasonable measure of complexity is the different number of components they contain, so as to be consistent with well-known Williston's law which predicts that very similar components will either merge or specialize. Staying on the ground of the idea of increasing complexity, the system's organization acts as a force which prevents loss of components and allows complexity increase by the integration of new ones. This leads to a principle stating that an organism with more of organs (e.g. pairs of legs) is more susceptible to evolution towards an increase in the number of these organs.

Yet, during reversible specialization of organs, the state of an organism can fall into the region of the catastrophic decrease of number of these organs. These catastrophes constitute the price of specialization. The likelihood of falling in the catastrophe region increases with the number of organs. This explains why organisms possessing large number of similar organs ultimately reduce this number, despite the fact that they are more susceptible to evolutionary increase in the organ number. This also agrees with the well-known formulation of Williston's law of evolution (Saunders and Ho 1976) that subsumes the results of observation and is confirmed by the excavation experiments. In the dynamical description of this problem an extremum principle provides a quantitative picture of biological development. It shows that a discrete gradient dynamics (governed by the entropy potential) can be predicted from variational principles for shortest paths and suitable transversality conditions.

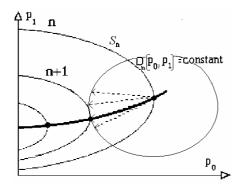


Figure 1. An original optimization problem for a system with *n* states is that of maximum change of entropy or complexity Γ between a point and the surface of constant distance from the point.

5. A VARIATIONAL APPROACH TO THE EVOLUTION DYNAMICS

Working in the dynamical context, (Szwast, Sieniutycz and Shiner 2002), we may analyze the evolution of living organisms as multi-organ or multi-limb systems by using the complexity criterion based on a potential, usually taken as the classical statistical entropy (of Shannon-Boltzmann) and the entropy-based complexity.

Here, however, in order to penetrate a vaster spectrum of stability (instability) properties, the generalized Tsallis entropy *S* is used (in k_B units) as a function of independent probabilities $p_0, p_1, ..., p_n$. In the analysis of this sort, classical thermodynamic quantities do not appear, yet the model used satisfies an extremum principle that, similarly as in thermodynamics, implies the maximum of entropy subject to the geometric constraint of a given thermodynamic distance.

More specifically, an original optimization problem for a system with *n* states is that of maximum change of entropy or entropy-related complexity Γ between a point and the surface of constant distance from the point (Fig.1).

Dual forms of this principle can also be considered, where one mimimizes the thermodynamic length subject to a fixed change of the system's complexity or entropy (Fig.2). In the dual problem one searches for minimum length between a point (for a system with nstates) and the entropy manifold of the system with n+1states. In this formulation specific properties of the shortest lines variational problems can directly be applied, (Lyusternik 1983), if one doesn't want to use standard theory of variational calculus (Elsgolc 1960).

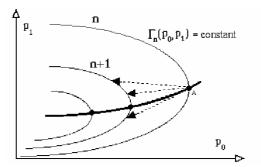


Figure 2. Dual optimization problem for a system with n states is that of minimum length between a point and the surface of constant entropy for the system with n+1states.

In the variational formulation, an s-dimensional evolution can be obtained via minimization of the length functional

$$J = \int_{p_0^n}^{p_0^{n+1}} a(p_0, p_1) \sqrt{1 + (dp_1/dp_0)^2} dp_0$$

$$\equiv \int_{p_0^n}^{p_0^{n+1}} L(p_0, p_1, dp_1/dp_0) dp_0$$
(25)

where independent probabilities p_i are constrained to reside on the constant-entropy manifold satisfying the constraint d \tilde{S} =0. (As in our example above we restrict to the system of two independent p_{i} .) The "conformal coefficient" $a(p_0, p_1)$ takes into account the deviation from the Euclidean measure of length in the simplest way possible. Regarding the problem of geodesic lines, see, e.g., (Lyusternik 1983). To handle the constraint d $\tilde{S} = 0$ one introduces the function $F_n(p_0, p_1) = \tilde{S} - \hat{S}_n$ whose numerical value equals zero for all states corresponding to the complexity-maximizing entropy. These are states residing on the evolution submanifolds or "reversible isolines". The direction coefficient of tangent to the submanifold \widetilde{S}_n (p_0 , p_1 ..) is the derivative $v_n \equiv (dp_1/dp_0)_n$. This derivative can be determined in terms of the partial derivatives functions \tilde{S}_n or F_n as

$$v_n = \left(\frac{d p_1}{d p_0}\right)_n = -\left(\frac{\partial \widetilde{s}_n(p_0, p_1)}{\partial p_0}\right) \left(\frac{\partial \widetilde{s}_n(p_0, p_1)}{\partial p_1}\right)^{-1}.$$
 (26)

To predict the location of a point on the submanifold n+1 when a point on the submanifold n is given, we consider *the variational problem* of the shortest line between the two points located on the submanifolds \tilde{S}_n and \tilde{S}_{n+1} . This corresponds with a minimum of the length functional (25).

The necessary extremum condition (the Euler equation) shows that any deviation from the Euclidean metric (measured in terms of a) influences, in general,

shapes of shortest-distance extremals which lead from the submanifold n to the submanifold n+1. Of course, upon restriction to the Euclidean metric and the Euclidean distance (a = 1), extremals are the family of the straight lines $p_1=C_1p_0 + C_2$. Generalization to nonflat spaces is given below, but we shall first consider *the transversality condition* for an arbitrary integrand L of (25) that may be associated with curvilinear spaces. An extremal which starts from a point on the submanifold nand terminates on the submanifold n+1 satisfies

$$\delta J = \{L - \frac{\partial L}{\partial (d p_1/d p_0)} (d p_1/d p_0)\} \delta p_0$$

$$+ (\frac{\partial L}{\partial (d p_1/d p_0)}) \delta p_1 = 0,$$
(27)

(c.f. Elsgolc 1960), where δp_0 and δp_1 are linked by condition (22) applied for n+1 rather than n.

For any length-type integral *J*, Eq. (27) defines the condition associated with the extremal which starts from a point on the submanifold *n* and terminates on the submanifold *n*+1. In view of arbitrary variations of p_0 the substitution of δp_1 from Eq. (26) into Eq. (27) yields the equality $u_{n+1} = -1/v_{n+1}$, where u_n is the slope coefficient of the normal to isoline \tilde{S}_{n+1} . This means the *orthogonality of the slopes* u_{n+1} and v_{n+1} in Euclidean spaces. In other words, in the case of an assumed or imposed Euclidean geometry (the transversality condition unaffected by the coefficient $a(p_0, p_1)=1$) the slope coefficient of the tangent to the extremal is

$$u_{n+1} = \left(\frac{d p_1}{d p_0}\right)_{n+1} = \frac{\partial \widetilde{S}_{n+1}(p_0, p_1)}{\partial p_1} / \frac{\partial \widetilde{S}_{n+1}(p_0, p_1)}{\partial p_0}.$$
 (28)

This condition implies the *gradient dynamics* in flat spaces, with probabilities changing with time in the form

$$\left(\frac{d p_i}{dt}\right)_{n+1} = \omega \frac{\partial \widetilde{S}_{n+1}(p_0, p_1)}{\partial p_i}$$
(29)

(i=0,1). The frequency-type coefficient ω has the interpretation of a kinetic constant. A related discrete dynamics of evolution contains the finite differences $\mathbf{p}(n+1)$ - $\mathbf{p}(n)$ instead of the time derivatives.

Next, it may be shown that the gradient dynamics also holds also in curvilinear spaces. In fact, admitting non-flat metrices (i.e. working with situation when a Lagrangian associated with a non-flat metric is effective) one may show (Gołąb 1956) that *the tensor generalization* of the continuous model (29) is

$$\frac{d p_i}{d\tau} = g_{ik} \frac{\partial \tilde{S} (p_0, \dots p_s)}{\partial p_k}, \qquad (30)$$

where $\tau = \omega t$ is a nondimesional time and ω is the frequency coefficient of Eq. (29) and g_{ik} is *s*-dimensional Riemannian tensor (Gołąb 1956). The consequence of this equation is the tensor form of the discrete evolution dynamics with the Onsager-like structure, where his symmetry matrix $L_{ik} = \Delta t \, \omega g_{ik}$ appears

$$p_{s}(n+1) - p_{s}(n) =$$

$$L_{s1} \frac{\partial \widetilde{S}_{n+1}(p_{0}, p_{s})}{\partial p_{0}} + \dots + L_{ss} \frac{\partial \widetilde{S}_{n+1}(p_{0}, p_{s})}{\partial p_{s}}, \quad (31)$$

as in the classical irreversible thermodynamics. Therefore, the evolution processes can be imbed quite naturally into a relatively large family of thermodynamic processes.

6. CONCLUDING REMARKS

By applying the tensor calculus, one can develop a discrete, nonlinear representation of evolution dynamics in metric spaces that may be curvilinear. Dynamic programming algorithms (Bellman's equations) can be derived and computer-aided simulations of their solutions can be performed. Systems governed by nonclassical *q*-entropies may exhibit irregular shape of entropy hill and show quantitatively distinct picture of instabilities than classical.

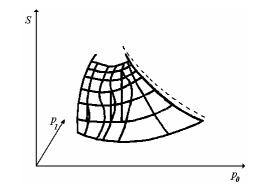


Figure 3. Szwast's (1997) computer simulation of instabilities in evolution systems. Trajectory of increase of number of pairs of legs (broken line), manifolds of reversible modification (specialization) of one pair of legs (lines of S=const) and vertical jumps describing a rapid decrease in number of pairs of legs (vertical lines).

Evolutions of living organisms can be described in terms of variational principles for maximum of generalized entropy along with suitable transversality conditions. General gradient dynamics (in curvilinear spaces), that governs the evolution problems, is of Onsager's structure and is consistent with the entropy principle of extremality as the driving factor in the discrete dynamics of complex and living systems, postulated recently (Szwast, Sieniutycz and Shiner 2002). We have shown that such a principle should be integrated with the evolution theory of biological systems.

Calculations of gradients of entropy or disorder versus number of organs, n, performed by Szwast (1997) show that these gradients increase with the number of multiple organs. This allows one to formulate the principle which states that organisms with more of organs are more susceptible to evolution towards an increase in the number of these organs. Yet, during reversible specialization of organs, the state of an organism can fall into the region of the catastrophic decrease of number of these organs. These catastrophes constitute the price of specialization. The calculations show, Szwast (1997), that the likelihood of the system's falling in the catastrophe region increases with n. Some of the related results are presented in Fig.3. This discussion explains why organisms possessing large number of identical organs ultimately reduce this number, despite the fact that they are more susceptible to the evolutionary increase in the organ number, in agreement with Williston's law. This law states that if an organism possesses many of the same or similar elements, a tendency appears to reduce the number of these elements along with the simultaneous modification (specialization) of these elements which are saved by the organism (Saunders and Ho 1976; Szwast, Sieniutycz and Shiner 2002; Szwast 1997). Entropy-based models, quantifying these critical phenomena, are enriched in this paper by inclusion of non-classical statistical entropies, e.g. q-entropies of Tsallis or Renyi, that may modify magnitudes of unstable regions in the space of process probabilities.

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His work with graduates has resulted in several PhD theses: Discrete Maximum Principle of Pontryagin's type (Z. Szwast 1979); Thermodynamic Liapounov Functions in Gas-Solid Systems (J. Komorowska-Kulik, 1979); Optimizations in Catalytic Cracking (A. Kebang 1980 and A. Dlugosz 1983): Modeling and Optimization in Separation of Coal Conversion Liquids (A. Dunalewicz 1989), Nonlinear Models of Mechanical Energy Production in Non-Ideal Generators Driven by Thermal or Solar Energy (M. Kubiak 2005 and P. Kuran 2006). Prof. Sieniutycz has contributed about 250 research papers in the field of chemical engineering and irreversible thermodynamics. He is also an author of several books: Optimization in Process Engineering (WNT Warsaw 1978 and 1991); Practice in Optimization Computations (with Z. Szwast; WNT, Warsaw 1982); Conservation Laws in Thermo-Hydrodynamics (Kluwer Variational Academic, Dordrecht 1995), and, recently, with Prof. J. Jeżowski, Energy Optimization in Process Systems, (Elsevier, Oxford and Radarweg, 2009) He has been a visiting professor in a number of schools: University of Budapest (Physics), University of Bern (Physiology), University of Trondheim (Chemical Physics), San Diego SU (Mathematics), University of Delaware (Chemical Engineering), and (several times at) The University of Chicago (Chemistry).