TRENDS IN THEORETICAL BIOLOGY: THE 20TH CENTURY

Kalevi Kull[*]

ABSTRACT

The paper gives a brief history of theoretical biology and examines the main trends in the search for a theory of general biology throughout the 20th century – the physicalisation on one hand, and the semiotisation on the other. These two approaches had their predecessors and were formed already in the 19th century biology, as Darwinian and Baerian biology. In theoretical biology, there are co-existing (however, asymmetrical) trends toward specifying solutions and generalising axioms. The inclusion of the biological organism as a subject into biological theory requires an analysis of the concept of scientific fact. The main periods of development of theoretical biology are briefly characterised, and the trend towards the theory of biological communication and meaning outlined.

I. INTRODUCTION: THE PEAKS AND PARADIGMS

How the theory of biology should look like? This is a problem which unceasingly participates in the discussions on theoretical biology during all of its existence. Where to find the metalanguage for all numerous models of biological mechanisms? What kind of language has a right to be called adequate (appropriate, or scientific) for explanation and understanding of living systems, the process of life?

Biological theories and theoretical concepts in biology are obviously as old as biology itself, since there cannot be any science without its theoretical part. However, theoretical biology as a discipline with its monographs, periodicals, professionals, and name arose mainly at the beginning of the 20th century. The works which launched the field were J. Reinke's 'Einleitung in die theoretische Biologie' [44] and J. v. Uexküll's 'Theoretische Biologie' [61].

The meaning of the term 'biology' has been reserved, already since

---

[*] University of Tartu Estonia (Institute of Zoology and Botany).

«AQUINAS», Anno XLIII, 2000, Fascicolo 2

the year 1800 when it was coined by K. F. Burdach (and a year later by J. B. Lamarck and G. R. Treviranus), to denote the integrity of various aspects and forms of life (including plants, animals and humans, morphology, physiology and behaviour, etc.). This is how the term has been interpreted both at the end of the 19th century (e.g., by a leading European journal 'Zeitschrift für Biologie', edited by W. Kühne), and later. In the same way, theoretical biology has set as its aim the development of a theory which can be applied for understanding the phenomenon of life wherever it occurs.

During the 100 years since its birth at the beginning of the 20th century, theoretical biology has experienced two remarkable peaks of interest. The first was in the 1930s, and the second in the 1960s and 70s. These peaks will be briefly characterised below (cf. [29]). The third peak of interest is just showing the first signs of its possible emergence now.

1.1. Diversity makes sense

To understand the atmosphere in biology in Reinke's and Uexküll's time, when 'theoretical biology' appeared on the scene, it is important to note that the decades around the turn of the century were very productive in starting simultaneously a series of new branches in biological research. Among them, the following can be listed:

(1) beginning of genetics through the rediscovery of Mendel's laws;
(2) beginning of mathematical biology and research into population variability, under the name of biometry; K. Pearson, F. Galton and W. Weldon established the first journal ('Biometrika') in this field (the first issue appearing in 1902, published until now);
(3) beginning of biophysics [11];
(4) the first book with the title 'theoretical biology' ([44]; cf. [2]);
(5) the boom of neovitalism (G. Bunge, H. Driesch);
(6) intensive work in the field of morphogenesis (W. Roux's 'Entwickelungsmechanik');
(7) ecology as an independent science took its first steps.

In 1919, the first series in the field of theoretical biology, "Abhandlungen zur theoretischen Biologie" (edited by J. Schaxel) started to appear, reaching 30 volumes by 1931. Also, influential works on philosophy of biology were published ([20, 21, 60]; see also [10]).

All these events had a long-lasting effect on biology, and influenced considerably theoretical discussions in biology. We may say, I suppose, that at that time theoretical biology as a branch of biology was born. Before that time, of course, there existed works on theory of biology which can be classified as theoretical biology, but as a branch with its specialised journals, books, name and devoted specialists it did not exist. This was development from the domain 'theory in biology' into the field 'theoretical biology'. This period of intensive diversification in biology at the turn of the century is somewhat comparable to the great peak in theoretical biology which took place in the 1960s and 1970s.

1.2. Mathematics meets evolution, ecology obtains dynamics

Between the establishment of theoretical biology close to 1900 and its peak in the 1960s–70s, there was also a remarkable wave in the 1930s. It was characterized by the publication of the influential monographs calling themselves 'theoretical biology' (L. v. Bertalanffy [5, 6], E. Bauer [4]), J. H. Woodger's 'The Axiomatic Method in Biology' [68], Rashevsky's mathematical biophysics [43], A. Lotka's [33] and V. A. Kostitzin's mathematical biology, and the start of several journals in this field. The journal "Acta Biotheoretica", established by a group of 'Jan van der Hoeven's Foundation of Theoretical Biology' in Leiden (the Netherlands), was first published in 1935, with its branch periodicals 'Folia Biotheoretica' and 'Bibliographia Biotheoretica' from 1938. The series 'BIOS: Abhandlungen zur theoretischen Biologie und ihrer Geschichte, sowie zur Philosophie der organischen Naturwissenschaften' was established in 1934 in Germany. In its first volume, A. Meyer [36] calls H. Driesch and J. v. Uexküll 'the pioneers of theoretical biology'. In the 1930s, the Theoretical Biology Club existed in England, with its members J. H. Woodger, C. H. Waddington, J. D. Bernal, J. Needham, D. M. Needham, L. L. Whyte, K. R. Popper, and few others [1]. Mathematical (and physical) biology, as belonging to theoretical biology and representing an important part of it, appeared in about the same period, including the works by A. Lotka, V. Volterra, S. Wright, R. A. Fisher, V. A. Kostitzin, J. H. Woodger, N. Rashevsky, and the 'Bulletin of Mathematical Biophysics' (the journal edited by N. Rashevsky from 1939, and after his death in 1972 continuing under the title 'The Bulletin of Mathematical Biology').

This has been called the golden age of theoretical ecology [50]. As a result of works by R. A. Fisher, S. Wright and J. B. S. Haldane, the Darwinian theory of natural selection obtained its mathematical basis, and the so-called modern synthesis took place, giving rise to the 'synthetic theory of evolution'. According to E. Mayr [34: 550], 'An unexpected achievement of the synthesis was its effect on the prestige of evolutionary biology. The 1920s and 30s experienced an absolute low in the esteem of evolutionary biology within biology'. Since that time, neo-Darwinism became the dominating view in biology for a considerably long time, and holism became unpopular.

At the same time, holistic views in biology were still quite strong, but this can be seen as late inertia from the neo-vitalist or organicist period of the beginning of the century. Besides Uexküll with his 'Bedeutungslehre' [64], there were also several other biologists developing organismic approaches, among them E. Dacqué, K. Friederichs, A. Meyer-Abich [37], R. Woltereck [67], and others. Of the more mathematically-biased holistic biologists, the works of D'Arcy Thompson [58], J. H. Woodger [68], L. v. Bertalanffy [5, 6] etc. should be mentioned (cf. [7]).

1.3. *Mathematics meets complexity, biology finds code*

As already noted, the 1960s precipitated the rise of a new powerful wave of theoretical biology, the cornerstones of that second period being the launch of 'The Journal of Theoretical Biology' in 1961, and the 4-volume proceedings 'Towards a Theoretical Biology' under the editorship of C. H. Waddington, 1968–72 [65]. This was a period of applied mathematics in every field of biology, together with a diversification of theoretical approaches. There were also a rise in the application of information theory in biology, and the quick development of mathematical biology, biophysics, biocybernetics, systems theory, etc. (see also below, 'Specifying solutions'). Due to the great influence of biocybernetics in this period, communication processes received much attention by biologists. Many new journals and book series were established: 'Theoretical Population Biology' (1969), 'Journal of Mathematical Biology' (1974), 'Lecture Notes in Biomathematics' (1974), 'Biological Cybernetics' (1975, from 1965 to this date it was titled as 'Kybernetik'), 'Progress in Theoretical Biology' (1967, edited by F. M. Snell and R. Rosen). R. Rosen published three volumes of 'Foundations of Mathematical Biology' [45].

This was also the start of extensive molecular biological research, with the deciphering and understanding of the genetic code and the principal ways of information transfer in a cell. At the same time, ethology became very popular.

Ecology, for which this period was also a time of large extension, is a branch of biology in which holistic views have had a strong influence, together with reductionist approaches, of course. E. P. Odum [39] 'clearly delineated these two camps and placed himself in the forefront of the holists' [35: 201]. However, these relationships are very complex and any superficial division is not correct. According to Bramwell [9], the organicist biology of Uexküll's time was that which gave the initial power to ecological views, extending far outside a professional biology[1].

The powerful introduction of cybernetic ideas and the concept of information into biology was thought to solve the eternal problems of the teleology of living together with the relationships of mind and matter. However, these problems, instead, resolved into many branches. Among them, an interesting book by Miller et al. [38] should be mentioned; this applied the notion of plan to the explanation of animal behaviour. Along the lines of this period, Uexküll's approach could be intepreted as an early development of some biocybernetic notions. Also, several notions of H. Driesch were taken into use in the theory of self-regulating systems (for instance, equifinality, by L. v. Bertalanffy, P. Weiss, and others). There were several scientific branchings emerging from biocybernetics, among them those represented by G. Bateson, and H. Maturana.

1.4. *Darwinian and Baerian biology: whether to start from phylogeny or from ontogeny*

There have generally been two diametrical approaches to understanding and delimiting life. According to the first, living systems (as a specific connection between special complex molecules, occurring in dissipative systems with special type of non-liner kinetics) represent a special and local case of the non-living physical world. According to the second, life is something in addition to the physical, is beyond the non-living, or is more general.

As a parallel, there are two ways of developing a theory (or of making a new one) – either by finding restricted, but not yet analysed, parts in the existing general theory and elaborating its conclusions, or, by making changes in the general axioms of the theory, showing that some of the axioms actually do not hold and should be replaced by other, or more general axioms.

Both these methods have been used in developing biological theory throughout its history. However, the traditions, or schools of thinking and research, which characterise these two different methods, are very much different – in popularity, in philosophical background, and even in the ethical predilections of the researchers. Also, I suppose, in their prospects.

Among the 19th century biologists, two have been considered to be great – Charles Darwin and Karl Ernst von Baer. Darwin's main interest was in the evolution, Baer's in the development of organisms. They

---

[1] On the relationship between theoretical biology and human ecology cf. [56].

esteemed each other highly, however, their views on life itself differed deeply, as deeply as two paradigms do. The heated discussions around the turn of the century subsided by the 1930s with the arrival of the synthetic theory of evolution and neo-Darwinian biology, and the forgetting of the opposite views for many decades. However, Baerian biology, still alive under the ashes, sometimes showed through the cracks of neo-Darwinism. Only at the very end of the 20th century, has the situation started to change, the critical notes against biological reductionism becoming more and more frequent (particularly in European biology), and ontogeny appears again as a field of new approaches [41, 48].

Up to now, the multitude of volumes on Darwinian biology have shed light on all the possible details of Darwin's research and views. There are no corners of biology which have not been reached by the Darwinian approach. The bibliographies published by M. T. Ghiselin [16] are great achievements indeed. An analogous work is all but missing in relation to Baerian biology (except some recent works by biology historians, e.g., P. J. Bowler [8], T. Lenoir [32], S. J. Gould [18], D. Ospovat [40]). If we want to reach at least a balanced situation in theoretical biology, then the wholistic understanding of biological life must also be developed. Or, for instance, as S. Salthe [49: 247] has formulated it: «Development, not evolution, could be considered as the central theoretical framework for biology. In this case Baer and not Darwin would become the central historical figure in theoretical biology» (cf. [19, 28]).

The opposition between these two main approaches largely coincides with the controversy between reductionistic and holistic views. However, in a good biology these two views are not as far from each other as a student of philosophy may think. The parts and wholes are intertwined in a really complex manner. Nevertheless, selection and self-organization [26] – the other names for the same context, which, when started respectively either from phylogeny and evolution, or from ontogeny and development, can create theoretical views rather opposite to each other.

II. SPECIFYING SOLUTIONS

The work by H. v. Helmholz, E. du Bois-Reymond, R. Wirchow and others at the end of the 19th century with the aim of putting physiology onto a physical scientific basis, was developed into a popular approach in biology which since the turn of the century is known as 'biophysics' (e.g., [11]). The demonstration of how the features of living systems can be deduced from the general laws of physics and chemistry as a result of particular constraints, has been a major aim of this branch of biology.

The application of dynamic models of chemical processes in the description of population dynamics, particularly by A. Lotka and V Volterra, has shown that many examples of non-linear dynamics are wel suited to biological theory.

After the work of A. Turing [59] and similar works by N Rashevsky [43], in which they added the diffusion process to the dynamic models of chemical reactions in order to model morphogenesis, the door was open for the theory of dissipative systems, non-equilibriur thermodynamics (I. Prigogine), and synergetics (H. Haken). In some special conditions of non-linear models phenomena called 'bifurcations appear, research into which has led to R. Thom's theory of catastrophes B. Mandelbrot's theory of fractals, and models of deterministic chaos These 'emergent' phenomena which have been seen as appropriate models for living systems can all be interpreted as specifying the condition and finding the solutions for models of physical systems.

However, it should be noted that complex (e.g., non-linear dynamics can be interpreted in two opposing ways: as a special case o more general dynamics which includes both linear and non-linear cases or as a generalisation of more simple (e.g., linear) systems.

Reductionism means several different things. Firstly, it means tha there is nothing else in the scientifically describable world than that whic behaves in accordance to the laws of physics. Secondly, it means that al that is going on in the world is deducible from the laws of physics.

It is important to stress that these two statements differ greatly i their consequences. I would state that biology can accept the first statement, whereas it should disagree with the second. All the behaviour o living organisms can be described and explained *post factum* on the basi of physics, but there is much in biology which can not be deduced fro the physical laws.

One of the things that is not deducible from physical laws is, fo instance, genetic code, i.e. the arrangement of aminoacids in the table o triplets. There have been many serious attempts to deduce the geneti code from some symmetry rules or physico-chemical forces – but withou success. (Of course, also, more than one genetic code exists. There i over a dozen versions of genetic code described from different organisms, among which the one in cell nucleus of eukaryots and the one i mitochondria are most well-known.) The same is true for other biologica or social codes. Also, the arrangement of species in the character space i not deducible from any laws of physics. And no one can say on the basi of physical knowledge and the ability to compute alone, whether th

Estonian (or the English) language is the one which would have appeared in the world or not.

J. R. Searle [51: 112] distinguishes between causal and intentional, or, when describing the types of causes, he analyses the features of intentional causality. I think we are speaking of exactly the same thing, when distinguishing between causal and interpretational (as one does in biosemiotics). According to Searle [51: ix], 'The correct solution of the "mind-body problem" lies not in denying the reality of mental phenomena, but in properly appreciating their biological nature.'

III. GENERALISING AXIOMS

An important aspect, the consequences of which are often not fully considered, is the *individuality* of almost every single genome. The size of any genome is so large, and the modifications (particularly in the case of sexual reproduction), however rare in a single locus, are nevertheless frequent enough to result in the individuality of each genome. The interconnectedness of the processes in the cells results in the individuality of the context in which the genes are read; i.e., the context of a particular allele can be different in every single individual (cf. [25]). Thus, no gene can have a constant meaning. Therefore, what can be selected in one generation, may not have the same meaning in the next one. Which may, in the extreme case, make the selection of a particular allele senseless.

A second aspect concerns *intransitivity* of the genome reproduction. R. A. Fisher's [14] theorems of natural selection make the unspoken assumption that reproduction is transitive. This assumption is used by the whole neo-Darwinian theory of natural selection. According to transitivity, if P gives Q, and Q gives R, then P gives R. However, due to the individuality of phenotypes, reproduction is generally intransitive. If A_1, A_2 and A_3 mark a particular allele A (considering here its primary structure only) in three sequential generations, the assumption of transitivity may still be correct. But if they denote the whole organisms as phenotypes, or the meaning of the allele, this will no longer hold. And since it is phenotypes that natural selection acts on, Fisher's theorems fail. Or, more correctly, they rely on an unrealistic assumption. Due to the individuality of genotypes, transitivity thus fails even without including the aspects of context.

The individuality of biological systems is a feature which makes it almost impossible to deduce any particular rules for biological systems when viewed as physical systems. There are also several other features of this kind, for instance *immenseness* as described by W. Elsasser [13].

These and other features of organisms have been a reason for a search for the foundations of biology, in which more general mathematical theories have been applied, the theory of categories and functors for example by R. Rosen [46], or the theory of fuzzy sets, etc.

Thus, it becomes very natural to ask, whether biology is a special case of physics, or vice versa. A. Meyer-Abich [37] has been one of several scientists who strongly claimed that physics is a special case of biology, and not vice versa. Holism, according to him and many other biologists, does not fit physics well. There are several other notions which have also met serious difficulties in attempts to give them a physical explanation. These include, for instance, intentionality, meaning, etc.

IV. THE EXTENDED CONCEPT OF FACT

Sooner or later, biology has to find the way to confess that an organism can be a subject, and accordingly to find a way to include the subject into its models and theory [22, 66]. The mind-body controversy and, together with this, the difficulty of explaining the whole sphere of mental phenomena is rooted in an assumption used in physics, according to which most of our (as well as other organisms') feelings are not considered as physical facts and, coupled to this, it is stated that there are no other facts in the world of science other than physical facts. A sentence in a novel or a strophe in a poem are physical facts, since these can be described repeatedly by another observer in another time, whereas the feeling or thought I experience as a result of my reading that strophe is not a physical fact since nobody else may have the same feeling or thought, or more exactly since this cannot be repeated in a controlled way. Thus, to go further in solving or understanding this basic controversy, I consider it interesting and important to look more carefully at the notion of fact, and its consequences. Namely, it seems reasonable to generalise the notion of fac (defining it as *something which can be, at least locally, represented*) Different types of facts, then, form a series or array with the most invarian (mathematical) facts at one end, and the least invariant ones (subjectiv and personal) facts at the other, whereas physical, biological, and probabl several other types of facts remain in between.

Accordingly, mathematical facts are those which can defined as th facts which are invariant in matter, time, language, and person; physica facts are invariant in time, language, and person; historical fact is invariant in person, and language, but not in time; subjective fact is invariant i