Boltzmann, Atomism, Evolution, and Statistics

Continuity versus Discreteness in Biology

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The 100 years' anniversary of Ludwig Boltzmann's death in Duino provides an opportunity to reflect on his view of nature, which he has very clearly expressed in two passages of a popular lecture that he gave in Vienna at the "Kaiserliche Akademie der Wissenschaften" on May 29, 1886.[1] The first statement expresses a remarkably deep admiration of Boltzmann for the genius Charles Darwin and his view of the world that in a free English translation reads:

> … If you would ask me about my heartfelt conviction, whether the nineteenth century will be called one day the iron century or the century of the steam engine or the century of the electricity, I answered without any doubt it will be called the century of the mechanistic conception of nature, the century Darwin's.…

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Today, nobody would claim that mechanics can explain nature but, as I shall try to argue later, the reductionists' program is close to being successful, at least in parts of biology. In his statement Boltzmann presumably meant, not *mechanics*' but an interpretation of Darwin's theory of evolution as the mechanism explaining changes in the appearance of species by phylogeny. The second statement by Ludwig Boltzmann is even more remarkable because it reveals the deep intuitive insight into biology that he apparently had. It reads, again freely translated into English:

> … The struggle for existence of the living beings is not a fight for basic materials—these materials are available in air, water and soil in sufficient quantities for all organisms—it is also not a fight for energy that is available in

[1] *The title of the lecture was "Der zweite Hauptsatz der mechanischen Wärmetheorie," and it is contained in a collection of Boltzmann's popular lectures [1].*

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the form of inconvertible heat in every body but it is a fight for [negative] entropy, which becomes available by the transition of energy from the hot Sun to the cold Earth. In order to exploit this transition as much as possible, the plants spread out the incredibly large surface of the leaves and force the energy of the Sun before it falls down to the temperature of the Earth in a not yet understood way to perform synthetic chemical reactions that are still completely unknown in our laboratories. …

"Negative" was inserted in order to correct for the fact that Boltzmann's H-function is equivalent to negative entropy ($S = -Nk_B H$). About 80 years later another theoretical physicist, Erwin Schrödinger, elaborated the issue of "negative entropy" again in his famous monograph "What is life?" [2]. Boltzmann's speculations about "synthetic chemical reactions" come remarkably close to our current knowledge about protein (and RNA) catalyzed reactions and the "struggle for the light of the Sun" found an unexpected confirmation by the discovery of light-harvesting proteins that support the photosynthetic center of bacteria in the collection of photons [3,4]. Only with respect to the availability of all basic materials, Ludwig Boltzmann was perhaps too optimistic.

Reflecting the historical development of evolutionary biology in the 20th century Boltzmann's deep admiration for Darwin is worth being examined. Boltzmann as the most prominent scholar of statistics in physics and fighter for "atomism" should have rather joined the other party in the battle between "selectionists" like Charles Darwin and his contemporary evolutionary biologists and "geneticists" that became dominant and verbally violent in the development of biological thought before World War II [5]. Indeed, Gregor Mendel and the geneticists were the "atomists" in evolutionary biology. Mendel—not unlike Boltzmann—postulated the existence of elements or "atoms" of inheritance that are transferred from generation to generation and recombined in the offspring. This process of recombination is nowadays understood as an inherent molecular feature of the so-called meiotic cell division. In addition, Mendel had discovered a statistical law, and because of his education in mathematics and physics he was able to draw the appropriate conclusions from his observations [6]. Apparently, Gregor Mendel's view of nature has been very close to Boltzmann's thinking. The most straightforward explanation simply is that Boltzmann was not aware of Mendel's work when he gave his lecture of 1886. Indeed Mendel's great discoveries remained known only to botanists until the turn of the 19th to the 20th century when Mendel's experiments were repeated or "rediscovered"[2] and gave rise to the development of genetics that soon led to a discipline in its own right.

Boltzmann's largest contribution to physics, in essence, was to show by means of statistics how the discrete and stochastic nature of elementary processes involving atoms and molecules gives rise to the deterministic laws of continuum physics.

As a matter of fact, Charles Darwin's theory of evolution differed from an "atomistic" view in two aspects: (i) He favored a gradualistic concept of phylogeny and (ii) his view of inheritance carried a strong element of continuity in the sense that he thought incorrectly that the properties of the parents were mixed through blending in the offspring. According to the selectionists' view evolutionary change is based on large numbers of small variations that accumulate over a long period of time through steady selection and eventually lead to observable alterations in the appearance of organisms. The reason for Darwin's preference for small variations seems to be explainable in the historical context of the 19th century. To get his theory of evolution accepted, he had to fight the "catastrophists," who considered catastrophes like the biblical "great deluge" as the only causes for extinction of otherwise unchangeable species [7]. In addition, Darwin has been strongly influenced by the geologist Charles Lyell, who was the proponent of slow but steady changes shaping the Earth's surface.

Variations, however, need not be small. The development of molecular biology in the second half of 20th century [8] provided entirely new insights into the mechanisms of evolution. Molecular genetics offers mechanisms for small and large changes in the genetic information stored in DNA. Single point mutations may have a minute effect; they can even be neutral with respect to selection. On the other hand, they can also have large effects when a sensitive part of the encoded biomolecule is hit. In addition, there is also evidence for large changes in the genetic information: Duplication events of whole genes and sometimes entire genomes seem to have occurred at times when new body plans of organisms appeared [9,10]. In the 1970s and 1980s the concept of "punctuated equilibrium" [11,12] received some attention in evolutionary biology. It was derived from the fossil record, and some paleontologists even thought that steps in the evolutionary optimization process might contradict the Darwinian principle. Since then evidence has been accumulated, for example, by computer simulation [13,14] and by recording the evolution of bacteria under constant conditions over many thousands of generations [15], that optimization can indeed be punctuated with long quasi-stationary epochs in finite populations.

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[2] *Mendel's two seminal papers appeared in the notes of two local scientific societies in 1865 and 1866 [5] and remained essentially unnoticed until they were 'rediscovered' in 1900 by the Dutch botanist Hugo de Vries, the German botanist Carl Correns and to a lesser extent also by the Austrian agronomist Erich von Tschermak-Seysenegg.*

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involving atoms and molecules gives rise to the deterministic laws of continuum physics. Thereby he developed the statistical interpretation of entropy and the origin of irreversibility. Continuity on the macroscopic level is apparently not always observed in biology: Stochastic phenomena originating from fluctuations at the microscopic scale appear macroscopically. Three features of biological processes are responsible for this entirely different relation between the microscopic and the macroscopic level in the life sciences: (i) Population sizes are smaller by many orders of magnitude in biology, (ii) biological systems are far away from equilibrium, and (iii) some of the nonlinearities in the dynamics of biological processes are self-enhancing. Consequently, the conditions for Boltzmann's statistics are commonly not fulfilled in living systems.

Returning to Boltzmann's statement about "the mechanistic conception of nature," it seems appropriate at present to replace "mechanistic conception" with the "reductionists' program." The second half of the 20th century brought the great breakthrough. It is worth referring to the deep thoughts of John Maynard Smith, who was one of the most influential scholars of evolutionary and social biology. He stated: [16]

Modern cellular biology is dealing with the cell in its full complexity and at the same time continues the bottom up approach initiated by the biochemists of last century.

> … What should be the attitude of biologists working on whole organisms to molecular biology? It is, I think, foolish to argue that we [the macroscopic biologists] are discovering things that disprove molecular biology. It would be more sensible to say to molecular biologists that there are phenomena that they will one day have to interpret in their terms. …

Apparently, this day has now come. Modern cellular biology is dealing with the cell in its full complexity and at the same time continues the bottom up approach initiated by the biochemists of last century. The same is true, in essence, for developmental and evolutionary biology. Because of the unexpected success of the reductionists' program, biologists are now approaching the synthesis between the molecular and the holistic view of nature. As a matter of fact, I believe, we are heading for a great synthesis of science. Quantum mechanics has rooted chemistry in physics and now molecular life sciences are going to root biology in chemistry. The reductionists' dreams in the sense of Ludwig Boltzmann's vision have indeed become true, but at the same time chemistry and biology have retained their independence as individual disciplines with their unique view of nature. Both are dealing with phenomena and notions that do not exist in physics or physics and chemistry, respectively. In chemistry this is, for example, the concept of reactivity that allows for planning pathways in synthetic chemistry. In biology unique features among others are the notion of genetic information, encoding of information, and information processing.

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