Published in final edited form as:
Q Rev Biol. 2007 December ; 82(4): 349–373.

ON THE MAKING OF A SYSTEM THEORY OF LIFE: PAUL A WEISS AND LUDWIG VON BERTALANFFY'S CONCEPTUAL CONNECTION

Manfred Drack,
Department of Theoretical Biology and Department of Neurobiology and Cognition Research, University of Vienna 1090 Vienna, Austria manfred.drack@univie.ac.at

Wilfried Apfalter, and
Department of Philosophy and Department of Neurobiology and Cognition Research, University of Vienna 1090 Vienna, Austria wilfried.apfalter@univie.ac.at

David Pouvreau
School of Advanced Studies in Social Sciences, Koyré Center 75231 Paris, France
david.pouvreau@wanadoo.fr

Abstract

In this article, we review how two eminent Viennese system thinkers, Paul A Weiss and Ludwig von Bertalanffy, began to develop their own perspectives toward a system theory of life in the 1920s. Their work is especially rooted in experimental biology as performed at the Biologische Versuchsanstalt, as well as in philosophy, and they converge in basic concepts. We underline the conceptual connections of their thinking, among them the organism as an organized system, hierarchical organization, and primary activity. With their system thinking, both biologists shared a strong desire to overcome what they viewed as a "mechanistic" approach in biology. Their interpretations are relevant to the renaissance of system thinking in biology—"systems biology." Unless otherwise noted, all translations are our own.

Keywords

organismic biology; theoretical biology; Biologische Versuchsanstalt; systems biology

Introduction

IN TERMS OF publications, "systems biology" is currently an exploding field (see, e.g., Chong and Ray 2002; Grant 2003). Note, however, that system thinking is not at all new in biology. In the sciences of life, it can be traced back at least to the German "teleo-mechanicist" tradition inaugurated by Immanuel Kant's *Critics of Judgement*, of which Johannes Müller and Karl von Baer were the main proponents (Kant 1789; Lenoir 1982). More generally, integrative (or "holistic") thinking is not a "discovery" of the 20th century. It has a rather long history going back to ancient Greek thinkers: Aristotle already claimed that "the whole is of necessity prior to the part" (Aristotle 1966:1253a20). Between the 14th and 16th centuries, it was a major intellectual trend, which strongly reemerged at the turn of the 19th century in German Romanticism and post-Kantian idealism. Among others, Nicholas of Cusa, Gottfried Wilhelm Leibniz, and Johann Wolfgang von Goethe are considered "precursors" of modern systems thinking (Bapp 1921; Bertalanffy 1926a; Harrington 1996). One of the leading figures, who recurrently referred to those thinkers, is the philosopher and theoretical biologist Ludwig von Bertalanffy (1901–1972), mostly known for his project on a "general system theory" (GST).

Unsurprisingly, he is still regularly quoted—although mostly laconically—by advocates of “systems biology” in the early 21st century (e.g., Chong and Ray 2002).

Pursuing the historical roots of biological systems theory inevitably leads to early 20th century Vienna. Ludwig von Bertalanffy lived there and was influenced by biologists Hans Leo Przibram (1874–1944), the founder of a laboratory for experimental biology, and his student Paul Alfred Weiss (1898–1989), both of whom were also based in Vienna. We will more closely examine the convergences of the experimental and theoretical works of Weiss—who allegedly claimed that “he was responsible for Bertalanffy’s initial appreciation of the systems nature of development and behavior” (Haraway 1976:38)—and Bertalanffy’s “system theory” of life; we extract basic concepts that were already developed long before the recent emphasis on “systems biology.” The early writings of Weiss and Bertalanffy can be fruitful for modern research: they already developed many concepts that can shed light on certain contemporary debates and perhaps only need to be adapted to current intentions.

The purpose of this article is therefore two-fold. We first provide a historical overview of the works of these system thinkers, and then reflect the early system conceptions on recent developments in biology.

Context of Early “Viennese” System Theory

The fin de siècle and the following years were characterized by innovations in many fields, among them science, arts, and politics. In particular, the developments in physics and psychology, together with problems in biology, provided an impetus that led to a sophisticated system conception of organisms.

An important revolution took place in physics, which many scholars from other disciplines liked to cite. A statement by Max Planck, inspired by the new quantum mechanics and referring to the false dictum that all physical processes can be displayed as a stringing together [*Aneinanderreihung*] of local processes, summarizes the relevance for system conceptions: “The physical world is not simply a sum of spatial and temporal single worlds running one besides the others, and many phenomena escape [*entziehen sich*] the understanding when one does not consider a physical object [*Gebilde*] as a whole” (Planck 1929:17).

At about the same time, a conceptual shift occurred in another field, namely psychology, which was also extended to the realm of physics. Based on the conceptions of the Austrian philosopher Christian von Ehrenfels, *Gestalt* theory was developed (Ash 1995); it emphasized the claim that an entity’s total characteristics cannot be discovered by simply summing up its partial characteristics. Wolfgang Köhler, one of this theory’s leading figures, derived concepts based on physical systems as known from thermodynamics and electrostatics. He considered Ehrenfels’s two criteria (“oversummativity,” i.e., the whole is more than the sum of the parts; and “transposition,” e.g., a melody can be played in a different pitch, but stays the same) as constitutive for *Gestalt* (Köhler 1920). Similarly, Bertalanffy (1928:69–70) characterized a *Gestalt* as comprising properties that cannot be found by simple addition of the components’ properties and that furthermore disappear when the *Gestalt* is destroyed; he used the term “*Gestalt*” synonymously to “systemic state” [*Systemzustand*] (Bertalanffy 1929c:89).

Bertalanffy witnessed a controversy among biologists at the turn of the century between “mechanicism” and “vitalism” (for contemporary analysis of this controversy see, in particular, Haldane 1884; Loeb 1906; Schaxel 1919; Needham 1928; Woodger 1929; Bertalanffy 1932; M Hartmann 1925; and M Hartmann 1937; for a recent discussion see Pouvreau 2005b). “Vitalism” can have two meanings, a metaphysical or a methodological one. Metaphysically, it asserts that biological phenomena cannot be explained without the action of a nonspatial principle harmonizing the matter and energies involved in living phenomena.

Methodologically, it is not antinaturalistic and only asserts that, at least provisionally, biology should have its own categories, methods, and laws. As for the term "mechanicism," it was sometimes loosely referred at that time to the opposed view that should be termed "physicalism" in order to avoid confusion; that is, the idea that the sole concepts, methods, and laws of physics and chemistry enable biological phenomena to be grasped. But this was not the only meaning. More generally and precisely, "mechanicism" seems (and seemed) to refer to a complex group of more or less coherently related positions. The more fundamental position is the "analytico-summative" approach to biological phenomena: its basis is the (methodological or metaphysical) postulate that any entity can be analyzed in parts whose properties can be studied in isolation from others without inconvenience (the relationships among the parts being "external," not "constitutive"). Through decomposition into "independent" causal chains and their "linear" composition, the properties of the whole are then supposed to be derivable from the knowledge thus acquired. "Mechanicism" would then be represented in a biology that combines the "analytico-summative" approach with one or several of the following positions: physicalism, determinism (each state is univocally derivable from previous states), and "reactivism" (the changes in the behavior of an entity are ascribable to the sole action of its environment). An extreme example is Jacques Loeb's theory of tropism, which combines all of these items.

A paradigmatic variant of mechanicism is a "machine-like" model applied to the organism. This model can be seen as a successor of Descartes's "bête machine," which explains life merely by means of physics and chemistry. Bertalanffy (1932:55) saw this Cartesian metaphor as one of the most unfortunate conceptions in the history of science and philosophy. Such a machine theory was opposed by many scientists. Some biologists in the late 19th century were considering a type of living molecule—e.g., Darwin's "gemmulae," Pflüger's "living proteins," or Haeckel's "Plastidulen" (Penzlin 2000:434)—although most physiologists rejected vitalism. Two findings were important for rejecting vitalism (see Lenoir 1982; Penzlin 2000): the first law of thermodynamics and successful physical-chemical analyses of vital functions. This was coupled with the Darwinian selectionist scheme of evolution, which is "analytico-summative" (selection and summation of single modifications) and "reactivist" (the phylogenetic adaptation of the organism is a mere reaction to the environment). In contrast, after experiments with early development stages of sea urchins, Driesch formulated a "neo-vitalistic" concept: he viewed the embryo as an "harmonic-equipotential" whole, i.e., a whole of cells in the embryo to which it does not matter whether some cells are removed or displaced, in which each event is finalized by a "wholeness causality" [*Ganzheitskausalität*] manifesting the operation of an immaterial agent, the "entelechy" (a term used by Driesch, as well as by Aristotle and Leibniz before him). A crucial experimental finding for his argument was when, in the two-cell stage of development, he separated the cells and found that each would eventually form a whole larva (Driesch 1899; Penzlin 2000).

INSTITUTIONS OF EXPERIMENTAL BIOLOGY

Another debate in biology at that time was on methodology. Since the 1850s, a lively discussion arose between proponents of two scientific approaches in biology: should mere observation or experimentation be employed (Nyhart 1995; Querner 2000)? Arguing for observation, traditional morphologists such as Ernst Haeckel saw no sense in artificial, violent, experimental studies of development because they considered it to be methodologically sufficient to thoroughly draw conclusions from observing nature's own diversity and genuine transformations. In their view, an experiment alters the events that normally occur during developmental processes and, thus, provides no causal explanation. Arguing for experimentation, scientists such as Hermann von Helmholtz, Sigmund Exner, and Wilhelm Roux favored well-constructed analytical experiments from which they hoped to derive causal explanations.

UKPMC Funders Group Author Manuscript

Apart from older institutions such as the Stazione Zoologica in Naples (founded in 1872) or the Marine Biological Laboratory in Woods Hole, Massachusetts (founded in 1888), a novel, avant-garde Viennese fin de siècle institution became famous for its experimental research on developmental and evolutionary processes. This Biologische Versuchsanstalt (Institute for Experimental Biology), or popularly “Prater Vivarium” (as there were other vivaria in Vienna, too), was situated in a Neo-Renaissance building at the so-called Prater, Vienna’s popular recreation and entertainment area (including parks, forest land, and fields) at the beginning of the Prater Hauptallee (Prater main avenue; Figure 1). Equipped with automatically regulated installations for controlling humidity and temperature, the Biologische Versuchsanstalt was an innovative research facility both methodologically and technologically. It was privately established as a new type of biological research institution in 1902, and opened in 1903, devoted exclusively to experimental research. It was founded by Przibram, along with his botanist friends Leopold von Portheim and Wilhelm Figdor (Reiter 1999;Hofer 2002;Gliboff 2005).

The “Prater Vivarium” was designed “to tackle all big questions of biology” (Przibram 1908–1909:234) by transdisciplinarily applying similar experiments to both plants and animals (e.g., with transplantation, breeding, processes of selection, orientation, and polarity in development). To perform those biological experiments, methods from physics and chemistry as well as physiology were applied to living organisms. Compared to physiological research, the “Vivarium” biologists needed long-term experiments to deal with questions of embryogenesis, regeneration, and evolution. This called for methods that allowed investigations over a series of generations.

There were several departments at the Biologische Versuchsanstalt: one each for zoology, botany, and physiology of plants. For some time, there were also physiology and physics/chemistry departments. Wolfgang Pauli Sr., a colloid chemist and close friend of Ernst Mach, headed the latter. Although Przibram, Paul Kammerer, and Figdor had already received their *Habilitation* (grand university teaching license) at the University of Vienna, the “Prater Vivarium” researchers—in many cases, liberal or left-oriented, open-minded individuals with a Jewish background (Reiter 1999; Coen 2006)—were subject to efficacious disadvantages orchestrated by established, and often anti-Semitic, academics from the university. However, effective January 1, 1914, the successively enlarged and highly productive Biologische Versuchsanstalt formally became a part of the Kaiserliche Akademie der Wissenschaften (Imperial Academy of Sciences) in Vienna. At the same time, the three founders were appointed as unsalaried heads of their departments, and Paul Kammerer was appointed *Adjunkt* (civil servant), which, at that time, was the only position with a salary.

There were also strong international activities and lively networking. About one-third of the positions were reserved for scholars from abroad. Those guests included people such as Karl von Frisch (Germany), Erich von Holst (Germany), A E Hopkins (U.S.), and Joseph H Woodger (UK); Woodger translated Bertalanffy’s *Kritische Theorie der Formbildung* (see Bertalanffy 1928; see also Pouvreau 2005b for discussion about their relationship). From 1920 to 1934, 39 of the 109 scientists (practicum students or research personnel) of the Biologische Versuchsanstalt were women (Rentetzi 2004:368). One example is Alma Mahler, who worked as an assistant in Paul Kammerer’s laboratory (Everdell 1997:325). Due to a series of public, high-level lectures— “big show-lectures” (Kammerer to Hugo Iltis on July 6, 1910, cited in Gliboff 2006:530)— the “Prater Vivarium” was quite popular in Vienna (Hofer 2002).

THE VISIONARY OF THE BIOLOGISCHE VERSUCHSANSTALT

One of the founders of the “Prater Vivarium,” Hans Leo Przibram, studied zoology in Vienna under the guidance of Berthold Hatschek, a well-known comparative morphologist with a special focus on vertebrate *baupläne* (body plans) and himself a student of Haeckel and Rudolf Leuckart. After studies in Leuckart’s laboratory (with its highly attractive microscopic equipment) in Leipzig, and after graduating from the University of Vienna in 1899, Przibram went to Strasbourg in order to study at the laboratory of physiological chemist Franz Hofmeister (Reiter 1999:591), which was very avant-garde at that time. In 1904, he received a *Habilitation* "for zoology with special consideration of experimental morphology" at the University of Vienna. He started his multivolume work *Experimental-Zoologie* (Przibram 1907) with the first volume on embryogenesis, researching issues that were later also addressed by Bertalanffy (e.g., 1937:91–99; 1942:289–291), such as growth rates and allometric growth. Although Hatschek followed the scientific style of Haeckel, Przibram was influenced by Loeb (Reiter 1999) and strove to put into practice Roux's program—integrating analytical approaches from mechanical anatomy and evolutionary morphology (Nyhart 1995). The goal was to find the specific "forces" that act upon the development of organisms. Loeb and Roux (also a student of Haeckel) both tried to find a physical, chemical, and physiological basis for ontogenesis. In particular, Roux conceived Darwin's principle of selection as also implying *internal* selection. When mentioning a "struggle of parts within the organism" (Roux 1881), he especially highlighted the "struggle" for nutrients and space. Bertalanffy, although in deep disagreement with the Darwinian selectionist scheme, later (the first time in Bertalanffy 1940b:56) refers to this "struggle of the parts," in which he sees an illustration of the metaphysical (Heraclitean and Cusean) principle of harmony through contradiction, when developing his theory of allometric growth. Arguing from Roux's point of view and considering living beings as highly active entities intimately related to their environments, the biologists of the Biologische Versuchsanstalt systematically questioned external selection as the crucial drive directing evolution (Gliboff 2005). This approach vaulted the "Prater Vivarium" staff directly into highly controversial central issues of developmental and evolutionary biology. Contemporary evolutionary developmental biology (EDB), or "evo-devo," examines this role of development in evolution and in the evolution of developmental mechanisms (Hall et al. 2003; Müller and Newman 2003). Wagner and Laubichler (2004) recognize the Vivarium program as a precursor of modern "eco-evo-devo." Describing the laboratory style at the Biologische Versuchsanstalt, Przibram programmatically declared: "No specialization, [but rather] a generalization of obtained experience is our goal" (Przibram 1908–1909:234). With experimental research, not only on one specific group of organisms, but rather on various plants and animals, he aimed at finding general answers to the "big" questions in biology.

Przibram proposed to ascribe "the Gestalt, developing under the influence of the inner forces, to a state of equilibrium [*Gleichgewichtszustand*]," so that "by viewing organic form as a state of equilibrium … a compensation of disturbance [*Störungsausgleich*] will become accessible to mathematical treatment" (Przibram 1923:22–23). In this context, note the influence of the German physiologist and psychologist Karl Ewald Hering on Przibram. Przibram quotes Hering, who in 1888 wrote: "An organism is a system, which is able to sustain its constitution [*Beschaffenheit*] (chemical thermal state) against influences from outside, and which shows a dynamic state of equilibrium of considerable stability" (Przibram 1906:222). The synonymous usage of the terms "*Gestalt*" and "form" is obvious in Przibram. He refers to the influence of the whole on the parts and how this can be dealt with mathematically. This notion—as discussed below—became important in Weiss's concepts, although he was less involved with mathematical details. Przibram committedly discusses the possibility of applying mathematics to biology in general and to morphogenesis in particular. He also considers laws of higher order in cases where the detailed underlying single processes are not known. "Anyway, the influence of the 'whole' on the 'part' turns out to be accessible to mathematical processing, grounded on our ideas from exact natural history [*Naturlehre*]" (Przibram 1923:23). Thus, he proposes a "mathematical morphology" by which the parameters of the developing forms (e.g., proportions) should be described, also in relation to physical measures such as surface tension. The investigation should reveal "constants" that explain similar forms in various species (Przibram 1923:23–25). Przibram also discusses Frederic Houssay's project of a "morphologie dynamique" (Przibram 1923:9–11); the fundamental idea here is to unite morphology and physiology, an improvement compared to D'Arcy W Thompson's approach of mathematical morphology. Thompson's theory, or rather inductive method, which has little predictive value, is likewise criticized by Przibram (1923:13–14) and Bertalanffy (1937). Przibram's outlook toward a "mathematical morphology" is very similar to the notion on which Bertalanffy (1932:105) later builds his concept of "higher order statistics" (i.e., describing the average behavior of higher units of cells or organisms, regardless of physicochemical single events). This is similarly already expressed by Przibram. His example is the first formulation regarding the course of organic global growth (precisely the field where Bertalanffy later brings his main contribution to mathematical biology, see Pouvreau 2005b; Pouvreau and Drack 2007): "It is, however, not always necessary to know the contribution or the nature of the involved components of morphogenesis [*Formbildung*] to arrive at mathematically formulated and theoretically usable laws" (Przibram 1923:25). With regard to the statistical view on nature since Ludwig Boltzmann, Przibram is influenced by his contemporary, physicist Franz Exner (Coen 2006). Przibram envisions and already initiates "a mathematical theory of the organic on the basis of quantitative inquiry, of tying up with geometry, physics, chemistry, and of sharp definitions of biological terms." He expects this "mathematical biology" to serve "as a safeguard of humankind against the forces of nature and namely as a bulwark against prejudice, superstition and untenable speculation" (Przibram 1923:64).

Furthermore, Przibram also opposes the idea of a mere passive organism. When talking about "'self-construction' [*Selbstgestaltung*] of organisms" (Przibram 1923:21), he emphasizes the pivotal agency (i.e., inherent activity) of living beings. In this view, living organisms are not mere playthings of environmental forces.

Paul Weiss's System Conceptions

In 1918, Weiss took up mechanical engineering, physics, and mathematics at Vienna's Technische Hochschule, now called Vienna University of Technology. After one year of training in engineering, he decided to study biology at the University of Vienna (for Weiss's background and professional career, see Brauckmann 2003). By 1920, he had already managed to receive one of the highly coveted permanent positions at the "Vivarium" laboratories, where he later conducted work for his doctoral thesis (Weiss 1922; Hofer 2000:149). After Paul Kammerer retired and left Vienna, Weiss, as his immediate successor, was appointed *Adjunkt* in early 1924. But he left the "Vivarium" in 1927 when he applied for dispense of his working duties (letter of March 25, 1928 and protocol no. 44 of January 31, 1929, Vivarium papers, K2) in Vienna in order to conduct research in Monaco, Paris, and Berlin. He definitively resigned from his salaried *Adjunkt* position in 1929. In 1931, he was appointed Sterling Fellow at Yale University. He went to the University of Chicago in 1933 and became an American citizen in 1939 (Haraway 1976; Brauckmann 2003).

The "Prater Vivarium" became especially important for Weiss and his later system thinking; so much so that at the Alpbach symposium in 1968, Bertalanffy, when discussing Weiss's talk, stated that, to his knowledge, Weiss was the first to introduce the term "system" in biology in 1924 (Koestler and Smythies 1969). As a matter of fact, Bertalanffy (e.g., 1932:87) knew very well that the philosopher Nicolai Hartmann (1912), with whom he was very much in line, had already held "system" as the fundamental category of biology as well as of other fields (Pouvreau 2005a). The concept of the "harmonic equipotential" system as applied to the biological organism was already the core of Driesch's thinking since the end of the 19th century (Driesch 1899). But even Driesch was not the first one to refer to the organism as a system; as mentioned above, Hering did so before him.

WEISS'S EARLY BUTTERFLY EXPERIMENTS

Weiss received his doctoral degree from the University of Vienna, supervised by Przibram and Hatschek, for an experimental study on the normal positions of butterflies in response to light and gravity, which greatly influenced his system conceptions. His experiments were designed to determine if and how much the normal position of butterflies is related to the direction and intensity of light and gravity. He therefore used one or two light sources and changed the angle of a wall on which the animals rested from vertical to overhanging horizontal. This experimental approach to the influence of external factors on organisms typifies the research approach at the "Prater Vivarium." On the one hand, this yields knowledge about external factors; by knowing the influence of these factors and abstracting from them, it also yields insight into the core of events—which he terms "specific vital" (Weiss 1922:1, 8–9)—that are not influenced by outside conditions.

In the experiments, he first investigated the influence of the single factors by excluding the others. In order to isolate the influence of light, he allowed the animals to attach only to the ceiling. The direction of gravity was normal to the light vectors and, therefore, played no role in the orientation of the butterflies. The influence of gravity was varied by changing the plane angle of the substrate from vertical to overhanging horizontal, thus altering the relevant component of gravity.

A result of Weiss's study was that the positions of the butterflies could not be precisely predicted by knowing the vectors of light and gravity alone. Nevertheless, he demonstrated that the vectors do play a role. When only one vector was applied, the animals responded to it; when both were applied, the positions of the animals were influenced by a combination of gravity and light. When altering the angle of the plane with constant light, there was a greater influence of gravity in the vertical position, while light became more important if the component of the gravitational force decreases. This allowed a rough estimate of the resting position:

> The experiments totally confirmed theoretical conclusions. It could be demonstrated that knowing the efficacy of single factors within a complex allowed unequivocal conclusions to be drawn about the efficacy of the entirety from which we previously isolated single parts; all positions [of the butterflies] turned out to be demonstrable as coming off the entirety of those partial effects, an exclusive efficacy of one single factor was never observed (Weiss 1922:19).

The experiment with two light sources and negligible gravity showed that the butterfly's position cannot be predicted based solely on light direction and intensity. The organism's "history" apparently plays a role. By taking into account the individual's preexperiences before taking the normal position, Weiss concluded that some kind of memory must play an important role. Nonetheless, the deviations from the calculated positions seemed to follow definite laws, and the butterflies oriented themselves toward the light source to which they were closer when crawling to their final position (Weiss 1922:8; 1925:223). When discussing the symmetrical position in relation to two light sources, Weiss claimed that, after disturbance, an equilibrium state is again found by the animals. "It is always a reaction of the affected *system* from within itself, which after each disturbance causes the return to a state of unique definiteness" (Weiss 1922:20, our emphasis).

NEW APPROACHES IN DEVELOPMENTAL BIOLOGY

With his early work in developmental biology, Weiss focused on regeneration and transplantation in vertebrates. Those studies proved certain prevailing concepts and discussions to be inaccurate (e.g., the debate on preformism versus epigenesis). Weiss also tried to overcome the debate on mosaic versus regulative development, which was also influenced by

Hans Spemann's "organizer effect." He argued that one cannot distinguish between them based on a strict timeline (such as the eight cell stage); rather, every developing organism at some time includes cells that are determined and cannot develop in other ways. Weiss's studies in developmental biology also use the system concept. He clearly states that ontogenesis cannot be understood by examining single isolated aspects only. Again, he refers to *Gestalt* theory and uses it to describe the occurrences found in the organism (Weiss 1926).

The developmental biologist Weiss notes that, in the organism, spatial heterogeneity is accompanied by substantial heterogeneity; thus, spatial form must not be viewed as separated from the variations in the involved materials or substances. With the morphological structure, certain functions are determined and everything that appears as distinct differentiation was, in a former phase, a latent ability. Biological form is defined as "the typical localization, i.e., arrangement and allocation of different sub-processes within the respective material systems." Accordingly, already the fact "that at this location these and only these and at that location those and only those processes are introduced is for us 'form'; not only that those different processes actually create a certain spatial Gestalt" (Weiss 1926:5). Developmental biology again harbors the concept of inseparable systems with an argument derived from the dynamic processes involved:

> If in the developmental process [*Gestaltungsprozess*] each part would simply be connected to its neighboring parts without taking a specific subordination within the whole system, then the smallest deviation of a partial process at the beginning would at the end lead to massive discrepancies. This contradicts the observation (Weiss 1926:7).

Weiss's criticism of misleading terms reflects his opposition to the concepts on which they are based. Terms like "equipotent" or "omnipotent" seem improper to him because the "material parts" of the early germ have no ability or potential to build up the whole in an organizational perspective. Rather, the parts should be called "nullipotent" because the specificity of their development is determined by their position, and differentiation is dominated by the factors prevailing at a certain position (Weiss 1926:10–11, 13). In this context, he derived a field theory for developmental biology comprising five aspects (Weiss 1926; Weiss 1928:1570; listed as "field laws" in Bertalanffy 1932:328):

1. Every field has axial structure, which leads to hetero-polarity [*Heteropolarität*] in at least one axis.
2. When material is separated from a field-bearing system, the field is contained in the remainder in its typical structure.
3. When unorganized but organizable material meets a field area, then it is included.
4. The field components are different according to their directions. When two fields are brought together they can add up or result in a mixed field depending on their orientation.
5. A field has the tendency to take up and incorporate equivalent fields from its surroundings.

He programmatically declared: "All field laws can be conceived as special cases of general system laws" (Weiss 1926:26). A field ascribes to every point in space a certain quality, direction, and intensity, which is very similar to the use of this term in physics. A whole responds to influences from the outside as a whole by inner reactions of the components in such a way that the former state is regained. The special cases in developing organisms are "morphogenetic organization fields." The field concept is considered to be completely in line with *Gestalt* psychology (Weiss 1926:23). During the developmental processes in an organism, various subfields can come into existence that govern certain areas of the material parts within the whole, subsequently leading to an "autonomisation" of those entities (Weiss 1926:31).

Note that Weiss was not the first to talk about fields in developmental biology. Boveri (1910) already postulated a concept of morphogenetic fields (see Gilbert et al. 1996:359), and in the same year, Gurwitsch started to use the field concept, which eventually led him to refer to an embryonic field [*embryonales Feld*] (Gurwitsch 1922). Spemann, who discovered the effect of embryonic induction and introduced the organizer concept, also used the term "field." However, Weiss is considered to be the originator of "field theory" in developmental biology (Haraway 1976:177)—he provided a theoretical basis for the concept (Gilbert et al. 1996:359).

FAR-REACHING CONCLUSIONS

Weiss's results from his butterfly experiments and further theoretical conclusions from his thesis were first published in German. The article was already written in 1922 (Weiss 1925:248), that is, before he came into contact with Bertalanffy—they very likely met each other in 1924 for the first time. At any rate, Bertalanffy regarded this work as an important contribution. This is reflected in the fact that an English translation was published in the *General Systems Yearbook*, the book series coedited by Bertalanffy (Weiss 1959). Weiss explained:

> That 80-page article stated the basic premises and principles of a holistic systems-theory which I could derive co-gently from my own studies of animal behavior and from cognate trends such as "Gestalt" Psychology so as to define in detail the scientific characteristics by which a singled-out fraction of nature can right-fully be accorded the designation of "system" (Weiss 1977:18).

Weiss concludes that his results "proved totally incompatible with the mechanistic doctrines—or rather, rationalizations—of animal behavior prevailing at that time" (Weiss 1977:17). With such doctrines, he refers especially to Loeb's tropism theory, by which the behavior of an animal is reduced to a mere physicochemical reaction triggered by factors exclusively coming from outside the organism, and where the mechanisms that govern orientation toward light and gravity are the same in plants and animals. Weiss (1925:171, 177–178) rejects this "fatal mistake," which consists of identifying similar phenomena [*Erscheinungsformen*] as the result of similar mechanisms. According to Weiss, the reduction of biological problems to mere physical and chemical aspects fails to touch the core of the problem of life.

Besides animal behavior, a field in which he performed only a few studies, Weiss is also similarly critical of developmental research, where his main interest lies, and to which Loeb also made contributions (Weiss 1922).

A CONCEPTUAL APPARATUS

Weiss points out the importance of theoretical considerations, but he uncritically holds that the description of facts does not change, whereas theories, which are formulated to integrate the findings into a larger context, may change (Weiss 1925:168–169). In contrast to the "reductionist" attitude, Weiss states that it is more promising and economical to first determine the laws in a certain research field such as biology, before separating it into physics and chemistry like Loeb did. Accordingly, it is important that biology develops its own scientific conceptual apparatus [*Begriffsbildung*] (Weiss 1922:2, 8). The basic terms of a conceptual apparatus from Weiss's perspective are listed below.

Even his early work contains the basis of a hierarchical order necessary to allow actions (such as locomotion) of an animal as a whole. This concept of hierarchy is also applied in his work in developmental biology. Accordingly, with each level (be it a physical or chemical reaction, a single muscle fiber contraction, a contraction of the muscle, a movement of the organ, or a move by the whole organism), new features appear that cannot be explained simply by constituents of lower levels alone. By splitting the whole into lower-level elements through quantitative analysis, the features of the whole may become lost even methodologically. This would also be true for inorganic entities such as molecules or atoms. Although a quantitative approach should be applied, it can never lead to a complete account of a complex entity, because when such an entity is fragmented, some characteristics are lost. “Higher complexes” can be viewed as units for which certain laws can be found without reducing them to their components (Weiss 1925:173–174).

Another possible term in a conceptual apparatus is the “system.” In his chapter on “laws of systems,” Weiss proposes an early system definition: “As a system we want to define each complex that, when parts of it are modified, displays an effort to stay constant with regard to its outside” (Weiss 1925:181, 183). In other words, the state of a system should be stable within and distinct from the outside conditions. Therefore, Weiss defines a system by its behavioral feature of reaction. This notion was not new and can be found in Hering, as mentioned previously; in Gustav Fechners’s “principle of tendency towards stability,” according to which every natural system, closed or open to external influences, tends toward relative stationary states (Heidelberger 2004); and in Henri Le Châtelier’s principle for chemical reactions, where the change in one of the parameters leads the others to modify in a direction that compensates this change and enables the system to return to an equilibrium state. As Weiss interprets it, a constant system state in the whole, when parts are altered, could only be achieved by inverse changes in its parts, which is done by the system itself (system reaction). He continues:

> The appearances of regulation and adaptation are typical system reactions of the organism. They are so widespread that their mere existence suffices to make the organism recognizable as a system (Weiss 1925:185).

Weiss distinguishes three different “system reactions.” In the first one, an outside factor applied to the system results in a reaction of a single part, such as in simple reflexes. In the second, more than one part of the system is affected by an outside factor. And in the final reaction, an outside factor does not trigger a reaction of single parts of the system, but of the whole system, where the reaction of the whole is not a result of the reactions of the parts: it is the other way around, and the reactions of the parts are a result of the overall reaction (Weiss 1925:175–181). The third reaction—which he illustrates by examples from physics and Köhler’s *Gestalt* theory—is important for his argument that an organism is not merely a conglomerate of cells, molecules, or atoms. This notion also allows laws to be found without knowing all of the details of the involved elementary processes, although the latter are important as well. Weiss emphasizes that the third case has no rigid mechanism. Rather, the parts show some plasticity, while the reaction of the whole is lawful. The physicist’s descriptions of processes based on “parts and their relations” is very much in line with that argument (Weiss 1925:186–187).

With regard to dynamic processes and Bertalanffy’s concept of open systems in “flux equilibrium” [*Fließgleichgewicht*], which was influenced by several authors, it is interesting that Weiss—when discussing system reactions—picks up Hering’s “schema of metabolism.” Equal rates of assimilation and dissimilation yield a metabolic equilibrium. The same idea is emphasized in 1920 by August Pütter, another organismic thinker, in his volume on growth equations, which had a significant influence on Bertalanffy’s own theory of growth: the end of growth corresponds to this equilibrium (see Pouvreau 2005b). For example, if dissimilation is accelerated by an outside change, then following the laws of chemical kinetics—which Weiss calls “system laws of chemistry”—assimilation is also accelerated (Weiss 1925:193–194). He argues that if this concept is viewed beyond the chemical context, it can serve as system law for living organisms.

The historical approach is also fundamental for biology. Weiss discusses teleology on the one hand and chance on the other, but he is not satisfied with either concept and claims that something such as an arch consisting of single bricks can never come into being. A mere mechanistic "causal analysis," however, cannot solve such a problem either. The solution of the contradicting perspectives is seen in the historical development of various processes where, from the very beginning, the parts are subordinated to the whole (Weiss 1925:190–191). The problem of reconciling the system perspective and the historical perspective was also mentioned by Jean Piaget when referring to the central problem of every structuralism: "have the totalities through composition always been composed, but how or by whom, or have they first been (and are they still?) on the way of composition?" (Piaget 1968:10). The importance of this problem is also emphasized by Leo Apostel (1970:167): According to him, structuralism is so dominated by the notion of equilibrium that it does not succeed to integrate genesis and history; the problem is central both to structuralism and system theory.

EPISTEMOLOGICAL CONSIDERATIONS

Weiss is deeply influenced by Mach; for example, he refers to the antireductionist program of the positivist thinker (Hofer 2000:151). Although Weiss contradicts the idea that biological activities can be explained by physics and chemistry alone, without further requirements, he leaves open the question whether or not physical or chemical terms could replace biological ones in the future. He does claim that the laws of complex issues will never be fully replaced (Weiss 1925:170).

With regard to prevailing positions of reducing biology, Weiss suggests that, notwithstanding progress within biophysics and biochemistry, the latter are only concerned with parts. The laws concerning the relationships among all parts are still the realm of biological research. But they must not remain mere "rules," they have to become "laws." The biological laws should be as strict as those of physics and chemistry, and should be able to unite several subdisciplines within biology without losing autonomy. This is the outlook that Weiss (1926:43) provides. The fundamental distinction between "rules" and "laws" had already been emphasized by Roux and Prizbram in biology, but also by physicists such as Walter Nernst (Przibram 1923; Nernst 1922); and it was a recurrent theme in subsequent reflections on theoretical biology, particularly by Max Hartmann (1925) and Bertalanffy (1928). It is another expression of the Kantian distinction between "natural science" as "a whole of knowledge ordered by principles" a priori, of which "the certainty is apodictic," and "natural history" as a "description of nature," of which the certainty is only empirical, and that is knowledge only in an inappropriate sense (Kant 1786).

We agree with Khittel when he states that Weiss's epistemological background is rather simple, and that he uncritically combines theory and experiment (Khittel 2000:160). Weiss is satisfied with posing questions to nature that are answered by the experiment and does not go deeper into epistemology.

The experimental biologist Weiss never developed a "system theory." Rather, from the insight he obtained by his experiments and observations, he described what such a theory must comprise and where the problems lie with the "analytico-summative" approach, as well as its abstraction and shortcomings. This sheds light on Weiss's statement that he only had "marginal contacts with the field [of general systems theory]" in his later life (Weiss 1977:18). Weiss was only minimally concerned with systems beyond the single organism, but he does consider them occasionally—for example, at the Alpbach symposium (Koestler and Smythies 1969); he also refers to communities and societies when talking about systems (Weiss 1970b:9). One of his last descriptions of systems broadens the scope even more: "a system is an *empirical entity which in our experience has sufficiently durable identity to be defined on a macroscale as a whole, although from our knowledge of the parts alone into which we can physically or* *mentally fractionate the entity on the microscale, we could never retrieve the rule of order discernible in the intact macrosystem*" (Weiss 1977:55). Furthermore, he states that this holds true throughout the hierarchy of natural systems, from stellar bodies, organisms, and molecules to subatomic units. As the following quotation demonstrates, Weiss advocated, in his late writings, system thinking on a broad and deep basis:

> It is an urgent task for the future to raise man's sights, his thinking and his acting, from his preoccupation with segregated things, phenomena, and processes, to greater familiarity and concern with their natural connectedness, to the "total context." To endow the epistemological foundations for such a turn of outlook with the credentials of validation by modern scientific experience, is thus a major step toward that goal (Weiss 1977:19).

Ludwig von Bertalanffy's Organismic Concepts

Ludwig von Bertalanffy, born to a family of lower nobility, was (from an early age) only interested in the works of Jean-Baptiste de Lamarck, Charles Darwin, Karl Marx, and Oswald Spengler (Hofer 1996; Pouvreau 2006). In his youth, Bertalanffy lived on his mother's estate outside of Vienna next to Paul Kammerer, one of the most prominent "Prater Vivarium" experimenters. Being a neighbor and friend of the family, Kammerer often talked to the young Ludwig about biological matters. Thus, Bertalanffy, even before his student years, was probably well aware of the specific style in which research was conducted at the Biologische Versuchsanstalt laboratories.

At the end of World War I, the Bertalanffy family temporarily left Vienna and moved to Zell am See (Salzburg, Austria) because of financial losses. Ludwig started his university studies, focusing on history of art and philosophy (especially metaphysics, logics, and philosophy of religion), in Innsbruck (Tyrol, Austria). To a lesser extent, he was also trained there in botany by the experimental morphologist Emil Heinricher and plant physiologists Adolf Sperlich and Adolf Wagner—the latter being one of the main advocates of a "psycho-vitalistic" philosophy of life. In 1924, Bertalanffy returned to Vienna, where he still focused on history of art and philosophy (especially philosophy of knowledge). As for biology, his only courses there (in 1925) can be labeled as "metaphysics of life" and dealt especially with Henri Bergson's thinking. Indeed, the student Bertalanffy was essentially what one might call a well-informed autodidact for biological matters. He earned his PhD in 1926 with a dissertation on Gustav Fechner's metaphysics of organization levels, which already stressed and discussed some contemporary ontological controversies in biology. Between 1926 and 1932, he devoted most of his studies to philosophy of biology, justifying and developing a project of "theoretical biology." He received his *Habilitation* in 1934, which was in "theoretical biology." He lived in Vienna until 1937, developing both his theoretical perspectives and some experimental applications in the field of animal organic growth. A Rockefeller scholarship was granted to him for one year. He worked in the United States from October 1937 on, especially in Chicago (with Nicolas Rashevsky and his coworkers) and in the Marine Biology Laboratory in Woods Hole (Massachusetts). After Hitler's *Anschluss* of Austria in March 1938, Bertalanffy tried to find a way to stay in the United States. But conditions were unfavorable in that regard, with priority being given to persecuted scientists: he was forced to return to Austria in October 1938. The dark period of Bertalanffy's life then started. Despite his deep disagreements with the essential parts of Nazi ideological commitments, he became a member of the Nazi Party in November 1938. It was a means to facilitate his promotion as a professor at the University of Vienna, which he was awarded in September 1940. During the war, in parallel to the elaboration of his theory of organic growth, he closely linked his "organismic" philosophy of biology to the totalitarian ideology in general and the *Führerprinzip* in particular. Bertalanffy lived in Vienna until 1948, when he decided to leave permanently. He was impatient regarding his career opportunities in post-1945 Austria because of unfavorable outcomes of his personal

UKPMC Funders Group Author Manuscript

"denazification" procedure and because of the enmities induced by his opportunistic behavior during the war (Hofer 1996; Pouvreau 2006). He then went through Switzerland and England to Canada.

Bertalanffy was influenced by many people (see Pouvreau and Drack 2007). From the philosopher's side, it was by no means only the Viennese Circle but, among others, also included neo-Kantian thinkers such as Hans Vaihinger and Ernst Cassirer. His organismic biology was largely influenced by Julius Schaxel, Emil Ungerer, Nicolai Hartmann, Hans Spemann, and Friedrich Alverdes, but to some extent also by the "Prater Vivarium" and Paul Weiss.

BERTALANFFY MEETS WEISS

When still a student, Bertalanffy met the recently graduated Weiss and they discussed system issues in biology, Weiss with an experimental and Bertalanffy with a philosophical background. Five years after Bertalanffy's death, the 79-year old Weiss remembers:

> Those days that a sparkling Viennese student, a little more than three years my junior, approached me for a meeting— Ludwig von Bertalanffy. We met in coffeehouses and "milked" each other. I soon found that his thinking and mine moved on the same wave-length—his coming from philosophical speculation, mine from logical evaluation of practical experience. And so it remained for half a century, each of us hewing his separate path according to his predilection. That is, I kept on as the empirical experimental explorer, interpreter, and integrator, for whom the "system" concept remained simply a silent intellectual guide and helper in the conceptual ordering of experience, while he, more given to extrapolations and broad generalizations, and bent on encompassing the cosmos of human knowledge, made the theory [general system theory] itself and the applicability of it to many areas of human affairs his prime concern. Does not this confluence here, once again, prove the "hybrid vigor" of the merger of ideas that, coming from a common source, have converged upon common ground, albeit by separate routes—the one offering a distillate of a life of study of living systems, the other the extensive elaboration of an intuitive philosophical ideology, tested in its pertinence to human evolution? (Weiss 1977:18–19).

During the last three months of Bertalanffy's initial U.S. visit (July through September 1938), he worked with Weiss at Woods Hole (Hammond 2003; Pouvreau 2006). This was their last meeting until 1952. In autumn of that year, they met again at the University of Austin (Texas), where Weiss was working. At that time, Bertalanffy was on a tour, making about 15 conference presentations in different parts of the country; he came to Austin at the invitation of the biochemist Chauncey D Leake. Weiss probably played a role in this invitation (Pouvreau 2006:76). Years after going abroad, Bertalanffy and Weiss met again in Austria at the small alpine village of Alpbach, Tyrol, on the occasion of a special symposium devoted to systems thinking, organized by Arthur Koestler in 1968 (Koestler and Smythies 1969).

Bertalanffy's written estate (Bertalanffy papers), which was found in 2004, yields no evidence of communication between Weiss and Bertalanffy after 1945. As for the period before 1945, no letters to or from Bertalanffy are conserved in this estate, because his home was burned at the end of World War II.

EARLY WORKS OF BERTALANFFY

In the course of his studies, Bertalanffy focused on philosophy, having Robert Reininger—the leader of neo-Kantianism in Austria and president of the Viennese Philosophical Society (1922–1938)—and Moritz Schlick among his teachers. Bertalanffy recognized his student days in Vienna as a time of high intellectual intensity, triggering many developments that later became important for him (Bertalanffy 1967). Concerning the positivist ideas of the “Vienna Circle” around Schlick, Bertalanffy logically regards empiricism as an erroneous doctrine. He holds that empirical data have to be ordered by laws, because “one cannot base and develop any science solely on experience and induction” (Bertalanffy 1927a:660). Referring to Kant (1787:A51/B75), he liked to say that, though theory without experience is mere intellectual play, experience without theory is blind (Bertalanffy 2003:101). Furthermore, when Bertalanffy outlines the difference between science and metaphysics, mythical thinking, and mysticism, he argues that a dialogue between them is necessary. For example, he writes: “The most noble task of science is that mysticism does not bring us back to the night of ignorance and faith, but that it becomes itself a means for the deepest understanding of nature” (Bertalanffy 1927b:264). Convergences with positivism can nonetheless also be found: especially a taste for logical analysis of concepts, the rejection of substantialism (see Mach 1906 and 1933), and the will to save the dignity of science in the face of the rise of irrationalism—a characteristic trend in the interwar German and Austrian context.

Bertalanffy’s doctoral thesis (Bertalanffy 1926a) was concerned with intriguing questions: Can units of higher order (integrating, from Fechner’s point of view, the living organism) be methodically investigated in an abstract manner? Can they be made empirically plausible? To what degree can an inductive metaphysics be based on a generalized concept of organization, as opposed to speculative metaphysics? His dissertation already covers the stratified levels of biology, psychology, and sociology, and he emphasizes the “perpetual recurrence of the same in all levels of integration [*Integrationsstufen*]” (Bertalanffy 1926a:49). To illustrate this, he employs the model of the atom as a small planetary system, reviving the ancient doctrine of the homology of macrocosmos and microcosmos. Note, however, that this model was already regarded as erroneous at that time in physics, after having been understood as a useful fiction.

After graduating, he wrote many articles in the field of theoretical biology. In 1928, he published his “critical theory of morphogenesis” (Bertalanffy 1928), which acquainted him with the Berlin Society for Scientific Philosophy and Hans Reichenbach—a counterpart to the Vienna Circle—and opened contacts with *Gestalt* psychologists (Hofer 2000:154). In that work, Bertalanffy regards the development of an organism out of a germ as a “paradigm” [*Paradigma*] illustrating the need for an “organismic” and “theoretical” biology. He therefore analyzes the various theories of development [*Formbildung*], among them the approaches of Przibram and Weiss (Bertalanffy 1928). Przibram’s analogy of a germ and a growing crystal is criticized because the first one consists of inhomogeneous parts, while the second is homogeneous, although both have a “vectorial potential” and tend to regenerate if disturbed. Also criticized is the lack of differentiation between life and the inorganic realm (Bertalanffy 1928:166–175). The “field theory” in Weiss’s developmental biology is categorized by Bertalanffy (1928:189–190) as an organismic theory (see below). Bertalanffy concludes from the analyzed theories of development that “wholeness [*Ganzheit*], Gestalt, is the primary attribute of life” (Bertalanffy 1928:225). He uses wholeness [*Ganzheit*] and *Gestalt* as synonyms (Bertalanffy 1929c:89).

In May 1934, Ludwig von Bertalanffy was the first academic at the University of Vienna to receive a *Habilitation* in “theoretical biology.” The basis for this licensing procedure was the first volume of his book on what he called *Theoretische Biologie*, which had already been published two years earlier (Bertalanffy 1932).

THEORETICAL BIOLOGY AND EPISTEMOLOGY

At a young age, Bertalanffy was probably introduced to the ongoing controversies in biology. The neo-Lamarckian Kammerer has already been mentioned above. Kammerer’s impact is clear in Bertalanffy’s early criticism of selectionist or mutationist theories of evolution

UKPMC Funders Group Author Manuscript

(Bertalanffy 1929a). But very early on, he distanced himself from the different kinds of neo-Lamarckism that were flourishing in the first two decades of the 20th century as a consequence of the inner weaknesses of Darwinism (related in particular to its apparent contradictions with the Mendelian theory of heredity). He therefore criticized Kammerer (Bertalanffy 1928:95) not only for his “Lamarckist” speculations, but also for his alleged “theory free” empiricism. As a consequence of his early contact with the (psycho-)vitalist botanist Adolf Wagner, Bertalanffy very likely had firsthand knowledge regarding the criticism of the Darwinian school and about attacks on biological “mechanicism” (Reiter 1999; Hofer 2000; Pouvreau 2006). Like Weiss, he was also very much influenced by Köhler, whom he regarded as a “precursor” of his “general systemology” (Bertalanffy 1945:5; 1949b:115). Köhler, who wanted to extend *Gestalt* theory toward biological regulation, coined the term *Systemlehre* (Köhler 1927), which Bertalanffy also used and that we translate as “systemology” (Pouvreau and Drack 2007). Köhler’s aim was to show that self-regulation by means of dynamic interactions is a common ability in both physical and organic systems.

An important figure regarding the need for a theoretical basis for biology was Schaxel, who in 1919 started a book series (Abhandlungen zur theoretischen Biologie; Treaties in Theoretical Biology) dedicated to implementing theoretical biology. It is not by chance that works of Przibram (1923), Weiss (1926), and Bertalanffy (1928) were published in that series. In the same year, he published an essay on the basics of theorization [*Theorienbildung*] in biology (Schaxel 1919). He also popularized the term “organismisch” (organismic), which was coined by the entomologist Ludwig Rhumbler in 1906 (Schaxel 1919:203). This term was used by Bertalanffy in order to characterize his own fundamental conceptions; the influences of both Schaxel and Ungerer (1922) are clear and explicit in the genesis of his ideas and his associated vocabulary.

Spemann’s works (1924) on “organizers of development” also influenced Bertalanffy. The dependency on the positions of the parts can only be understood when considering the organism as a whole, including processes of differentiation and hierarchization.

Bertalanffy’s first book, in which he emphasized the need for a theoretical biology, appeared in 1928. His motivation for going into biology is much related to the fact that biological categories (especially wholeness and organization) were very often and uncritically used in areas beyond biology, and often served as a basis for dogmatic ideologies.

> The science of life has nowadays to a certain extent become a crossroad, in which the contemporary intellectual developments converge. The biological theories have acquired a tremendous ideological [*weltanschauliche*], yes even public and political significance… . The condition of biology, problematic in many respects, has led to the situation that the “philosophies of life” were until now by no means satisfactory from the scientific as much as the practical point of view; we see all the more clearly the importance of the theoretical clarification of biology (Bertalanffy 1930:4–5).

Another consideration demanding a sound epistemological basis in biology was its mere descriptive or experimental character, which, according to Bertalanffy, had to be overcome. He argues in the same line as Weiss in so far as both think that biology has to be autonomous, and that life cannot be reduced to the realm of physics and chemistry alone, as “mechanicists” (or rather, “physicalists”) would like. There are two main justifications for this. First, biology needs to be seen with different methodological perspectives: physicochemical, *ganzheitliche* (integrative or “holistic” in a broad sense) or organismic, teleological, and historical (e.g., Bertalanffy 1928:88). The “analytico-summative” approach expressed by the physical and chemical investigation of isolated processes leaves aside organization, which is a core problem of biology. Second, Bertalanffy regarded the conflict between “mechanicism” and “vitalism” as an essentially metaphysical one, which cannot be solved empirically—this can also be seen as a criticism of empiricism. A new approach was therefore necessary. Bertalanffy called it "organismic biology" (Bertalanffy 1932).

In starting his theoretical program, he was convinced that biology's right to exist as a science requires a theoretical background that had not been established yet, although many so-called "theories" were around. For him, biology of this time was little more than some kind of natural history in a precritical ("pre-Copernican"—note the allusion to Kant) stage (Bertalanffy 1928:1–3, 51–56, 90–100; 1932:1–9, 20–35). Empirical data have to be ordered by laws, and Bertalanffy distinguished between "empirical rules" and laws, a distinction that empiricists usually do not make—as mentioned, Weiss did so but not in an elaborated way—and that consequently leads to confusion.

> The rule is derived inductively from experience, therefore does not have any inner necessity, is always valid only for special cases and can anytime be refuted by opposite facts. On the contrary, the law is a logical relation between conceptual constructions; it is therefore deductible from upper [*übergeordnete*] laws and enables the derivation of lower laws; it has as such a logical necessity in concordance with its upper premises; it is not a mere statement of probability, but has a compelling, apodictic logical value once its premises are accepted (Bertalanffy 1928:91).

Another confusion involves mixing description, which is "the mere reporting of facts," and explanation, which "means the logical subsuming of the particular under the general, the ordering of the facts standing in our way in more general relations" (Bertalanffy 1932:23–24).

The role of the experiment is overestimated by empiricists and, from a logical point of view, not justified. The law does not belong to the empirical realm. Furthermore, it cannot be induced because, in such a procedure, the "disturbances" in reality have to be known before the law is derived from empirical data, which is logically impossible (Bertalanffy 1928:93). Laws therefore have to be derived "hypothetico-deductively," with experiments being an incentive and instance of proof (Bertalanffy 1932:27–28). A final mistake of empiricists is the illusion that a "hypothesis free" science could possibly exist. All the activities of science contain a certain theoretical momentum. Scientists who are unaware of that instance might easily become victims of metaphysical or ideological bias.

According to Bertalanffy, biology must also become an exact nomothetic science (Bertalanffy 1928:55). On the one hand, a theory of knowledge and methodology of biology is required. On the other, general principles and laws of life for deriving particular laws are also part of a theoretical biology, within which the different fields of biology should also be synthesized and unified in a coherent system. Theoretical biology has to plan experiments and strive for the conceptual mastery of the phenomena. Furthermore, the unstructured accumulation of empirical data and the specialization into various fields, which obscures the links among the problems, must be overcome (Bertalanffy 1932:32–34). Nevertheless, establishing "exact laws" does not mean that biology has to be reduced, by "causal analysis," to physics and chemistry. The essential and sufficient character of a law is "to link univocally a definite initial state with a definite final one," thereby "it is not indispensable" for such a determination "that all intermediary processes are known" (Bertalanffy 1930–1931:400). This is similar to Prizbram's position but, of course, also to Boltzmann's statistical approach in thermodynamics to which Bertalanffy repeatedly refers, or to the contemporary approaches in quantum mechanics.

Bertalanffy alleges that his "organismic" biology, where the *Ganzheit* (wholeness) is held as a fundamental characteristic of biological entities, is beyond "mechanicism" and "vitalism." His "organismic program" aims at determining the corresponding laws that are complementary (in Niels Bohr's sense) to the analytico-summative approach. Furthermore, the concept of

UKPMC Funders Group Author Manuscript

teleology is rehabilitated: not in a vitalistic way (in the metaphysical sense), but as a logical form of the maintenance of the whole. The basic assumption that the world is stratified (N Hartmann 1912) is used in order to connect causality and finality in connection with the concept of dynamic equilibrium: "What in the whole denotes a causal equilibrium process, appears for the part as a teleological event" (Bertalanffy 1929b:390; 1929c:102). His "de-anthropomorphization" of teleology—it might be less confusing to employ the word "teleonomy" instead, which was introduced by Pittendrigh (1958)—and use of a systemic category is in line with other authors such as Ungerer, Schaxel, Weiss, and Nicolai Hartmann.

> Just like the concept of energy is the form of expression for the causal law ruling the inorganic world, the concept of organism is the form of expression for the finalist [*finale*] perspective, which we have to apply to the organism besides the causal one. The characteristic of the organism is first that it is more than the sum of its parts, and second that the single processes are ordered for the maintenance of the whole (Bertalanffy 1928:74).

Important in this context is the idea that an "equifinal" state of the whole may be reached independently of the initial states of the parts and in the way they reach it. This conception is crucial in developmental biology and clearly contradicts a "mechanicist" attitude.

The epistemology of "organismic biology" is based on the conception of the organism as a system, and can thus be called a "system theory" of life. The term *Systemtheorie* ["system theory"] first appears in Bertalanffy's writings in 1930–1931 (p 391), although he does not explicitly define what is meant by system before 1945—where a system is described as a complex of elements in interaction (Bertalanffy 1945). Mathematics also plays an important role. Inspired by thermodynamics, he aims at the determination of "higher order statistics," where the causalities driving the single part are left aside, "exact laws" are nevertheless derived without reduction to the physicist and chemist realm. Clearly, Bertalanffy's thinking and the attempts of Przibram converge. With his growth equations, Bertalanffy (1934, 1941) later shows how a mathematical approach in that direction can be implemented in the field of the dynamics of morphogenesis (Pouvreau 2005a,b).

It should also be mentioned that Bertalanffy rejects emergentism and holism in their original sense (Lloyd Morgan 1923; Smuts 1926). He considers them as belonging to metaphysics and as sterile in science—both implying an ontological irreducibility of the whole to its parts and relationships, even when they are exhaustively known (radical qualitative *novelty*). He also easily resists critiques such as those of Phillips (1976). Although that latter critique— toward a simple-minded Hegelian attitude of holistic thinkers—focuses on the late works of both Weiss and Bertalanffy, it should be discussed here because it also provides insight into their early works. Bertalanffy's position might be interpreted as echoing Georg W F Hegel's "doctrine of internal relations" (according to which the whole relational structure is constitutive of each "part") as well as holism, which is not the case. In contrast to Phillips's critique, Bertalanffy's statements are purely epistemological. Weiss was probably too pragmatic and too much an experimentalist to incorporate any Hegelian attitude. But the chief argument brought forward against "Hegelian thinking"—namely, against the idea that the parts gain certain properties when combined to a whole—cannot be sustained for the two biologists. Bertalanffy understood the "whole" as the sum of its "parts" *and* their relations, and thought that this is all that can be tackled by science. The only problem lay in the epistemological difficulties posed by "organized complexity"—as Warren Weaver (1948) calls it—which sets into practice the impossibility to satisfy the required condition of knowing all the parts and their relations in order to know the whole:

> The properties and modes of action of the higher levels are not explainable by the summation of the properties and modes of action *of their components as studied only*

> *in isolation*. But if we know *all* the components brought together and *all the relations existing between them*, then the higher levels are derivable from their components (Bertalanffy 1932:99; 1949a:140).

The system laws thus deal with the relationships among the parts: the existence of such laws relies on the idea that the relational structure may change, while the parts stay "intrinsically" the same (i.e., as studied in isolation from the whole), so that the whole has properties of its own. Only in that sense is emergence tangible by science, and not in the mentioned metaphysical sense (Bertalanffy 1932:99). A later statement by Weiss is interesting in this context, which is very much in the same line. In the phrase "the whole is more than the sum of its parts," Weiss interprets "more" not as an algebraic term, but refers to the "more" information that is needed to describe the whole compared to the parts. With this conception, Weiss bridges the gap between reductionism and holism (Weiss 1970a:20).

Bertalanffy is also very much in line with Weiss (see above) when he states that biological system laws are not once and forever irreducible to physics, although Weiss refers to biological terms that in the future might be replaced, but he holds that the laws of complex issues will never be fully replaced by physics and chemistry (Weiss 1925:170).

> To the question whether the concepts of physics are at present sufficient for scientific biology, the answer is no… . To the question whether the [purely biologically applied] concepts can anyway be replaced by physical ones, the answer is: wait and see (Bertalanffy 1932:113–114 following Woodger).

> If the system laws of the organism cannot today be formulated in a physico-chemical way, then a biological version of those laws is justified. The question whether an ultimate reduction of the biological system laws is possible … is of secondary importance (Bertalanffy 1932:115).

ORGANISMIC PRINCIPLES

Bertalanffy formulates two general organismic "principles" or "working hypotheses" (Bertalanffy 1932:331), which should more appropriately be regarded as conceptual models of biological organization. These "principles" had already been previously mentioned by others, but Bertalanffy unifies them and extends their scope from the single organism to biological organizations in general (from cell to biocoenosis), thereby opening the way from organicism to systemism. The first one is the "principle" of the organized system as an "open system" in "flux equilibrium" [*Fließgleichgewicht*] (Bertalanffy 1929c:87; 1932:83–84, 116, 197; 1940a:521; 1940b:43). This equilibrium cannot be compared to chemical equilibria because the latter are characterized by a minimum of free energy. In contrast, the organism is an open system that maintains itself through a continuous flux of matter and energy, by assimilation and dissimilation, distant from true equilibrium, and is able to supply work. Metabolism is thus an essential property of the organism.

The second "principle," also first enunciated in 1929, is the "striving of the organic *Gestalt* for a maximum of formness [*Gestaltetheit*]" (Bertalanffy 1929c:104). This is thought to play a role in ontogenesis as well as in phylogenesis, and later becomes the "principle of hierarchization" or "principle of progressive organization (or individualization)" (Bertalanffy 1932:269–274, 300–320). The dynamic interactions in the system give rise to order. The principle is very much related to epigenetic phenomena and comprises the development from an initial equipotential state (with maximum regulation abilities) over segregation processes. This is followed by differentiation and specialization, where some sort of centralization, with "leading parts" that control the development of other subsystems, can also occur. Characteristic is the inherent trend toward an ever-increasing complexity— a trend that he later (Bertalanffy 1949a) calls "anamorphosis," after Richard Woltereck had coined the term in 1940.

Besides the “principles” of wholeness and dynamics, a third one, namely that of primary activity of the organism, becomes explicit only later when Bertalanffy’s organismic thinking has matured (Bertalanffy 1937:14, 133–134). It was nonetheless implicit in many of his writings between 1927 and 1932, and also has ancient roots. It must be viewed in opposition to a mere passive concept of organisms that merely react to the outside world. The concepts are not new, but were already forwarded by researchers of *Lebensphilosophie* (“philosophy of life”), which was an intellectual fashion in the first two decades of the 20th century (Pouvreau and Drack 2007). Weiss and Przibram also argue along the lines of primary activity, but Bertalanffy does not refer to them in this regard. Bertalanffy largely cites Weiss when discussing the theory of the morphogenetic fields (e.g., Bertalanffy 1928), although he at least once clearly writes about system theory with regard to animal behavior without mentioning Weiss (Bertalanffy 1932:57–58). There, he refers to the *Erstarrung* (congealment) into a machine as a secondary process and the *Fähigkeit zum Ganzen* (ability toward being a whole) as primary to the plasticity and regulation abilities of the most rigid, machine-like reflexes and instincts of the organisms. But Weiss’s theory of animal behavior is never explicitly mentioned. Bertalanffy (1937:136–142) provides detailed criticism of Loeb’s theory, but only Friedrich Alverdes is mentioned, not Weiss. In the 1920s and 1930s, Alverdes was the main German advocate of an organismic approach to animal behavior (individual, but especially social); his entire body of work is dedicated to it.

BEYOND WEISS’S CONCEPTIONS

Note that Bertalanffy’s concerns went beyond the convergences with Weiss’s concepts. The program of his “organismic biology” comprises four dimensions. It is (1) a scientific program for opening the way toward constructing exact theories of biological systems of different levels. It also is (2) a natural philosophy of the biological world, where the two principles mentioned above “probably have in the organic realm a similar basic importance as the physical fundamental laws for inorganic nature” (Bertalanffy 1932:282). Essential for this philosophy is the stratified character of reality and the autonomy of its levels, where fundamental system laws can be found at each level—a scheme already discussed in his doctoral thesis (Bertalanffy 1926a). Furthermore, the dimension of (3) a basis for developing an inductive metaphysics has to be mentioned. Metaphysics can, according to Bertalanffy (1932:283), find a solid fundament in “organismic” biology for renewing answers to old problems. Finally, there is (4) an ideological dimension, insofar as “organismic” biology is supposed to lay the foundations of an alternative worldview beyond “mechanicism”—a foundation in which the *Ganzheit* [wholeness] plays a central role (Pouvreau and Drack 2007).

The fact that Bertalanffy’s “organismic biology” was not an empty program is exemplified by his theory of organic growth, which even today remains a central reference in that field. In this theory, global growth and relative (allometric) growth are tackled not only by finding growth constants, but also by linking growth with anabolism and catabolism. This step had not been made before, and combines the open system concept with equifinality (see Pouvreau 2005a,b; Pouvreau and Drack 2007). As already described above, this is in line with “laws of higher order” and “mathematical morphology” as mentioned by Przibram.

Conceptual Connection

The fields of interest of Bertalanffy and the “Vivarium” biologists overlapped considerably. The “Vivarium” tackled some of the basic questions in biology experimentally and Bertalanffy strived to set up a theoretical basis of biology. Unsurprisingly, they argue in similar fields, such as developmental biology, which comprises fundamental biological questions; indeed, observations from embryology also influenced Bertalanffy’s “system theory of life.” The research style at the “Vivarium” clearly offered one, although not the only one, introductory approach to issues of “system theory.” When Weiss and Bertalanffy met in 1920s Vienna, their discussions very certainly centered around concepts that later converged in Bertalanffy's "system theory." Bertalanffy, however, was also well acquainted early on with the works of Przibram, and first mentioned Przibram in his first paper in the field of biology (Bertalanffy 1926b).

Bertalanffy's concepts in his "system theory" are not all congruent with those of Weiss. Nevertheless, some ideas converge, and Weiss's work probably provided motivation. Otherwise, Bertalanffy would not have mentioned him at the Alpbach symposium as a key figure regarding the system approach in biology. Weiss was one of the first researchers who not only described but effectively grasped the organism as a system. The experiments that he performed support the system approach of the organism and, thereby, also Bertalanffy's "organismic biology." Like Bertalanffy, Weiss addresses "system theory" later on in his career. However, the development of both thinkers was more parallel, and the influence of one on the other was only minor.

The conceptual connections between Weiss and Bertalanffy can be summarized as follows: Both think dynamically and in hierarchical terms, and both consider "wholeness" as a key conception for understanding living systems or organisms as systems, as opposed to a "mechanicist" approach. In this regard, the principle of primary activity is crucial for both. The idea of "conservation" is also fundamental to their system concepts. Weiss's tentative definition of system and formulation of "system laws" also has a certain generality, which is paralleled in Bertalanffy's later effort toward a "general system theory." Both also argue for biology as an autonomous discipline with its own conceptual apparatus, which cannot be reduced to physics and chemistry; and for biologists to find laws of "higher order." Nevertheless, Bertalanffy was much more interested in establishing a theoretical biology than Weiss and, therefore, his epistemological attempt was more sophisticated.

Potential Contribution to Future System Approaches in Biology

As the conceptual connection between Weiss and Bertalanffy arises from both experimental and philosophical considerations, these can serve as a useful framework for further research regarding biological systems. In recent years, "systems biology" (see Kitano 2002) and "biocomplexity" research (see Michener et al. 2001) have appeared as new fields, often in order to provide quantitative (computer) models for complex biological phenomena.

Although there is currently no widely accepted definition (Kirschner 2005), "systems biology" can be described as the study of the interactions among the components of biological systems and the consequent function and behavior of the system as a system (i.e., how a biological whole behaves over time). This already shows that "systems biology" goes beyond a mere "analytico-summative" approach. Still, quite often concepts only from engineering or cybernetics are used to model biological systems; for example, when feedback loops are introduced or when robustness is investigated. These concepts are often derived from physics and do not comprise central characteristics of life. Woese (2004) criticizes this engineering approach, which he already observes in the Human Genome Project, a pivotal kickoff impulse for "systems biology." Some scientists aim to explain life within "systems biology" on the basis of molecular interactions with emphasis on genes and proteins. Furthermore, the question of how the phenotype is generated from the genotype is important within "systems biology," as is the correspondence between molecules and physiology at a larger scale.

Kirschner (2005) notes that the performance of a protein is not only determined by a gene, but that it depends on the context in which it occurs, and this context is history dependent. The historical dimension of all living systems can be detected in the work of Weiss and Bertalanffy as well.

The concept of hierarchy was already central to Weiss and Bertalanffy. Thus, they were far removed from what Mesarovic and Sreenath (2006) criticized as a “flat earth perspective in systems biology.”

In addition to the concept of control, as stemming from engineering feedback systems, the importance of coordination in living systems has recently been pointed out by Mesarovic and Sreenath (2006:34): “Coordination … provides motivation/incentives to the parts to function in such ways that they contribute to the overall system’s goal while at the same time they pursue their local objectives.” This parallels the concepts of “wholeness” and “conservation” of Weiss and Bertalanffy.

An engaged warning has been uttered against a possible new “regression into over-simplification” (Newman 2003:12) that might prevail in “systems biology.” Here, the concepts of Weiss and Bertalanffy might help avoid the risk of “mechanicism.” As shown, some of these concepts have already been incorporated or encouraged to be integrated in “systems biology.” Primary activity, however, is not an issue in “systems biology” today, but was acknowledged as important by Weiss and Bertalanffy.

Although skeptical about earlier system attempts in biology, O’Malley and Dupré (2005) emphasize that further philosophical efforts have to be made within “systems biology.” This is what they call “systems-theoretic biology,” as opposed to “pragmatic systems biology,” which is concerned with interactions of molecules on a large scale.

As we have demonstrated, Bertalanffy already contributed much to epistemological issues in his early German publications on organismic biology that approached the organism as a system. The data-driven approach found in modern “systems biology” is often seen as a necessary first step. Theory from (not only) Bertalanffy’s point of view, however, clearly plays an important role especially at the start of a new scientific endeavor: theoretical work must be combined with experimental efforts at every stage. This is precisely what he intended with his theoretical biology based on an organismic approach.

As Kirschner (2005) remarks, “systems biology” is not a branch of physics. In the view of Weiss and Bertalanffy, it was self-evident that biology is an autonomous discipline and has to work with its own conceptual apparatus. This prompted them to develop a system theory of life.

Acknowledgments

This research was supported by Austrian Science Fund (FWF) Grant P18149-G04 to Rupert Riedl (1925–2005), who unfortunately passed away shortly after the research project was initiated. Riedl was one of Bertalanffy’s students in 1940s post-war Vienna and later on actively emphasized the importance of “*Systemtheorie*” [system theory] and “*Längsschnitttheorien*” (longitudinal-section theories)—not only in biology, but also in other sciences and in humanities as well (e.g., Riedl 1978, 2000). His emphasis on the importance of establishing a theoretical biology was also influenced by Bertalanffy. Later on, Weiss, a fatherly friend as Riedl liked to say, also exerted an influence on him. We furthermore wish to thank Ludwig Huber and Gerd B Müller for their support.

REFERENCES

Apostel L. Structuralisme et théorie générale des systèmes. Morale et Enseignement: Annales de l’Institut Philosophique de l’U.L.B 1970:163–174.

Aristotle. Politics. Revised Edition. Clarendon Press; Oxford (UK): 1966. The Works of Aristotle, Volume 10

Ash, MG. Gestalt Psychology in German Culture, 1890–1967: Holism and the Quest for Objectivity. Cambridge University Press; Cambridge (UK): 1995.

Bapp, K. Aus Goethes griechischer Gedankenwelt. Dieterich; Leipzig (Germany): 1921.

Archive of the Bertalanffy Center for the Study of Systems Science (BCSSS). Department of Theoretical Biology, University of Vienna; Austria: Bertalanffy papers. http://www.bertalanffy.org

von Bertalanffy, L. PhD diss. University of Vienna; 1926a. Fechner und das Problem der Integration höherer Ordnung.

von Bertalanffy L. Zur Theorie der organischen Gestalt. Wilhelm Roux' Archiv für Entwicklungsmechanik der Organismen 1926b;108:413–416.

von Bertalanffy L. über die Bedeutung der Umwälzungen in der Physik für die Biologie. Studien über theoretische Biologie II. Biologisches Zen-tralblatt 1927a;47:653–662.

von Bertalanffy L. über die neue Lebensauf-fassung. Annalen der Philosophie und philosophischen Kritik 1927b;6:250–264.

von Bertalanffy, L. Kritische Theorie der Formbildung. Gebrüder Borntraeger; Berlin (Germany): 1928. Abhandlungen zur theoretischen Biologie, Volume 27 Translated by J H Woodger as Modern Theories of Development: An Introduction to Theoretical Biology. Oxford (UK): Clarendon Press, 1933.

von Bertalanffy L. Der heutige Stand des Entwicklungsproblems. Teil I: Die klassischen Theo-rien; Teil II: Neuere Anschauungen und die Zukunft der Entwicklungslehre. Scientia 1929a;46:97–110. 171–182.

von Bertalanffy L. Die Teleologie des Lebens. Eine kritische Erörterung. Biologia Generalis 1929b; 5:379–394.

von Bertalanffy L. Vorschlag zweier sehr allgemeiner biologischer Gesetze. Studien über theoretische Biologie III. Biologisches Zentralblatt 1929c;49:83–111.

von Bertalanffy, L. Lebenswissenschaft und Bildung. Kurt Stenger; Erfurt (Germany): 1930.

von Bertalanffy L. Tatsachen und Theorien der Formbildung als Weg zum Lebensproblem. Erkenntnis 1930–1931;1:361–407.

von Bertalanffy, L. Theoretische Biologie, Band I: Allgemeine Theorie, Physikochemie, Aufbau und Entwicklung des Organismus. Gebrüder Borntraeger; Berlin (Germany): 1932.

von Bertalanffy L. Untersuchungen über die Gesetzlichkeit des Wachstums I. Allgemeine Grundlagen der Theorie. Mathematisch-physiologische Gesetzlichkeiten des Wachstums bei Wassertieren. Wilhelm Roux' Archiv für Entwicklungsmechanik der Organismen 1934;131:613–652.

von Bertalanffy, L. Das Gefüge des Lebens. B. G. Teubner; Leipzig (Germany): 1937.

von Bertalanffy L. Der Organismus als physikalisches System betrachtet. Die Naturwissenschaften 1940a;28:521–531.

von Bertalanffy, L. Vom Molekül zur Organismenwelt; Grundfragen der modernen Biologie. Akademische Verlagsgesellschaft Athenaion; Potsdam (Germany): 1940b.

von Bertalanffy L. Untersuchungen über die Gesetzlichkeit des Wachstums, VII. Teil: Stoffwechseltypen und Wachstumstypen. Biologisches Zentralblatt 1941;61:510–532.

von Bertalanffy, L. Theoretische Biologie, Band II: Stoffwechsel, Wachstum. Gebrü-der Borntraeger; Berlin (Germany): 1942.

von Bertalanffy L. Zu einer allgemeinen Systemlehre. Blätter für deutsche Philosophie 1945;18(3/4) Unpublished, but preserved in the Bertalanffy papers.

von Bertalanffy, L. Das biologische Weltbild – Die Stellung des Lebens in Natur und Wissenschaft. A. Francke; Bern (Switzerland): 1949a.

von Bertalanffy L. Zu einer allgemeinen Systemlehre. Biologia Generalis 1949b;195:114–129.

von Bertalanffy, L. Robots, Men and Minds: Psychology in the Modern World. G. Braziller; New York: 1967.

von Bertalanffy, L. General System Theory: Foundations, Development, Applications. G. Braziller; New York: 1969.

Boveri, T. Festschrift für Richard Hertwig III. G. Fischer; Jena (Germany): 1910. Die Potenzen der Ascaris-Blastomeren bei abgeänderter Furchung, zugleich ein Beitrag zur Frage qualitativ-ungleicher Chromosomen-Teilung; p. 131-214.

Brauckmann S. The scientific life of Paul A. Weiss (1898-1989). Mendel Newsletter 2003;12:2–7. [PubMed: 12856679]

Chong L, Ray LB. Whole-istic biology. Science 2002;295:1661.

Coen DR. Living precisely in fin-de-siècle Vienna. Journal of the History of Biology 2006;39(3):493–523.

Driesch H. Die Lokalisation morphogenetischer Vorgänge – Ein Beweis vitalistischen Geschehens. Archiv für Entwickelungsmechanik der Organismen 1899;8(1):35–111.

Everdell, WR. The First Moderns: Profiles in the Origins of Twentieth-Century Thought. University of Chicago Press; Chicago (IL): 1997.

Gilbert SF, Opitz JM, Raff RA. Resynthesizing evolutionary and developmental biology. Developmental Biology 1996;173(2):357–372. [PubMed: 8605997]

Gliboff S. "Protoplasm … is soft wax in our hands": Paul Kammerer and the art of biological transformation. Endeavour 2005;29(4):162–167. [PubMed: 16271762]

Gliboff S. The case of Paul Kammerer: evolution and experimentation in the early 20th century. Journal of the History of Biology 2006;39(3):525–563.

Gurwitsch A. über den Begriff des embryonalen Feldes. Archiv für Entwickelungsmechanik der Organismen 1922;51(1):383–415.

Grant SGN. Systems biology in neuroscience: bridging genes to cognition. Current Opinion in Neurobiology 2003;13(5):577–582. [PubMed: 14630221]

Haldane JS. Life and mechanism. Mind 1884;9(33):27–47.

Hall, BK.; Pearson, RD.; Müller, GB., editors. Environment, Development, and Evolution: Toward a Synthesis. MIT Press; Cambridge (MA): 2003.

Hammond, D. The Science of Synthesis: Exploring the Social Implications of General Systems Theory. University Press of Colorado; Boulder (CO): 2003.

Haraway, DJ. Crystals, Fabrics, and Fields: Metaphors of Organicism in Twentieth-Century Developmental Biology. Yale University Press; New Haven (CT): 1976.

Harrington, A. Reenchanted Science: Holism in German Culture from Wilhelm II to Hitler. Princeton University Press; Princeton (NJ): 1996.

Hartmann, M. Biologie und Philosophie. Springer; Berlin (Germany): 1925.

Hartmann, M. Philosophie der Naturwissenschaften. J. Springer; Berlin (Germany): 1937.

Hartmann, N. Philosophische Grundfragen der Biologie. Vanderhoeck and Ruprecht; Göttingen (Germany): 1912.

Heidelberger, M. Nature from Within: Gustav Theodor Fechner and his Psychophysical Worldview. University of Pittsburgh Press; Pittsburgh (PA): 2004.

Hofer, V. Organismus und Ordnung: Zur Genesis und Kritik der Systemtheorie Ludwig von Bertalanffy's. University of Vienna; 1996. PhD diss.

Hofer, V. Der Beginn der biologischen System-theorie im Kontext der Wiener Moderne. Diskurslinien und Wissenschaftsgemeinschaften als intellektueller Hintergrund für Ludwig von Bertalanffy. In: Edlinger, K.; Feigl, W.; Fleck, G., editors. Systemtheoretische Perspektiven: Der Organismus als Ganzheit in der Sicht von Biologie, Medizin und Psychologie. P. Lang; Frankfurt am Main (Germany): 2000. p. 137-158.

Hofer, V. Rudolf Goldscheid, Paul Kammerer und die Biologen des Prater-Vivariums in der liberalen Volksbildung der Wiener Moderne. In: Ash, MG.; Stifter, CH., editors. Wissenschaft, Politik und Öffentlichkeit: Von der Wiener Moderne bis zur Gegenwart. WUV Universitätsverlag; Vienna (Austria): 2002. p. 149-184.

Kant, I. Metaphysische Anfangsgründe der Naturwissenschaft. F. Meiner Verlag; Hamburg (Germany): 1786. [1997 reprint.]

Kant, I. Kritik der reinen Vernunft. Reclam; Stuttgart (Germany): 1787. [2003 reprint.]

Kant, I. Kritik der Urteilskraft. Reclam; Stuttgart (Germany): 1789. [1963 reprint.]

Khittel, S. Paul Weiss: Der Beginn seiner System-theorie des Organismus in den 20er Jahren. In: Edlinger, K.; Feigl, W.; Fleck, G., editors. Systemtheoretische Perspektiven: Der Organismus als Ganzheit in der Sicht von Biologie, Medizin und Psychologie. P. Lang; Frankfurt am Main (Germany): 2000. p. 159-170.

Kirschner MW. The meaning of systems biology. Cell 2005;121(4):503–504. [PubMed: 15907462]

Kitano H. Systems biology: a brief overview. Science 2002;295:1662–1664. [PubMed: 11872829]

UKPMC Funders Group Author Manuscript

Köhler, W. Die physischen Gestalten in Ruhe und im stationären Zustand. Friedr. Vieweg und Sohn; Braunschweig (Germany): 1920.

Köhler W. Zum Problem der Regulation. Wilhelm Roux' Archiv für Entwicklungsmechanik der Organismen 1927;112(1):315–332.

Koestler, A.; Smythies, JR., editors. Beyond Reductionism: New Perspectives in the Life Sciences. Hutchinson; London (UK): 1969.

Lenoir, T. The Strategy of Life: Teleology and Mechanics in Nineteenth Century German Biology. D. Reidel Publishing Company; Dordrecht (The Netherlands): 1982.

Lloyd, Morgan C. Emergent Evolution. Williams and Norgate; London (UK): 1923.

Loeb, J. Vorlesungen über die Dynamik der Lebenser-scheinungen. Verlag von Johann Ambrosius Barth; Leipzig (Germany): 1906.

Mach, E. Die Analyse der Empfindungen und das Verhältnis des Physischen zum Psychischen. Fifth Edition. G. Fischer; Jena (Germany): 1906.

Mach, E. Die Mechanik in ihrer Entwicklung. Ninth Edition. Brockhaus; Leipzig (Germany): 1933.

Mesarovic M, Sreenath SN. Beyond the flat earth perspective in systems biology. Biological Theory 2006;1(1):33–34.

Michener WK, Baerwald TJ, Firth P, Palmer MA, Rosenberger JL, Sandlin EA, Zimmerman H. Defining and unraveling biocomplexity. BioScience 2001;51(12):1018–1023.

Müller, GB.; Newman, SA., editors. Origination of Organismal Form: Beyond the Gene in Developmental and Evolutionary Biology. MIT Press; Cambridge (MA): 2003.

Needham J. Recent developments in the philosophy of biology. Quarterly Review of Biology 1928;3(1): 77–91.

Nernst W. Zum Gültigkeitsbereich der Naturgesetze. Die Naturwissenschaften 1922;10(21):489–495.

Newman SA. The fall and rise of systems biology. GeneWatch 2003;16(4):8–12.

Nyhart, LK. Biology Takes Form: Animal Morphology and the German Universities, 1800-1900. University of Chicago Press; Chicago (IL): 1995.

O'Malley MA, Dupré J. Fundamental issues in systems biology. BioEssays 2005;27(12):1270–1276. [PubMed: 16299766]

Penzlin, H. Die theoretische und institutionelle Situation in der Biologie an der Wende vom 19. zum 20. Jahrhundert. In: Jahn, I., editor. Geschichte der Biologie. Third Edition. Spektrum Akademischer Verlag; Berlin (Germany): 2000. p. 431-440.

Phillips, DC. Holistic Thought in Social Science. Stanford University Press; Stanford (CA): 1976.

Piaget, J. Le structuralisme. Presses Universitaires de France; Paris (France): 1968.

Pittendrigh, CS. Adaptation, natural selection, and behavior. In: Roe, A.; Simpson, GG., editors. Behavior and Evolution. Yale University Press; New Haven (CT): 1958. p. 390-416.

Planck M. Aus der neuen Physik. Forschungen und Fortschritte 1929;5:16–17.

Pouvreau, D. Mémoire de DEA. E.H.E.S.S.; Paris (France): 2005a. Vers une histoire de la "théorie générale des systèmes" de Ludwig von Bertalanffy.

Pouvreau D. Eléments d'histoire d'une fécondation mutuelle entre "holisme" et biologie mathématique. Sciences et techniques en perspective 2005b;9:143–242. fascicule 2. 2esérie

Pouvreau, D. La "tragédie dialectique du concept de totalité": Une biographie non officielle de Ludwig von Bertalanffy (1901-1972) à partir de ses textes, de sa correspondance et de ses archives. BCSSS; Vienna (Austria): 2006.

Pouvreau D, Drack M. On the history of Ludwig von Bertalanffy's "General Systemology." and on its relationship to cybernetics – Part I: Elements on the origins and genesis of Ludwig von Bertalanffy's "General Systemology.". International Journal of General Systems 2007;36(3):281–337.

Przibram H. Kristall-Analogien zur Entwick-lungsmechanik der Organismen. Archiv für Entwickelungsmechanik der Organismen 1906;22(1–2):207–287.

Przibram, H. Experimental-Zoologie: Eine Zusammen-fassung der durch Versuche ermittelten Gesetzmäßigkeiten tierischer Formen und Verrichtungen, Band 1: Embryogenese. Franz Deuticke; Leipzig (Germany): 1907.

UKPMC Funders Group Author Manuscript

Przibram H. Die Biologische Versuchsanstalt in Wien: Zweck, Einrichtung und Tátigkeit wáhrend der ersten fünf Jahre ihres Bestandes (1902-1907), Bericht der zoologischen, botanischen und physikalisch-chemischen Abteilung. Zeitschrift für biologische Technik und Methodik 1908–1909;1 (3–5):234–264. 329–362, 409–433.

Przibram, H. Aufbau mathematischer Biologie. Gebrüder Borntraeger; Berlin (Germany): 1923. Abhandlungen zur theoretischen Biologie, Volume 18

Pütter A. Studien über physiologischeÄhnlichkeit VI. Wachstumsähnlichkeiten. Pflüger's Archiv für die gesamte Physiologie des Menschen und der Tiere 1920;180:298–304.

Querner, H. Die Methodenfrage in der Biologie des 19. Jahrhunderts: Beobachtung oder Experiment. In: Jahn, I., editor. Geschichte der Biologie. Third Edition. Spektrum Akademischer Verlag; Berlin (Germany): 2000. p. 420-430.

Reiter WL. Zerstört und vergessen: Die Biologische Versuchsanstalt und ihre Wissenschaftler/innen. Österreichische Zeitschrift für Geschichtswissen-schaften 1999;10(4):585–614.

Rentetzi M. Gender, politics, and radioactivity research in interwar Vienna: The case of the Institute for Radium Research. Isis 2004;95(3):359–393. [PubMed: 15747771]

Riedl, R. Order in Living Organisms: A Systems Analysis of Evolution. Wiley; New York: 1978.

Riedl, R. Strukturen der Komplexität: Eine Morphologie des Erkennens und Erklárens. Springer; Berlin (Germany): 2000.

Roux, W. Der Kampf der Theile im Organismus: Ein Beitrag zur Vervollständigung der mechanischen Zweckmäßigkeitslehre. Engelmann; Leipzig (Germany): 1881.

Schaxel, J. Grundzüge der Theorienbildung in der Biologie. G. Fischer; Jena (Germany): 1919.

Smuts, JC. Holism and Evolution. Macmillan; New York: 1926.

Spemann H. über Organisatoren in der tierischen Entwicklung. Die Naturwissenschaften 1924;12(48): 1092–1094.

Ungerer, E. Die Teleologie Kants und ihre Bedeutung für die Logik der Biologie. Abhandlungen zur theoretischen Biologie, Volume 14. Gebrüder Borntraeger; Berlin (Germany): 1922.

Biologische Versuchsanstalt. Archive of the Austrian Academy of Sciences (AÖAW); Vienna, Austria: Vivarium papers.

Wagner GP, Laubichler MD. Rupert Riedl and the re-synthesis of evolutionary and developmental biology: body plans and evolvability. Journal of Experimental Zoology Part B: Molecular and Developmental Evolution 2004;302B(1):92–102.

Weaver W. Science and complexity. American Scientist 1948;36:536–544. [PubMed: 18882675]

Weiss, PA. Richtungbestimmende Einflüsse äußerer Faktoren. Die Ruhestellung der Vanessiden. University of Vienna; 1922. PhD diss.

Weiss PA. Tierisches Verhalten als "Systemreaktion." Die Orientierung der Ruhestellungen von Schmetterlingen (Vanessa) gegen Licht und Schwerkraft. Biologia Generalis 1925;1:165–248.

Weiss, PA. Morphodynamik: Ein Einblick in die Gesetze der organischen Gestaltung an Hand von experimentellen Ergebnissen. Gebrüder Borntraeger; Berlin (Germany): 1926. Abhandlungen zur theoretischen Biologie, Volume 23

Weiss PA. Morphodynamische Feldtheorie und Genetik. Zeitschrift für induktive Abstammungs- und Vererbungslehre 1928;2(supplement):1567–1574.

Weiss PA. Animal behavior as system reaction: Orientation toward light and gravity in the resting postures of butterflies (*Vanessa*). General Systems: Yearbook of the Society for General Systems Research 1959;4:19–44.

Weiss, PA. Das lebende System: Ein Beispiel für den Schichten-Determinismus. In: Koestler, A.; Smythies, JA., editors. Das neue Menschenbild – Die Revolutionierung der Wissen-schaften vom Leben. Fritz Molden; Vienna (Austria): 1970a. p. 13-70. Also published as Beyond Reductionism: New Perspectives in the Life Sciences. London (UK): Hutchinson, 1969.

Weiss PA. Life, Order, and Understanding: A Theme in Three Variations. The Graduate Journal 1970b; 8(supplement) Austin (TX): University of Texas.

Weiss, PA. The system of nature and the nature of systems: Empirical holism and practical reductionism harmonized. In: Schaefer, KE.; Hensel, H.; Brady, R., editors. A New Image of Man in Medicine.

Futura Publishing Company; Mt. Kisco (NY): 1977. p. 17-63. Volume 1: Towards a Man-Centered Medical Science

Woese CR. A new biology for a new century. Microbiology and Molecular Biology Reviews 2004;68 (2):173–186. [PubMed: 15187180]

Woodger, JH. Biological Principles: A Critical Study. K. Paul, Trench, Trubner and Company; London (UK): 1929.

UKPMC Funders Group Author Manuscript

Figure 1.
The Biologische Versuchsanstalt
The “Prater Vivarium” is depicted in the left foreground as seen from the Riesenrad, Vienna’s giant ferris wheel. © Österreichische Nationalbibliothek/Wien L 39.274-C.

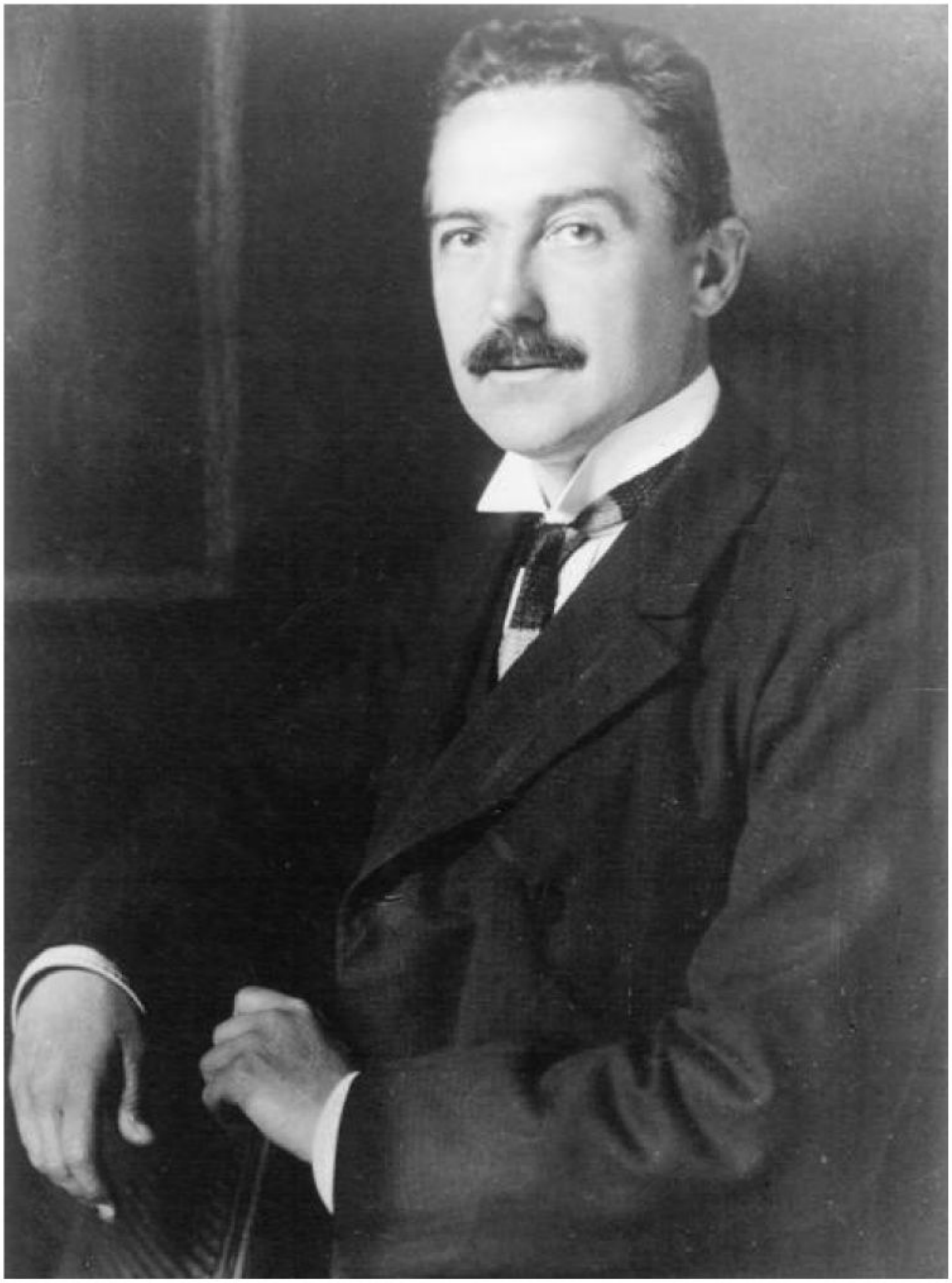

Figure 2.
Hans Leo Przibram (1874–1944)
© Österreichische Nationalbibliothek/Wien NB 510.429-B.

Figure 3.
Paul Alfred Weiss (1898–1989)
© Courtesy of the Rockefeller University Archives.

Figure 4.
Ludwig von Bertalanffy (1901–1972)
© Österreichische Nationalbibliothek/Wien NB 533.771-B.