Journal of the History of Biology
https://doi.org/10.1007/s10739-018-9549-4

O Organism, Where Art Thou? Old and New Challenges for Organism-Centered Biology

Jan Baedke[1]

Abstract

This paper addresses theoretical challenges, still relevant today, that arose in the first decades of the twentieth century related to the concept of the organism. During this period, new insights into the plasticity and robustness of organisms as well as their complex interactions fueled calls, especially in the UK and in the German-speaking world, for grounding biological theory on the concept of the organism. This new organism-centered biology (OCB) understood organisms as the most important explanatory and methodological unit in biological investigations. At least three theoretical strands can be distinguished in this movement: Organicism, dialectical materialism, and (German) holistic biology. This paper shows that a major challenge of OCB was to describe the individual organism as a causally autonomous and discrete unit with consistent boundaries and, at the same time, as inextricably interwoven with its environment. In other words, OCB had to conciliate individualistic with anti-individualistic perspectives. This challenge was addressed by developing a concept of life that included functionalist and metabolic elements, as well as biochemical and physical ones. It allowed for specifying organisms as life forms that actively delimit themselves from the environment. Finally, this paper shows that the recent return to the concept of the organism, especially in the so-called "Extended Evolutionary Synthesis," is challenged by similar anti-individualistic tendencies. However, in contrast to its early-twentieth-century forerunner, today's organism-centered approaches have not yet offered a solution to this problem.

Keywords Organism · Organicism · Dialectical materialism · Holistic biology · Biological individual · Life · Extended Evolutionary Synthesis

Contemporary biology is in a state of crisis.
A general biology, a science of life as such, exists in name only.
– Julius Schaxel 1919

Jan Baedke
jan.baedke@rub.de

[1] Department of Philosophy I, Ruhr University Bochum, Universitätsstr. 150, 44801 Bochum, Germany

Published online: 21 November 2018

Introduction

In the early twentieth century, and especially in the interwar period, comprehensive experimental investigations allowed new insights into the plasticity of organisms, their robustness and regeneration, and their symbiotic and collective forms of interaction with one another. These investigations triggered the theoretical development of a new organism-centered biology (OCB). This movement was made up of a heterogeneous group of biologists, especially in the UK and the German-speaking world (and, to a lesser extent, in the US) that held a number of theoretical viewpoints different from both vitalism and mechanism. These included organicism, dialectical materialism, and (German) holistic biology. A central topic for this group was the interest in developing a theoretical framework that allowed for conceptualizing organisms as the most central unit in biology—a starting point of all methodologies and explanations. This idea rests on the argument that many (if not all) biological processes cannot be investigated effectively without considering the causally efficacious unit of the organism, which not only transcends the properties of its interacting parts but mediates its material organization in coordination with environmental cues, constructs its material and social environment, and assembles with other organisms to form new kinds of individuals, among other things.

In the recent past, historians of biology have shown a growing interest in single elements of this OCB. This especially includes the British tradition of organicism (Nicholson and Gawne 2015; Peterson 2016) as well as the work of single German-speaking members of the OCB community, such as Adolf Meyer-Abich[1] (Amidon 2008), Jakob von Uexküll (Brentari 2015), or Julius Schaxel (Hopwood 1997; Reiß 2007). This paper does not directly contribute to this research, nor does it seek to add a new chapter to the comprehensively-investigated debate between vitalism and mechanism (see Hein 1972; Allen 2005; Nicholson and Gawne 2015). Instead, it seeks to draw a larger picture of the international and multi-disciplinary research community during the first decades of the twentieth century (especially from the 1910s to the late 1930s) that, despite its heterogeneity, clustered around a shared interest in the concept of the organism. In particular, this paper includes a number of little-known German-speaking authors, including Emil Ungerer, Friedrich Alverdes, and Karl Linsbauer.

In addition, this paper aims to carve out so-far undiscussed conceptual challenges (as well as their solutions) that arose in the OCB community. In fact, developing an organism-centered framework was not as easy as it seems, as biologists could not consistently and unambiguously identify the unit denoted by the concept of the organism. In many cases, the organism seemed to completely blend into its context. Ironically, the effect of this insight led some organism-centered biologists to adopt anti-individualistic positions. At least three such anti-individualistic arguments can be distinguished: (1) organisms are reciprocally and inextricably linked with their

[1] Adolf Meyer changed his name to Meyer-Abich in 1937 (Abich is the name of his maternal family). "Meyer-Abich" is always used in the text. The references list his name in the form originally used in the publications.

environment (Uexküll 1909), (2) organisms and their environments are individuals that share the same (or very similar) properties (Henderson 1913), and (3) organisms have no discrete and continuous boundaries to one another (Schaxel 1931). Thus, in this organism-centered theoretical movement, the status of the concept of the organism turned out to be ambiguous. The organism was a causally autonomous and active unit with consistent boundaries and, at the same time, an externally determined entity that was sometimes even completely dissolved into the environment. I will show that advocates of organism-centeredness in organicism, dialectical materialism, and holistic biology were quite aware of this conceptual problem. They tried to delimit more precisely the organisms from their environments by clarifying what it meant for organisms to be alive. Therefore, among members of these three streams of OCB, a concept of life was discussed that integrated functionalist and metabolic elements as well as biochemical and physical ones. It allowed the organism to be more clearly identified and located as a lifeform in its environment—a particularly organized, metabolic unit that actively resists the environment in a state far from equilibrium. This characterization also gave the organism the task of actively shaping itself as well as its surroundings in order to stay alive.

Besides clarifying this international and interdisciplinary conceptual debate about the organism, this paper covers the demise of OCB after the Second World War up to the return of the organism in contemporary biological theory. Today, a new version of OCB has emerged, the so-called "Extended Evolutionary Synthesis" (EES; see Pigliucci and Müller 2010; Laland et al. 2015). Interestingly, this new trend of emphasizing the centrality of the organism faces similar anti-individualistic challenges to those faced by the advocates of OCB in the early twentieth century. Again, the environmentally-sensitive organism faces the threat of merging with its environment and with other organisms, losing its agency as an independent active unit and no longer standing out in complex interdependencies of causal reciprocity. Despite these similarities, the old and new versions of OCB differ substantially. Besides arising as opposite standpoints to different positions (reductionist cell theory and biochemistry in the nineteenth and early twentieth centuries, on the one side, and genecentrism in the late twentieth and early twenty-first centuries, on the other side), the older version of OCB recognized that the above conceptual challenges had to be addressed in order to avoid "losing" the organism. In contrast, the recently emerging approach, EES, has not (yet) developed this awareness. Given these differences, the history of early-twentieth-century OCB should not be written in the light of today's organism-centered approaches. However, because a number of older conceptual challenges about the unit of the organism remain important today, the new OCB can learn something from earlier theoretical debates.

In the following analysis, I first describe the empirical findings that triggered the emergence of OCB in the early twentieth century. I then discuss the basic tenets underlying this OCB and identify three anti-individualistic challenges to this movement within organicism, dialectical materialism, and holistic biology. Theorists including Ludwig von Bertalanffy, Julius Schaxel, and Joseph Needham, among others, countered these challenges by strengthening the concept of life and thus clarifying what an organism as a life form is. Finally, I discuss the fall of OCB in the 1940s and 1950s and the recent reemergence of organism-centeredness in biology in the form of EES. I show that EES suffers from the same ambiguities of simultaneously highlighting and losing the organism.

New Studies on Plastic, Robust, and Collective Organisms

Since the end of the eighteenth century, the concepts of the biological individual and the organism were often used interchangeably, as organisms were treated as paradigmatic individuals (see Cheung 2006).[2] Later, beginning in the 1890s and especially in the interwar period of the twentieth century, new experiments on developmental phenomena, as well as ecological field studies, triggered a growing interest in the question of what constitutes organisms and biological individuals respectively (see Fig. 1).[3] These studies focused on various properties that organisms show when interacting with their environment that had previously been under-investigated. These properties were plasticity or environmental responsiveness, developmental robustness, and symbiotic and/or collective forms of cell–cell or organism–organism interaction.

The ability of organisms to be modified by the environment—what is today known as "plasticity"—became a crucial point of heated discussion through Hans Driesch's (1892) experiments on sea urchins. Driesch separated blastomeres at the two-cell stage of sea urchin embryos. Even though the larvae were reduced in size, nearly normal embryos were formed. Driesch argued that this result showed the potential of the embryo's cells to regulate their own development. He later concluded that these experiments offered an empirical proof of vitalism (in contrast to nonvitalist views in OCB; see below). According to Driesch, the fate of cells is not determined at an early cell stage but through the cell's relationship to the whole. The parts do not seem to exist "only for the sake of their own preservation," as argued by Wilhelm Roux (1881, p. 220), but rather for that of the whole organism. Even though the observed plasticity was found to have limits, it became obvious that in many cases the developing organism does not work like a machine.

During this period, moreover, modifications of plastic development were investigated with respect to the environmental responsiveness and heritability of developmental processes. Woltereck (1909), for example, found out that the development of some traits in the water flea *Daphnia*, such as head shape, depended not on "internal" conditions of the organism but on the presence of an "external" inducing factor (i.e., a particular predator). In addition, this and other environmentally inscribed traits were found to be inherited (although in most cases only for a few

[2] The Latin word *Organismus* ("organism") was introduced by Stahl (1684). During the Enlightenment this term was rarely used, in contrast to "organization" and "organized bodies" (see Kant 1902; AA 5, p. 409).

[3] As Fig. 1 shows, the University of Cambridge Libraries Collection (UCLC) lists significantly fewer monographs on organisms compared to the German Union Catalogue (GVK). In fact, the total numbers of entries in the UCLC match with the numbers of entries in the British Library (data not shown). This result suggests that during this period, a significant part of empirical and theoretical debates about organisms was being discussed in German publications (at least in the form of monographs).

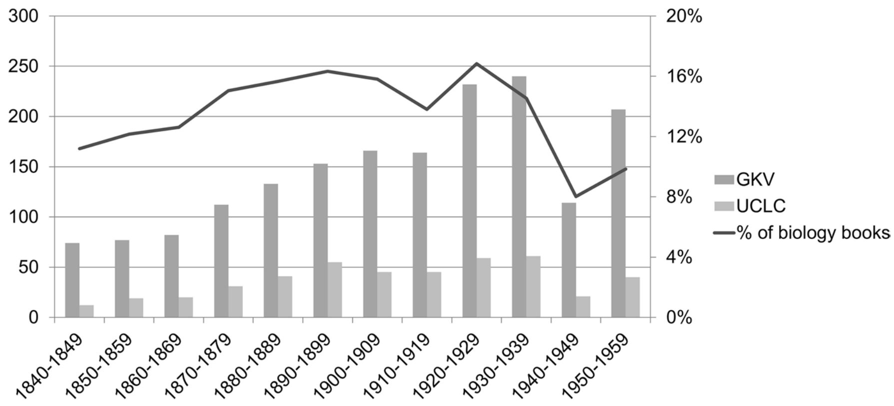

Fig. 1 The use of the concept of the organism between 1840 and 1959. Depicted is the number of monographs containing *organism*, *organisms*, *Organismus*, or *Organismen* in their titles. Entries are taken from two bibliographic databases: University of Cambridge Libraries Collection, UCLC (light grey bars) and German Union Catalogue, GVK (dark grey bars). Only biological books are considered. Multiple counting of single monographs is possible, as they may appear more than one time in each database. The black line shows the percentage of all "organism books" (in GVK and UCLC) compared with all biological books published per year (i.e., entries in both databases matching keyword or substance for "biology" or "Biologie")

generations). Other induced transgenerational effects were described by Kammerer (1907) in Vienna. In a series of experiments at the Vivarium in 1903 and 1912 which provoked a wide academic and public interest, he investigated environmentally-induced transgenerational effects in different salamander species (for example, *Salamandra atra* and *S. maculosa*) and the midwife toad (*Alytes obstetricans*). For example, in one of his contested but widely discussed studies, Kammerer described that when mothers and offspring in fire salamanders were prevented from accessing water, more completely developed larvae with lungs and legs were born after four generations.[4]

Besides these investigations, which suggested a high level of responsiveness and embeddedness of the biological individual in its environment, other experimental findings showed that the unit of the organism was able to delimit itself from (changes in) its environment and to maintain its developmental trajectory. This phenomenon—today described as the "developmental robustness" of the organism—was noted by the American embryologist Stockard (1921), who observed that embryos of many species can resist oxygen deprivation in some developmental stages without leading to embryonic malformations. Beginning in the 1890s, Hans Spemann and his colleagues also demonstrated organisms' capacity to compensate for changes in their environment or in themselves. In one of many transplantation experiments, Spemann and Schotté (1932) showed that if the non-determined

[4] On the contested story of Kammerer's experiments, see Koestler (1971), and on the question of whether the transgenerational parent-of-origin effects described by Kammerer were due to (what is known today as) epigenetic inheritance, see Vargas et al. (2016).

epidermis (prospective belly region) of a frog (*Bombina pachypus*) is transplanted to the future mouth region of a newt (*Triturus alpestris*), the newt develops mouth and teeth. Even though the teeth were similar to those of frogs, the receiving organism could maintain in large part its normal developmental pathway by integrating "building material" from a different species and a different ("presumptive") body part.

Findings like these were flanked by a growing number of experiments and ecological field studies that conveyed a deeper understanding of the complex relationships between organisms and how collectives (on a cellular and multicellular level) come into existence. For example, when Huxley (1912), inspired by a similar experiment by Henry Van Peters Wilson, dissociated cells in a sponge, he observed that, after some days, the separated cells reunited to form a fully functioning sponge, similar in every way to the one developed before (Gibson et al. 2013). Huxley concluded: "there seems to be a strange organizing power superior in kind to the powers of the cells themselves—an idea of the whole, informing the parts" (1912, p. 97). In such cellular collectives Huxley sees a "unity, an individual of a higher order than the cell" in which the "whole is greater than the sum of its parts" (Huxley 1912, p. 92). A similar observation was made by myrmecologist Wheeler (1911) when studying the coordinated social behaviors of ants and termites. He understood these organisms as being part of a higher-level, multi-species individual, suggesting the "ant-colony is a true organism" (Wheeler 1911, p. 310). What is more, such so-called "super-organisms" (Wheeler 1920) may contain not only functionally relevant non-living components, like mounds of the higher termites, but also multiple species that show symbiotic relations to one another, such as that between individual termites and their intestinal flora. Wheeler highlights that "[e]very organism manifests a strong predilection for seeking out other organisms and either assimilating them or cooperating with them to form a more comprehensive and efficient individual" (1911, p. 142; see Gibson et al. 2013, pp. 510–517, which discusses these cases). These studies shared the idea that through the agency and activities of particular parts (cells or organisms), a greater whole—and new individual—is formed, be it a multicellular organism or a colony. These newly found abilities of biological individuals—environmental sensitivity and (transgenerational) plasticity, robustness and regeneration, as well as cell–cell and organism–organism interaction and organismic activity and agency—led to an increasing interest in the concept of the organism (see Fig. 1).

The Rise of Early Twentieth-Century Organism-Centered Biology

In a series of papers on "The Concept of Organism" (1930–1931), Joseph Woodger complained about what he felt to be the still marginal interest of biologists in the unit of the organism: "In the past the concept of organism has not been employed by the majority of biologists …. In histories of biology in the dim future there will probably be a chapter entitled 'The Struggle for Existence of the Concept of Organism in the Early Twentieth Century,' which will relate how this concept came to be neglected …" (1930–1931, p. I:6). Given the newly-discovered multi-faceted ways in which organisms delimit themselves from the environment as robust individuals, integrate various environmental components in a plastic manner to maintain their existence, actively construct their intra- and extra-organismic contexts, and collectively form new kinds of individuals, an increasing number of biologists, especially in Great Britain and the German-speaking world, shared Woodger's worries about the unjustified neglect of the organism. They came to highlight the organism as the right level of organization from which most (if not all) processes in nature should be understood. This assumption was the starting point of a new kind of OCB. Central works of this movement discussing the concept of organism or biological individuality are provided in Table 1.

At least three different theoretical strands can be identified in this organism-centered movement: organicism, dialectical materialism, and (German) holistic biology, represented in the work of different biologists.[5]

Organicism	Ludwig von Bertalanffy Charles Manning Child Lawrence J. Henderson William Emerson Ritter Edward Stuart Russell Conrad Hal Waddington Paul Alfred Weiss Joseph Henry Woodger
Dialectical materialism	John Desmond Bernal John Burdon Sanderson Haldane Joseph Needham Marcel Prenant Julius Schaxel Boris Zavadovsky
Holistic biology	Friedrich Alverdes Bernhard Dürken Kurt Goldstein John Scott Haldane Adolf Meyer-Abich Jan C. Smuts Jakob von Uexküll Emil Ungerer William Morton Wheeler

[5] For studies of different aspects and members of organicism, see Hein (1972), Abir-Am (1987), Peterson (2011, 2016), and Nicholson and Gawne (2014, 2015). For dialectical materialism, see Allen (1980), Hopwood (1997), Reiß (2007), and Sheehan (2007). For holistic biology, see Amidon (2008), Sölch (2016), and Rieppel (2016). In contrast to the Anglophone tradition of holism (Smuts 1926; Lloyd Morgan 1926), German holistic biology, so-called "Ganzheitsbiologie," was closely linked to Nazi ideology (Rieppel 2016, pp. 187–242). As described above, this paper does not seek to directly contribute to this body of literature by offering more insight into individual members of this early twentieth century OCB (or their disciplinary or political backgrounds), but by clarifying conceptual debates and theoretical challenges shared across different strands of this movement.

Table 1 Central Works on the Concept of the Organism or Biological Individual, 1908–1945

Hans Driesch	*The Science and Philosophy of the Organism*	1908
William Morton Wheeler	"The Ant Colony as an Organism"	1911
Julius S. Huxley	*The Individual in the Animal Kingdom*	1912
Lawrence J. Henderson	*The Fitness of the Environment*	1913
Hans Driesch	*The Problem of Individuality*	1914
Charles Manning Child	*Individuality in Organisms*	1915
John Scott Haldane	*Organism and Environment as Illustrated by the Physiology of Breathing*	1917
Lawrence J. Henderson	*The Order of Nature*	1917
Julius Schaxel	*Fundamental Features of Theorizing in Biology*	1919
William Emerson Ritter	*The Unity of the Organism*	1919
Oscar Hertwig	*The State as Organism*	1922
Edward Stuart Russell	*The Study of Living Things*	1924
Alfred North Whitehead	*Science and the Modern World*	1925
Julius S. Huxley	"The Biological Basis of Individuality"	1926
Emil Ungerer	*The Regulations in Plants*	1926
Ludwig von Bertalanffy	*Critical Theory of Form Construction*	1928
Joseph Henry Woodger	*Biological Principles*	1929
Jakob J. von Uexküll	*Theoretical Biology*	1928
Ludwig von Bertalanffy	"Facts and Theories of Form Construction as a Path Towards the Problem of Life"	1930
Joseph Henry Woodger	"The 'Concept of Organism' and the Relation Between Embryology and Genetics. Part I-III"	1930–1931
Julius Schaxel	"The Biological Individual"	1931
Ludwig von Bertalanffy	*Theoretical Biology,* Vol. I	1932
Friedrich Alverdes	*The Holistic View in Biology*	1932
Ludwig von Bertalanffy	*Modern Theories of Development* (Woodger, trans.)	1933
Kurt Goldstein	*The Structure of the Organism*	1934
Karl Linsbauer	"Individual—System—Organism"	1934

Table 1 (continued)

Adolf Meyer-Abich	*Periods of Crisis and Turning Points in Biological Thought*	1935
Bernhard Dürken	*Developmental Biology and Wholeness*	1936
Joseph Needham	*Order and Life*	1936
Alfred Edwards Emerson	"Social Coordination and the Superorganism"	1939
Adolf Meyer-Abich	"Keynotes of Holism"	1940
Paul A. Weiss	"The Problem of Cell Individuality in Development"	1940
Conrad Hal Waddington	*Organisers & Genes*	1940
Ludwig von Bertalanffy	*Theoretical Biology,* Vol. II	1942
Ralph S. Lillie	*General Biology and Philosophy of Organism*	1945

All German titles have been translated into English. This table includes those biotheoretical and biophilosophical publications (monographs and papers) during the first decades of the twentieth century (until 1945) that both (1) treated the concept of organism and/or biological individual as a theoretically and ontologically central (if not the most central) concept in biology (including issues like the organism's criteria of individuation, its boundaries, diachronic identity, etc.), and (2) were widely (that is, internationally) discussed. For deeper similarities among (but also differences between) the authors listed, see below

These groups, however, should not be understood as homogenous or clear-cut. In addition, in a number of cases the theoretical viewpoints of authors cannot be attributed to a single group only (for example, when their views changed over time). Despite the heterogeneous character of this movement (see below), these three strands nonetheless shared the following three views:

"A third way"	Neither vitalism nor reductionist mechanicism is the right theoretical or methodological framework for biology.
Organism-centeredness	"Organism" is (one of) the most central theoretical concept(s) in biology.
Wholeness	Biology should study the organism as a whole; all relationships between biological entities (within organisms and between organisms and environment) are compositional (i.e. between parts and wholes).

"*A third way*": Driesch (1899, 1908) attempted to conceptually grasp the plastic and regenerative properties of developing organisms by invoking an *Entelechie*, a non-material influence or "individualizing force" that preserved the development of the whole organism.[6] This vitalism was an attempt to protect the autonomy of biological phenomena from physicochemical reduction, such as those defended in Wilhelm Roux's research framework of *Entwicklungsmechanik*. Most members of OCB shared the general critique of Driesch, but also criticized his idea that explaining the special character of the organism necessitates presupposing built-in "entelechial" forces. They were instead looking for a viewpoint between (or apart from) the two extremes of vitalism and mechanism (see Nicholson and Gawne 2015). For example, Austrian biologist Ludwig von Bertalanffy noted that the mechanism-vitalism issue had been discussed like a debate between "religious sects" with distinct and extreme "dogmas" (1932, p. 41). In a similar manner, German theoretical biologist Adolf Meyer-Abich argued that the two "completely depleted ideals of knowledge [*Erkenntnisideale*]" (1942, p. 205) had to be replaced by a new and better theoretical framework.[7] Theoretical biologist and embryologist Julius Schaxel criticized previous theoretical approaches as being so fascinated by the new "abundancy of material" that they forgot to develop a general conceptual framework that allowed for categorizing and analyzing empirical findings, rather than simply collecting them (1919, p. 4). This commonly-targeted new framework, which was given a number of different names (for example, "kritische Biologie" by Schaxel [1917]), should be grounded on the concepts of organism and wholeness.

Organism-centeredness: While this OCB acknowledged the special characteristics of organisms as features that legitimate the autonomy of biology (like vitalism), these organisms were understood to be subject to the same natural laws as physical systems. At the same time, however, OCB argued that organisms are wholes

[6] On the concept of *Entelechie* and its imprecise use by Driesch, see Freyhofer (1982).

[7] Unless otherwise noted, all translations from the original German are my own. Still further, botanist Linsbauer (1934) understands the distinction between vitalism and mechanicism as a pseudo problem that results from the incommensurability of two distinct conceptual frameworks for describing organisms (i.e. "organo-centered" and "physico-chemical" concepts). Both frameworks work on different levels of integration of complex systems with their own unique set of laws (see also Bertalanffy 1928).

that—due to metaphysical reasons (Meyer-Abich 1948) and/or epistemological reasons (Needham 1936)—cannot be simply reduced to their physical components. Nevertheless, the special unit of an organism can be understood in purely naturalistic terms by focusing on the systemic processes of organisms' parts (inside and outside of their bodies), such as self-organization and self-regulation. To understand these processes—the interrelatedness of the parts and their relation to the whole—this novel "third way" had to be rooted in a strengthened concept of biological individuality and/or organism.[8]

> [T]he living individual [is] the fundamental unity of biology… the individual is essentially a functional unity, whose activities are co-ordinated and directed towards the development, maintenance and reproduction of the form and modes of action typical of the species to which it belongs. (Russell 1930, p. 166)

In a similar way, Bertalanffy (1928) wrote that *Organismus* is a special way of thinking—a "proto concept" or *Urbegriff* (Bertalanffy 74; cited in Toepfer 2011, p. 810). A biology that is based on this proto concept has the potential for true autonomy, as all other attempts to ground biology are rooted in other disciplines: Darwinism in sociology, mechanism in physics, and vitalism in psychology (Bertalanffy 1932, p. 113). Others, like William Morton Wheeler, British developmental geneticist Conrad Hal Waddington, and theoretical biologist Joseph Henry Woodger, were deeply influenced by Whitehead's (1925) process metaphysics—a view he labeled "philosophy of organism."[9] By drawing on the work and concepts of Claude Bernard and even earlier French theorists, John Scott Haldane coined this newly envisioned biology "organicism" (1917, p. 3); William Emerson Ritter labeled it "organismalism" (1919, p. 1:28); Bertalanffy "organismische Biologie" (1932, p. 80); and Jena-based embryologist and theoretical biologist Julius Schaxel spoke of an "organismic basic conception" ("organismische Grundauffassung"; Schaxel 1919, p. 125) that biology should adopt.

Wholeness: According to these views, the wholeness of the organism and its indivisibility sets the methodological and explanatory standard for investigating biological phenomena. For example, the organism as a whole constitutes the background for investigating and explaining the causal roles of single genes and the robustness of developmental pathways (Waddington 1942) as well as its relationship to the environment (Haldane 1931). Ritter summarized this idea as follows:

[8] While in the history of biology there have been many definitions given for what biological individuals are, especially in order to identify them as physiological or evolutionary units (see Lidgard and Nyhart 2017; Baedke, forthcoming), many members of the OCB community used the concepts of biological individual, organism, and individual organism interchangeably, or they treated organisms as exemplars of biological individuality (see Woodger 1930–1931; Schaxel 1931). For example, the following quote, which emphasizes the role of the individual, is taken from a chapter in Russell (1930) titled "The Organismal Point of View."

[9] Whitehead's "philosophy of organism" represents a systemic view of the organism that emphasizes the complex interrelatedness of its developing parts with each other and the environment. On the influence of Whitehead's metaphysics on organicist Waddington, see Peterson (2011); on Wheeler, see Sölch (2016); and on Woodger, see Nicholson and Gawne (2014).

> The organism taken alive and whole is as essential to an explanation of its elements as its elements are to an explanation of the organism … all attempts to assign explanatory value to the elements in their relation to the whole organism, while at the same time denying either expressly or tacitly, similar values to the entire organism in its relations to the elements, must fail in large degree. (Ritter 1919, p. 1)

In a similar holistic manner, Bertalanffy wrote: "The organism is a system, in which the elements and processes are organized in a particular manner, and in which, in the end, every single part, every single event, depends on all other parts and all other events" (1932, p. 2).[10] Chemist Lawrence J. Henderson described the organism as "an autonomous unit in which every part is functionally related to every other and exists as the servant of the whole" (1917, p. 21). While the activities of the organism as a whole were considered to be "more" than the activities of the parts, this "more" was not understood to arise from mysterious vitalist forces (as described above), but simply from the complex relations between the parts (see, for example, Waddington 1940, pp. 142–146). Thus, one had to develop a systemic perspective that focused on the complex dynamics and dependencies of parts in order to understand (changes in) the properties of biological individuals.

While the members of OCB agreed on these three points, their positions differed in a number of ways. With respect to their holistic compositional viewpoint, organicists, such as Waddington (1940), usually showed no preference for whether the relationship between part and whole should be investigated as "bottom-up" or "top down." By contrast, a number of members in (the quite heterogeneous group of) holistic biology stressed the importance of investigating and conceptualizing living systems as top-down. For example, the developmental biologist Bernhard Dürken wrote: "It should not be said that the organism as a whole is built up of parts, but that the organism, which is characterized through a consistent wholeness, develops parts and then, subsequently, has parts" (1936, p. 17; see also Meyer-Abich 1935, p. 88). In other words, the whole is temporally before the parts (Dürken) or ontologically prior compared to the parts (Meyer-Abich). Thus, wholes always have to be investigated first (see also Ungerer 1965, pp. 80–82). These differences affected the role that the concept of organism played. While organicists in large part focused on compositional analyses of organisms and their parts, holistic biologists saw organisms as one—albeit important—part of many in a compositionally organized whole universe (see Uexküll 1928; Haldane 1931; Meyer-Abich 1948, p. 377).

In addition, the philosophical motivations varied among (but also within) the three different strands. Some organicist thinkers of the so-called "Theoretical Biology Club" (or, as it was originally called, "Biotheoretical Gathering"), like Woodger and Waddington, were deeply influenced by Whitehead's process philosophy (see Peterson 2011, 2016), while other holistic thinkers, like theoretical biologist Jakob von Uexküll, started from a study of Immanuel Kant's transcendental analysis and

[10] For other views in this OCB highlighting the importance of compositional relationships, see Woodger (1929), Dürken (1936), Needham (1937) and Meyer-Abich (1940).

his critique of teleology (Brentari 2015; see also Ungerer 1926; Haldane 1931). Yet another group, the dialectical materialists, started from readings of Schelling's and Hegel's Romantic philosophies of nature and, especially, from the work of Karl Marx and Friedrich Engels. Dialectical materialists argued that all processes in nature should be thought of as confrontations of antagonists leading to new and qualitatively different forms of order that are in need of their own conceptual framework. As Needham stated: "We have repeatedly seen that biological order is a form of order different from those found in physics, chemistry, or crystallography …. Translated into terms of Marxist philosophy, it is a new dialectical level" (1936, p. 45). Dialectical materialists, such as Schaxel (1931), zoologist and parasitologist Marcel Prenant (1938), crystallographer Bernal (1935), and embryologist Zavadovsky (1931), closely linked their left-wing political opinions and socio-economic worldviews with their experimental and theoretical work (Hopwood 1997; Sheehan 2007).[11] As a consequence, the views of some members of the OCB differed radically, like those between dialectical materialists and, for example, holists like Meyer-Abich and Uexküll, or organicist Bertalanffy, who, at least at some point in their careers and personal lives, endorsed nationalist and anti-communist feelings or had close ties with the Nazis (Pouvreau 2009; Brentari 2015).

Due to these different theoretical and political dimensions, today it is quite difficult to disentangle the three strands of this organism-centered movement unambiguously. In fact, even in the early twentieth century, the advocates of an OCB themselves seemed to be divided about where exactly to draw such boundaries and how to link philosophical frameworks with biological investigation. For example, Needham thought that organicism and dialectical materialism were "closely similar" (1936, p. 45). Somewhat more cautiously, his colleague Waddington acknowledged similarities between the two when, for example, it came to describing how levels of organization arise, but also issued a warning that philosophical theories such as dialectical materialism should not guide biological thought [as, for example, Needham (1937) had done in his theory of integrative levels]. Instead, philosophical reasoning should follow biological investigations (Waddington 1940, pp. 142–148).[12] However, such ambiguities should not hide the fact that all members of OBC not only

[11] For an overview of topics discussed among Soviet scientists who defended dialectical materialism, see Bukharin (1931). While agreeing with their European colleagues on the basic thesis on the dialectical relationship between levels of organization (and the claim of the complicity of science with capitalist exploitation), the debates among biologists in the early years of the Soviet Union until the mid-1930s (organized by the Timiriazev Institute for the Study and Propaganda of Natural Science from the Viewpoint of Dialectical Materialism) did not primarily concentrate on the concept of the organism. Instead, Soviet biologists focused more on issues such as the border between biological and social evolution, modes of inheritance (in particular Lamarckism), and (from the early 1930s onwards) agriculture; see Joravsky (1963). On later dialectical approaches in biology, see Levins and Lewontin (1985); see also Graham (1987). On the importance of dialectical materialism for recent developments in evolutionary theory, see Svensson (2018); see also "Losing, Finding, and Losing the Organism" below.

[12] Stronger disagreement on how to interpret the relations between different strands within OCB can be found after the Second World War, as, for example, dialectical materialists retrospectively treated quite similar holistic views, like that of Meyer-Abich, as nothing but a continuation of Driesch's vitalism (see, Sershantow 1978). Even the holist Ungerer (1965) retrospectively discredited other holistic approaches as flawed.

shared basic theoretical assumptions (see above), but formed one lively international research community. They collaborated with one another (Woodger with Bertalanffy [Bertalanffy 1933]); translated each other's work (Meyer-Abich translated J. S. Haldane [1931]); made research visits (members of the Theoretical Biology Club, like Woodger or Dorothy M. Wrinch, visited the Biologische Versuchsanstalt in Vienna) and exchanged letters with one another (Bertalanffy with Ritter and Needham, or Needham with Meyer-Abich); and edited each other works (for example, the monographs of Weiss, Bertalanffy, Ungerer, Alverdes, Goldstein, Uexküll, and Meyer-Abich were published by Schaxel in his comprehensive book series *Abhandlungen zur theoretischen Biologie* [Contributions to Theoretical Biology, 31 monographs, 1919–1931]).[13] Most importantly, advocates of organicism, dialectical materialism, and holistic biology read and discussed each other's work in a lively and productive manner.

In many cases, members of OCB actively sought interactions after finding surprising similarities between their views and that of other theoretical strands of OCB. For example, when meeting Russian biologists in London in 1931, Needham was highly surprised by the striking similarities between British organicism and dialectical materialism, as obviously biologists "in other countries" had come to "similar conclusions" (1937). Even earlier, in 1928, Needham, astonished by their similar theoretical viewpoints, wrote to German holistic biologist Meyer-Abich, who immediately replied, saying: "For a researcher few things are as exhilarating as the fact to find a scholar in a different country who is working on the same scientific aims and who, completely independently, comes to the same results. Without any doubt this is a strong proof of the correctness of the pathway we follow."[14]

The joint reaction of the OCB community on the newly-uncovered dimensions of biological individuals—the active and plastic integration of and interaction with the environment—was to conceptualize them neither in a mechanistic nor a vitalistic framework. Instead, they decided to develop a new theoretical framework for biology that was based on the unit of the organism. However, as we will see, this third way was rocky, as theoretical integration of the newly observed phenomena turned out to be difficult and led to ambiguities.

Anti-Individualistic Challenges for Organism-Centered Biology

The new OCB understood the biological individual—the organism—as (one of) the most fundamental units in biological theorizing. Nature's mysteries were thought to be revealed and explained by the perspective of the organism's development, actions, interactions, and evolution. At the same time, however, as a reaction to the new data available from fields like genetics, cytology, and embryology, the organism-centered movement also highlighted the organism as interwoven with its environment and

[13] For other relationships between the members of OCB, see Nicholson and Gawne (2015, pp. 368–373).

[14] Letter from Meyer-Abich, 25 November 1928, Joseph Needham Papers and Correspondence, GB 12 MS.Needham, M 60, Cambridge University Library, Cambridge, England.

with other organisms. Accounting for these features created several problems for conceptualizing the organism as an identifiable unit with unambiguous properties and activities. These challenges are mirrored in at least three anti-individualistic theoretical positions defended in OCB. These are: (1) Organisms are reciprocally and inextricably linked with their environments, (2) organisms and their environments are units that share the same (or very similar) properties, and (3) organisms have no discrete and continuous boundaries with one another. Let us describe these theses in some detail.

(1) *The organism is inextricably interwoven with the environment.* As described above, various members of OCB conceived of organisms as (more or less) autonomous and active units. However, this view of the organism and its boundaries to the environment was contested within the organism-focused community. For example, by drawing on the coordinated character of the organism-environment relationship, John Scott Haldane emphasized that "the relation between organism and environment is no mere mechanical relation in which we can separate the influences of organism and environment—of 'nature' and 'nurture'.… In biological interpretation we can never separate organism from environment" (1935, p. 31; see also Haldane 1931). In his book *Order and Life,* Joseph Needham restated Haldane's point: "We cannot separate organic from environmental structure, for no sharp line can be drawn between organism and environment" (1936, p. 10). Such statements are somewhat surprising, as they directly challenged the targeted organism-centeredness of biological theory. They emerged from the insight that the organism is not only a starting point of causal arrows in nature but is reciprocally interwoven with its surroundings. In fact, this idea was common in OCB. For example, as early as 1884 Haldane noted: "The organism is thus no more determined by the surrounding than it at the same time determines them. The two stand to one another, not in the relation of cause and effect, but in that of *reciprocity*" (pp. 32–33; emphasis added). Also Uexküll's position included the element of reciprocity, through which the environment forms an "*inextricable whole* with the animal itself." Thus, "[o]ne cannot picture to oneself an animal isolated from its environment …" (1909, p. 196; cited in Toepfer 2011, p. 801). But if we cannot do so, how can we establish biological theory on the concept of organism?

This problem arises from an expansion of the traditional reciprocal structure of organisms on higher levels of organization. In the history of biological reasoning, at least since Kant (1902), it has become common to describe reciprocity as a form of organization distinctive of organisms. Through the reciprocal interaction of its parts, the organism is created and maintained as a whole. This tradition has widely influenced our understanding of the organism's boundaries to the environment. In contrast, as many advocates of organism-centeredness have argued, we should also use this traditional conceptual framework of reciprocity to understand higher levels of organization, like organism-environment relationships, which were traditionally understood as unidirectional. In other words, both the individual organism's relations to its internal parts as well as its relations to the external environment were understood to be of the same kind. As a consequence, it became more difficult to distinguish between the two.

(2) *The organism and its environment are units that share the same (or very similar) properties*. This second tendency in early twentieth century OCB was directly related to (1). It emerged from older discussions of biological individuality (among others). For example, as Haeckel (1866) had already stressed, individuality can appear on various levels of organization, including cells in multicellular organisms or colonies of insects.[15] In this hierarchical view individuals are composed of smaller individuals, which themselves are made up of even smaller ones, etc. Each individual contributes to the process of forming an object at a higher level (Woodger 1929, p. 316; Linsbauer 1934, p. 67). This view was common, especially in holistic biology (Rieppel 2016, pp. 187–242). It developed its most radical form in emergent evolutionism (Smuts 1926; Lloyd Morgan 1926) and in Whitehead's (1925) process philosophy. Advocates of these positions defended a wider understanding of the concept of the organism. The whole universe was understood to be made up of "organisms"—organized units whose components are related to one another and to the whole universe at a certain point in time. According to this view, "[b]iology is the study of larger organisms; whereas physics is the study of the smaller organisms" (Whitehead 1925, p. 103; see also Needham 1928, p. 88).

This somewhat inflationary use of the concept of the organism was accompanied by a strong trend to parallel properties of nature and even the universe as a whole with properties of organisms (or their parts). Therefore, various analogies and metaphors were introduced. Wheeler (1928, p. 230) suggested that the insect colony was a "super-organism" (see also Wheeler 1911), whose parts show the same division of labor as the parts of organisms. Plant ecologist Frederic Edward Clements noted that "organic development is essentially alike for the individual and the [plant] community" (1916, p. 6; see also Gibson et al. 2013, p. 516). Like an organism, the plant community arises, grows, matures, and dies. In addition, Oscar Hertwig (1922) considered the state to be an organism. Henderson even described the whole environment by an analogy to the organism. He argued that an adapted organism inhabits an adapted environment that has (especially physico-chemical) properties that support the development of life: "Darwinian fitness is a perfectly reciprocal relationship. In the world of modern science a fit organism inhabits a *fit environment*" (1913, p. 132; emphasis added). Even more radical, Meyer-Abich (1948, p. 377) described reality as a whole as a huge universal organism. In the context of such common metaphors and analogies between the organism and extraorganismic entities, it became more difficult for OCB to specify what organisms actually are and how they differ from one another.

(3) *Organisms have no discrete and continuous boundaries to one another*. Some traditional definitions of biological individuals, such as morphological or

[15] Haeckel distinguished between physiological (self-maintaining) and morphological individuals, which can be found on different levels of organization. For example, he identified six different morphological individuals ("Morphons"): cells, organs, so-called "Antimere" (for example, homotypic parts of an animal), "Metamere" (for example, body segments), "Personen" (for example, higher organisms), and colonies (see Haeckel 1866, p. I:266). While many advocates of OCB adopted similar multi-level views of biological individuality, they often highlighted, not the differences between individuals (including organisms) located on different levels, but their similarities, as described below.

genetic definitions, conceived of organisms as discrete and/or homogenous units with consistent boundaries. However, this idea of individuals as concrete entities in time and space was increasingly challenged by observations and experiments in which biological individuals interact or even integrate with one another to form and maintain themselves. Examples are Wheeler's cooperative ants, the behavior of dissociated cells in sponges (Huxley 1912), or symbioses, as between a fungus and an alga in lichens that form a new "amalgamated unit" (Linsbauer 1934, p. 73; see also Schaxel 1931, p. 489). Such findings made the relationship between different individuals problematic for members of the organism-centered movement:

> If … we believe that in the course of evolution individuals of a higher grade [for example, an ant community] have developed by unification of an aggregate of individuals of a lower grade … we should expect to find cases in which it was impossible to say whether the old individuality of the aggregated parts or that of the system as a whole was the more fundamental. (Huxley 1926, pp. 309–310)

Given such far-reaching problems, and inspired by Whitehead's (1925) idea that all entities have global (rather than intrinsic) properties and that the nature of these entities is essentially processual and permanently changing, some authors, like Woodger (1929), argued that one should avoid any criterion that assumes individuals to be static things that show discreteness or concreteness. For example, to Woodger the cell was "not a concrete entity" (1929, p. 296). Others, like Wheeler, were even willing to abandon the project of establishing criteria of the unit "organism" completely: "It is obvious that no adequate definition can be given, because the organism is neither a thing nor a concept, but a continual flux or process, and hence forever changing and never complete" (1911, p. 310; see also Sölch 2016, p. 497). However, if no "adequate definition" could be given, how, at all, could OCB specify the relationship between the organism and its environment—(1) and (2), above—or, as a special case of this, the relationships between different organisms (3)?

A paper that nicely uncovers these three conceptual tensions in early-twentieth-century OCB is Schaxel's 1931 paper "Das biologische Individuum." He described various dimensions in which the organism is dissolved in biology: "historically, genetically, with respect to its form, and—in the species that have progressed most in natural history—socially. It is made up of parts and is itself only a part in a bigger context. We always see it *relative* and *never absolute*" (Schaxel 1931, p. 492; emphasis added). To exemplify the "dissolution of form" as a boundary between organisms, he conducted a number of parabiosis experiments in which he linked vessels and tissues of two axolotls in early development. He thus created a cardiovascular system with one heart that connected two morphological individuals (see Fig. 2). To his surprise, this new unit stayed alive for 7 years. From this result, Schaxel concluded that morphological boundaries convey no insight for identifying biological individuals and the boundaries between them. In addition, the individual is dissolved into its larger environment, as in supra-individual social communities characterized through labor division and symbiosis or biocenosis. Inspired by a socialist political agenda, he wrote: "When the masses build such a community, a new life form is built. Quantity

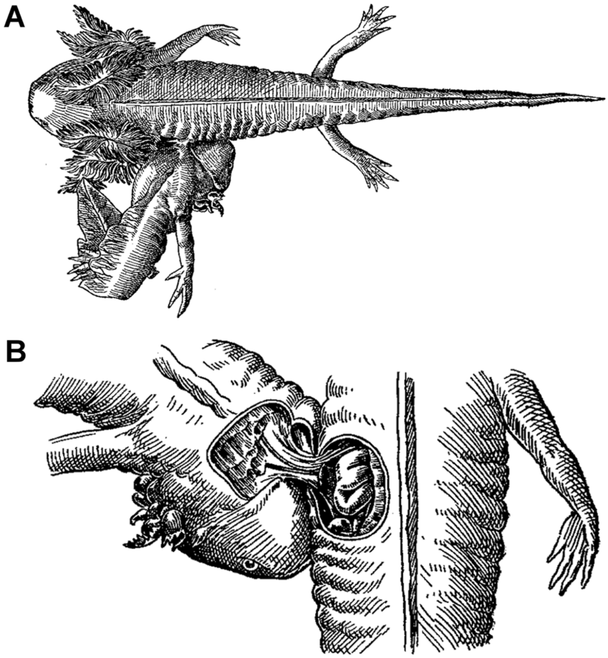

Fig. 2 Axolotl parabiosis experiment by Schaxel. **A** Axolotl 172 days after creation of parabiosis. **B** Parabiosis died after 7 years. Adhesion area opened. Left animal has no circulatory system. Gill area (left animal) and splenic (right animal) are connected through vessels (**A** Schaxel 1931, p. 486; **B** Schaxel 1931, p. 487)

is transformed into quality. In social progression it comes to the *dissolution of the individual in the collective*" (Schaxel 1931, p. 490; emphasis added).

According to such prominent views in OCB, the organism loses its "Gestalt" and clear boundaries to one another and to its larger environment. The individual is inextricably interwoven and dissolved in a multi-faced environment, ranging from symbiotic to social relationships. As a consequence, there simply is no clear unit to which we can attribute properties like autonomy or agency. Paradoxically, this amounts to a seemingly anti-individualistic biology, which, ironically, understands itself to be organism-centered.

One may, however, argue that one must distinguish between ontological and methodological (anti)individualism. That means, in principle, that one does not need to eliminate the organism as an object of interest just because one believes that there are no ways to segregate individuals from their contexts. This could be legitimized through an assumed high heuristic value of the organism concept for reasoning about the target system. Unfortunately, this view is limited. Given that one takes a realist stance, it becomes quite confusing to understand how, in fact, the target system is supposed to look, especially if it is not a separable and discrete ontological unit with intrinsic properties but, at the same time, shows characteristics that can be investigated best as such a discrete unit. This problem is enhanced by the claim, common in OCB, that organisms are not only a node or reading frame in a network, but the causally most efficacious unit in nature—a starting point of various biological processes, ranging from molecular to ecological and evolutionary ones.

In addition, it is important to highlight that the anti-individualist tendencies in OCB did not simply arise from the idea of considering more seriously the context-dependency of the organism. Instead, some members of OCB argued that the organism and its environment are so deeply interwoven (1), share so many or substantial properties with one another (2), and/or have boundaries that can hardly be identified or cannot be traced at all (for example, due to process-ontological or ideological assumptions) (3), that it makes little sense to single out any of the two units and/or to separate them in a dichotomous manner. As a consequence, claims arose for no longer distinguishing, for example, individuals from collectives and nature from nurture. Unfortunately, these positions were in stark contrast to the common aim that biological theory should rest on the identifiable unit of the individual organism. Against this background, the paradox of anti-individualism was a crucial ontological and theoretical challenge for early-twentieth-century OCB. To solve this problem, members of this theoretical movement were in desperate need of an integrative and unifying concept that was able to rescue the biological unit of the organism and, thus, their organism-centered framework. This unifying concept was "life."

The Unifying Concept of Life

Life is often considered a concept that is not very precise. When life begins, when it ends, and which entities are alive are issues still debated today. However, for OCB the concept of life played a crucial theoretical role. Many defenders of organismic biology seemed to realize that the concept of individuality or organism alone cannot found an organism-centered framework. Thus, they turned to the concept of life to specify in greater detail the boundaries of organisms. In other words, they tried to grasp the unit of organism better by characterizing what it means for an organism to be alive.[16] As Schaxel put it: "Only in the organism life exists" (1919, p. 143). The basic idea was to understand why the organism shows certain properties (such as plastic or robust integration of environmental cues as well as interaction with and incorporation of other organisms) by characterizing it as a life form.[17]

Since the late nineteenth century, a number of authors have characterized the biological individual as a unit of life (see, for example, Hertwig 1906, p. 371). In early-twentieth-century OCB at least three different definitions of life can be distinguished: (1) a functionalist view of life, (2) a metabolic view of life, and (3) a biochemical and physical view of life.[18] Let us briefly describe these views:

[16] Please note that although the difference between "organism" and "living organism" seems to be minor and negligible, moving from one to the other is an important conceptual step, as we will see below.

[17] While the German-speaking advocates of OCB were widely using the term "Lebensform." the English-speaking ones rarely used the term "life form." Rather, they discussed the concept of life in general or what it means to be alive (i.e. a "living organism").

[18] Each of these definitions should not be understood as a necessary and sufficient condition for the organism-centered movement to specify the unit of organism as a life form. In fact, in many cases more than one definition was adopted.

(1) *Functionalist view of life*: Most members of OCB highlighted the fact that in order to understand why the organism is alive, one should focus on its functional organization rather than its matter.[19] For example, Bertalanffy stated: "There is no 'living substance,' because the characteristic of life is the organization, the order, the orderliness (Uexküll), or the framework. The distinctiveness of life is not based on a chemical mystery, but on organization" (1928, pp. 68–68). In a similar manner, Schaxel said: "All life is organized, has organization […] There is no living substance, no living processes as such, but only as a means and expression of organisms" (1919, p. 143). Biochemist Frederick Gowland Hopkins, who was Needham's mentor, highlights that life is "a property [for example] of the cell as a whole, because it depends upon the organization of processes" (1913, p. 715). Accordingly, an organized individual is a functional unit in which the parts through their interaction collectively keep the unit alive.

While some authors, like Bertalanffy, argued that organization could be described by invoking laws of nature, others, like Waddington, were more skeptical. Waddington admitted that organization is a more fundamental concept than organism, but he considered it to be "not truly a part of science" (1940, p. 143). It has heuristic value as "a philosophical idea" or scheme "into [which] all phenomena can be fitted." However, merely saying "that a specific entity is organized does not attribute to it any specific properties" (Waddington 1940, p. 146). This is certainly true. While a focus on organization denies that morphological definitions and essentialist intuitions of individuality are helpful for characterizing life forms, it has to clarify how the organization of interconnected parts actually keeps the whole unit alive. The solution is to understand organization as a whole that endures through self-regulation.

(2) *Metabolic view of life*: According to OCB, in order to understand what makes organisms alive, one should not only shift away from matter and towards organization, but also towards activities (see Nicholson 2018). Thus, the focus lay on all regulatory activities—eating, drinking, breathing, assimilating, etc.—that allow organisms to preserve themselves over time. For example, animal psychologist Friedrich Alverdes called this ability the physiological "Auswahlvermögen" (selective potential) of organisms, which ensures that the "organism takes the suitable amount of oxygen from the breathing air; the plant extracts from its environment nutrients in a particular dosage; [and] in the gut of animals digestible and indigestible things are separated from one another" (1932, p. 111). In other words, living organisms are open systems with the ability of self-organization through metabolic procedures. This allows them to keep a dynamic stability and to separate themselves from their environment (see also Hopkins 1913; Haldane 1917; Woodger 1929; Bertalanffy 1932, 1942). In other words, the "metabolism of life [in organisms] is a sub-process of the metabolism of the earth" (Schaxel 1931, p. 487).

In one of his later publications, botanist Ungerer (1965) nicely expressed the relationship between the unit of the organism and the—even more

[19] Note that in early-twentieth-century OCB "organization" was sometimes used not only to describe organic life, but also inorganic objects, such as crystals (see, for example, Woodger 1929, p. 292).

important—self-preserving unit of life. He stated that while it is important to consider the organism as a whole, it is even more important to realize that “the life process as a whole is preserved in the form of organisms and that the single occurrences and forms of life are defined through their relation to the preservation of this overall life process” (Ungerer 1965, pp. 70–71). Thus, the organism (pre)serves life. By doing so it comes to be a life form.

(3) *Biochemical and physical view of life*: An additional step to specify the unit of the organism and its boundaries was to analyze the chemical processes and physical components that partake in the self-regulatory patterns of living organisms described, for example, by Ungerer. As J. B. S. Haldane put it: “Life is a pattern of chemical processes” (1947, p. 56). Against this background, some members of OCB argued that the dynamic stability of living organisms—their “homeostasis”—can be described by natural laws: “It is crucial to understand life forms as unitary systems” and to “find *the physico-chemical laws* that determine organic events as a whole” (Bertalanffy 1930, p. 387; emphasis added). These laws should describe the homeostatic steady state—the “thermodynamic niche”—in which the open living system maintains its order:

> The living organism has as it were a certain niche in its physico-chemical surroundings, and to that it will always return provided that the disturbing influence has not been so great as to throw it out of gear altogether. Its normal hydrogen ion concentration, its normal osmotic pressure, its normal concentration of glucose or salts, its normal physiological constants, these it will always tend to preserve unchanged. (Needham 1928, p. 85)

In other words, living organisms have actively to maintain their dynamic stability and internal order as open systems far from equilibrium (see also Schrödinger 1944). This view highlighted the fact that the emergence and maintenance of life forms is (not determined but) constrained by the laws of physics, especially those of non-equilibrium thermodynamics. Organisms have to obey these laws actively in order to stay alive in a state far from equilibrium.

According to these three views of life (1–3), which were widely discussed in OCB, the living organism can be characterized as a functionally, metabolically, and thermodynamically organized unit. From this definition it directly follows that the organism as a life form is a unit of activity. As an open system with “equifinality” (Bertalanffy 1942, p. 37), it is driven towards activity and functioning. All its activities are directed towards this goal. The organism cannot do otherwise. If it refuses, it dies. This teleological, but non-vitalist, idea was ubiquitous in OCB:

> the concept of organism is the form of expression for the *finalist 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, p. 74; emphasis added)

> If we look at living things quite simply and objectively we cannot but be struck by one feature of their *activities*, … this basic element of *directive striving*,

> usually unconscious and blind, only rarely emerging into consciousness to become intelligently purposive. (Russell 1950, p. 108; emphasis added).[20]

> In my action I, myself, am life. (Leben bin ich selbst in meinem Handel.) (Schaxel 1919, p. 139).[21]

Many of these views were fueled by neo-Kantian or Aristotelian traditions in OCB that understood the organism as a unit with a clear "telos" in development and evolution (see also Haldane 1931). Besides the above authors, for example, psychologist Goldstein (1934) thought that the organism is characterized through a fundamental "drive" to actualize its own capacities. For Uexküll (1909), the way each organism perceives its environment leads to individual and spontaneous self-movement in this very environment. In a similar manner, Whitehead (1925, pp. 109–110) highlighted the various ways in which organisms as agents shape their environment. According to these teleological and constructionist views, the organism is a clearly identifiable unit that purposefully molds itself and its environment. Meyer-Abich called these "active environment-related" units "subjects" (1948, p. 39).

Most importantly, this clarification of the organism as an active, living "subject" makes the challenging phenomena of plasticity, robustness, and (symbiotic and/or collective forms of) interaction between individuals (see above) integrable into an organism-centered theory of biology. First, active, living organisms need to regulate their material setup permanently to maintain their internal organization. This "self-modification" is made possible through procedures such as plasticity and robustness. Second, they need to regulate external matter input in a particular manner to maintain their order. This means that they have to interact actively with (or even integrate) other life forms and shape their environment individually or collectively. For example, Bertalanffy stated that a "living organism … remains or establishes its state, by means of *constant change* of those substances and energies that build up the system as well as during external perturbations" (Bertalanffy 1932, p. 86; emphasis added). Thus, again, the organism is driven to live, actively. This is a truly organism-centered view that allows understanding developmental and organismic activity as processes of life.

In addition, grounding biological theory on the unit of the living individual allowed members of OCB to evaluate the usefulness of particular methodologies. For instance, soon after the First World War, novel tissue culture techniques were developed that allowed growth and, as some have even argued, "permanent life" (Eberling 1913) of cells outside the organisms. At first, this result seemed to speak in favor of mechanistic and reductionist views, as each part (i.e., a single cell) did not seem to need the whole organism to exist and grow. According to organism-focused biologists, however, this reductionist approach was limited in its understanding of how organisms work: "An organism is something which the scientific method cannot deal with; it is a hard, round, smooth nut, which experimental analysis can neither

[20] Russell (1924, p. 61) also argued that the organism should be understood as "clay modeling itself.".

[21] Note that Schaxel's view on the concept of life also included criticism of the attempts of vitalism and life-philosophy (for example, by Driesch and Bergson) to describe the teleological characteristics of life in idealist ways and/or by means of personal experiences (see Hopwood 1997, pp. 375–380).

crack nor lever open any point. As soon as a hole is made in it, it explodes like a Prince Rupert drop and vanishes away" (Needham 1929, p. 82). What vanishes away in this case is life. Most members of OCB would have agreed that we can learn something from cutting organisms into pieces, but we never learn anything from cutting life into pieces. Only the living individual as a whole is a fruitful methodological starting point and conveys a deeper understanding. Not considering this rule has a serious consequence, as the history of tissue culture shows. By the beginning of the Second World War, "Tissue Culture lay becalmed in the doldrums for a time" (Willmer 1965, p. 8) due to its one-sided reductionist methodology. It turned out that simply placing a group of cells in serum, plasma, embryo juice, or another "natural" medium to simulate an organismic context was not sufficient for learning more about cell and tissue behavior.

As we have seen, OCB in the early twentieth century did not, in fact, try to build biological theory on the unit of the organism, but, more specifically, on that of life or the living organism: "Should biology be mounted from scratch by means of the organismic approach, … the laws of *autonomy of life* have to be clarified" (Schaxel 1919, p. 160; emphasis added). Only through its specific actions of living—continuous and goal-directed self- and environment-reorganization—can the unit of organism be characterized with sufficient consistency to separate itself from other individuals as well as the environment. In other words, the "achievements of autonomous life prove to be unified, whole, and individualized" (Schaxel 1919, p. 142). Thus, for this OCB, the concept of organism played a double role (see also Haldane 1931, p. 12). First, the organism exemplifies characteristics of life (ready to be investigated). "If a hypothetico-deductive system is possible in biology, the concept of organism will have to be its highest concept, because the *characteristic being of life* lies in the [organism's] organization of substances and processes" (Bertalanffy 1932, p. 86; emphasis added). Second, the organism is unified by these characteristics as a living whole. It is a distinctive active and constructive unit, a starting point of various causal processes in nature, ranging from developmental to evolutionary processes.

Losing, Finding, and Losing the Organism

This golden era of the organism lasted only a relatively short period of time. In the course of the 1940s and 1950s, it came to an abrupt halt. This was due to various reasons. Many older members of OCB had died (J. S. Haldane in 1936; Wheeler in 1937; Henderson in 1942; Schaxel in 1943; Ritter, Dürken, and Uexküll in 1944; Alverdes in 1952), while others turned their interest to new topics—Woodger to logic, Needham to the history of China, Bertalanffy to systems rather than organisms (see Nicholson and Gawe 2015), or to politics and/or popular science writing (Schaxel and Bernal). Yet others simply left the OCB community (J. B. S. Haldane went to India in 1957 as a reaction to the Suez crisis).[22] For many of the

[22] On changes in J. B. S. Haldane's theoretical positions in his early career, as well as his view on dialectical materialism, see Sarkar (1992).

German-speaking advocates of holistic ideas, the end of the Second World War was a *caesura,* a break with the past. Among those few scientists who continued defending holistic and organism-centered views of biology, Meyer-Abich (1948, 1956) was the most active. When Schaxel's book series ended in 1931, Meyer-Abich tried to take over (see Amidon 2008). From 1934 to 1947 he published the book series *Bios: Abhandlungen zur theoretischen Biologie und ihrer Geschichte, sowie zur Philosophie der organischen Naturwissenschaften* (Bios: Contributions to Theoretical Biology and its History, as well as to the Philosophy of the Organic Natural Sciences) in Leipzig (Laubichler 2001), and, after 1935, he co-edited the journal *Acta Biotheoretica* in Leiden (Reydon et al. 2005). Both worked as platforms for book and paper publications of members of OCB (for example, Uexküll, Ungerer, Alverdes). However, these efforts could not keep the OCB community alive. Nor could, for example, Waddington's later writings (Waddington 1957).[23] In the 1940s and 1950s the (relative) number of monographs discussing organisms significantly dropped (see Fig. 1).

Another reason for the decreasing interest in the concept of organism was the rise of molecular biology and the population genetic framework of the Modern Synthesis (see Nicholson 2014; Peterson 2016). While the former highlighted a reductionist research program that abstracted from the context of the whole organism, the latter focused on the transmission of genes and its effect on populations rather than on the developing organism (which was often held to be nothing but a product of genetic programs). As a consequence, the organism (and organismic individuality) was no longer understood as a major ontological and theoretical challenge that had to be addressed by biological theory, as in earlier OCB. Looking back at this development, Brian Goodwin, a former student of Waddington, noted:

> Organisms have *disappeared as fundamental entities*, as basic unities, from contemporary biology because they have no real status as *centres of causal agency*. Organisms are now considered to be generated by the genes they contain. … Thus organisms are arbitrary aggregates of characters, generated by genes, which collectively pass the survival test in a particular environment. … there is *no causally efficacious unit* that transcends the properties of the interacting parts. This is the sense in which organisms have disappeared from biology. (Goodwin 1999, p. 230; emphasis added)

This situation, however, has changed radically in recent years due to new insights into the very same phenomena that triggered the rise of OCB in the early twentieth century. Again, this includes studies on the environmental responsiveness and (transgenerational) plasticity of organisms, the various activities and processes that underlie their organizational robustness, as well the numerous ways in which organisms actively shape and interact with their environment (including other organisms). Biologists in fields like epigenetics, evolutionary developmental biology (evo-devo),

[23] In addition, after Schrödinger (1944), the concept of life (but not the question about origin of life) was discussed less in biology, and more in fields such as (non-equilibrium) thermodynamics or complexity sciences (however, see Bertalanffy 1952).

and niche construction theory now seriously investigate these phenomena. However, they are generally not aware of the earlier theoretical debates these phenomena triggered. Epigenetics studies (among other things) the environmental plasticity and heritability of changes in regulatory non-DNA factors, including disease etiology and sex-linked inheritance patterns, and, more generally, the role of non-genetic inheritance in evolution (Jablonka and Lamb 2005; Baedke 2018). Like epigenetics, evo-devo emphasizes the neglected role of development in the theory of evolution. It focuses on the processes through which organizational patterns arise and persist during onto- and phylogenesis (Minelli and Fusco 2008). In addition, niche construction theory seeks to understand the self-perpetuating and reciprocal effects of organisms that construct their own niche (and/or that of other species) during development and thus bias natural selection (Laland et al. 2016).

This reoccurring interest in the plasticity and agency of developing organisms has triggered calls for reworking the conceptual framework of evolutionary theory. A novel, so-called "Extended Evolutionary Synthesis" (EES) is currently being developed (Pigliucci and Müller 2010), at the heart of which lies the concept of the organism (Bateson 2005; Laland et al. 2014, 2015; Sultan 2015). For example, Kevin Laland and his colleagues focus on "organismal causes" of evolution (2015, p. 2), "the ability of an organism to shape its own developmental trajectory" (6), and how "organisms modify environmental states" (4). In other words, the EES is "characterized by the central role of the organism in the evolutionary process" (8).

This new kind of OCB—a new "Organism-centred perspective" (Laland et al. 2015, p. 2)—arises as an opposite standpoint against theoretical positions that are different from those in the early twentieth century. For example, it opposes not reductionist biochemistry and cell theory or vitalism but gene-centrism. Thus, the history of early-twentieth-century OCB is decoupled to a certain degree from today's OCB. But nonetheless, the new OCB can learn something from older theoretical debates because similar things are being discussed, such as the structure of organism-based explanation and ontological and methodological challenges to theoretically (re)integrating the concept of organism into (evolutionary) biology (see, for example, Pepper and Herron 2008; Huneman 2010; Nicholson 2014; Walsh 2015; Baedke, forthcoming). Thus, the future of the organism in biological theory seems to be promising. However, this appraisal is elusive. The EES is more and more challenged by anti-individualistic tendencies that provide an indication of unsolved conceptual problems. In fact, these fundamental problems are very similar to the ones the earlier version of OCB faced a century earlier (as previously discussed). Again, the organism seems to be (1) inextricably interwoven with and (2) indistinguishable from its environment. In addition, (3) the boundaries between organisms become blurred. Let us conclude by taking a brief look at these recent trends.

(1–2) It seems that the EES supports a switch from an externalist to a constructionist perspective, in which the organism actively molds its internal states and external environment (see Laland et al. 2014, 2015). However, this idea about organisms' autonomy and distinctness from the environment is not as clear cut as it seems. Thanks to the new emphasis on organisms' sensitivity to environmental change, views of epigenetic or environmental determinism are also emerging (Waggoner and Uller 2015). Based on findings of environmentally-induced and long-lasting (heritable) epigenetic modifications, as well as seemingly heteronomous organisms, the properties of organisms face the threat of being distributed across their complex environments. Against this background, Niewöhner (2011) argues that a new concept of the human body is currently emerging, the so-called "embedded body." According to this concept, the human individual can no longer be grasped in isolation from its material and social environment. Instead, the formerly external environment—the milieu—is now literally penetrating humans' skin and the individual is no longer "skin-bound" (see Baedke 2017).

This idea of environmental interwovenness of organisms is even further enhanced by niche construction theory, which shows how the active organism and the environment permanently construct each other. A common example is a beaver that shapes its ecosystem, which then in turn acts on the beaver and its offspring through novel selection pressures. In accordance with claims common in early-twentieth-century OCB, members of EES (see especially Laland et al. 2014, 2015) argue that biologists should accept the idea of causal reciprocity between organism and environment as the most fundamental principle in biological theory. As a consequence, as in the earlier OCB, unambiguous and consistent boundaries between organisms and higher levels, such as ecosystems, disappear, as reciprocally organized organisms reciprocally interact with their environments. In other words, organisms and environments become increasingly similar to one another as organisms blend with their surroundings as "extended organisms" (Turner 2000). Some authors actually embrace this development. Similar to Haldane (1931, 1935) and Needham (1936, p. 10), for example, Griffiths and Gray claim that "[t]here is *no distinction* between organism and environment" (2001, p. 207; emphasis added). Moreover, Laland and Brown (2018) argue that it is not possible to distinguish the "biological" from the "environmental/cultural" (see also Lewens 2017).

(3) Finding the boundaries between organisms also becomes more difficult in the new OCB. Novel high-throughput technologies revealed that multicellular organisms have multiple persistent symbionts that are closely linked to their host. In such "holobionts" (i.e., multicellular and multi-species eukaryotes), many persistent symbionts are found to be crucial to the organism's normal development, immune system, and evolution. Through these findings, definitions of multicellular organisms as bound and tidy entities become problematic. Against this background, Gilbert and colleagues argue with respect to humans that "we have never been individuals" (2012, p. 325). Instead, humans should be understood as integrated supraindividual and interspecies collectives. An example for such a unit is the mother-fetus-microbes community. The mother's diet affects the embryo, the embryo in turn actively modifies the mother's immune system, and bacteria help regulate pregnancy. In addition, Gilbert (2014) questions the standard human birth narrative in which an individual gains independence. "There is no such thing as 'independence.' It's mutual dependency all the way down, and birth is the exchanging of one symbiotic system for another" (Gilbert 2014, p. 5).

As these examples show, as in the original version of OCB, the currently-emerging new version of organism-centeredness faces serious anti-individualistic challenges. On the one hand, in EES it is argued that organisms' various abilities to actively mold themselves, their offspring, and environment should be understood (again) as the starting points of biological theorizing (especially about evolution), rather than genes. On the other hand, this special status of the organism and its causal agency is threatened by the fact that the organism is understood to be fully embedded in and inextricably connected with its environment. This leads to new (but in fact old) problems to distinguish organisms from their environment and from one another.

The major difference between old and new OCB seems to be that older approaches were aware of the conceptual inconsistencies underlying their theoretical framework, as they tried to better conceptualize the boundaries of organisms by specifying what it meant for organisms to be alive. In contrast, the advocates of EES (at least so far) seem to assume that concepts like causal reciprocity are sufficient to secure organisms as unambiguously identifiable "causally efficacious units" in nature (Goodwin 1999). As the debates in early-twentieth-century OCB have shown us, we should be critical about this assumption. In other words, the ESS should be careful not to lose the organism once again.

Conclusion

In the early twentieth century, and especially in the interwar period, a number of theoretical approaches tried to establish organisms as the central unit in biological theorizing. This OCB—different from both vitalism and mechanism—arose from new insights into the various causal roles organisms play in nature. This includes studies on the plasticity and robustness of organisms as well as their collective and symbiotic activities in the environment. However, as it turned out, the attempt to develop a consistent concept of the organism struggled with a number of cases in which the biological individual seems to be dissolved. As a consequence, at least three anti-individualistic arguments arose within early-twentieth-century OCB: (1) organisms are reciprocally and inextricably linked with their environments, (2) organisms and environments are units that share the same (or very similar) properties, and (3) organisms have no discrete and continuous boundaries to one another. Thus, the status of the concept of the organism in this organism-centered movement turned out to be somewhat paradoxical. The organism was understood as a causally autonomous and active unit with unambiguous and consistent boundaries and, at the same time, as an externally dependent unit that is sometimes even completely dissolved in the environment. As I have tried to show, the earlier version of OCB was aware of this situation. Several of its members tried to overcome anti-individualistic tendencies by further clarifying what an organism is and where its boundaries lie. They attempted this by introducing a multilayered concept of life that unified the organism as a life form—a particularly organized, metabolic unit that actively resists the environment at a state far from equilibrium. This qualitatively distinct unit has the "duty" to actively shape itself as well as its surroundings to stay alive. Thus, "life" secured the organism as a causally influential unit in development and evolution.

As this golden era of the organism shows, building biological theory on the concept of the organism is a challenging project. Recent enthusiastic announcements of the "return of the organism" in twenty-first century biology should be more aware of this. As a novel OCB—EES—appears on the horizon, we should not forget that an emphasis on the organism is easily associated with the organism's disappearance. In fact, organisms are ambiguous units. Often, once we approach them, they vanish away, merging with the environment and with each other. As new anti-individualistic tendencies show, the EES has not yet developed a satisfying conceptual solution to these problems. Today, again, OCB "seems to be reaching a point where radically new types of thinking are called for" (Waddington 1940, p. 148). Against this background, comprehensive historical and philosophical analyses are needed to secure the unit of the organism as a fruitful explanatory and methodological starting point of a new biological theory.

Acknowledgements I thank Daniel Brooks, Abigail Nieves Delgado, Richard Gawne, Nick Hopwood, Alessandro Minelli, Erik L. Peterson, Helmut Pulte, and two anonymous reviewers for constructive comments on earlier versions of this paper. I also thank the session audiences at the meeting of the International Society for the History of Philosophy of Science in São Paulo (Brazil, 2017) and at the workshop 'New Styles of Thought and Practices in Early 20th century Biology: Epistemologies and Politics' in Bochum (Germany, 2016) for feedback on presentations on this topic. In addition, I gratefully acknowledge financial support from the German Research Foundation (DFG; Project No. BA 5808/1-1) and the Konrad Lorenz Institute for Evolution and Cognition Research (KLI), Vienna.

References

Abir-Am, P.G. 1987. The Biotheoretical Gathering, Transdisciplinary Authority and the Incipient Legitimation of Molecular Biology in the 1930s: New Perspective on the Historical Sociology of Science. *History of Science* 25: 1–70.

Allen, G.E. 1980. Dialectical Materialism in Modern Biology. *Science and Nature* 3: 43–57.

Allen, G.E. 2005. Mechanism, Vitalism and Organicism in Late Nineteenth and Twentieth-Century Biology: The Importance of Historical Context. *Studies in History and Philosophy of Biological and Biomedical Sciences* 36: 261–283.

Alverdes, F. 1932. *Die Ganzheitsbetrachtung in der Biologie*. Berlin: Elsner.

Amidon, K.S. 2008. Adolf Meyer-Abich, Holism, and the Negotiation of Theoretical Biology. *Biological Theory* 3: 357–370.

Baedke, J. 2017. The New Biology of the Social: Shaping Humans' Future, Science, and Public Health. In *Imagined Futures in Science, Technology and Society*, eds. G. Verschraegen, F. Vandermoere, L. Brackmans, and B. Segaert, 45–64. London: Routledge.

Baedke, J. 2018. *Above the Gene, Beyond Biology: Towards a Philosophy of Epigenetics*. Pittsburgh: University of Pittsburgh Press.

Baedke, J. forthcoming. What is a Biological Individual? In *Old Questions and Young Approaches to Animal Evolution*, eds. J.M. Martín-Durán and B.C. Vellutini. Dordrecht: Springer.

Bateson, P. 2005. The Return of the Whole Organism. *Journal of Biosciences* 30: 31–39.

Bernal, J.D. 1935. *Engels and Science* (Labour Monthly Pamphlets 6). London: Trinity Trust.

Bertalanffy, L.v. 1928. *Kritische Theorie der Formbildung*. Berlin: Borntraeger.

Bertalanffy, L.v. 1930. Tatsachen und Theorien der Formbildung als Weg zum Lebensproblem. *Erkenntnis* 1: 361–407.

Bertalanffy, L.v. 1932. *Theoretische Biologie*. Vol. 1. Berlin: Borntraeger.

Bertalanffy, L.v. 1933. *Modern Theories of Development*. Trans. J.H. Woodger. Oxford: OUP.

Bertalanffy, L.v. 1942. *Theoretische Biologie*, 2 vols. Berlin: Borntraeger.

Bertalanffy, L.v. 1952. *Problems of Life*. New York: Harper and Brothers.

Brentari, C. (ed.). 2015. *Jakob von Uexküll*. Dordrecht: Springer.

Bukharin, N.I. (ed.). 1931. *Science at the Cross Roads*. London: Kniga.

Cheung, T. 2006. From the Organism of a Body to the Body of an Organism: Occurrence and Meaning of the Word ‘Organism’ from the Seventeenth to the Nineteenth Centuries. *British Journal for the History of Science* 39: 319–339.
Child, C.M. 1915. *Individuality in Organisms*. Chicago: University of Chicago Press.
Clements, F.E. 1916. *Plant Succession*. Washington: Carnegie Institute of Washington.
Driesch, H. 1892. Entwicklungsmechanische Studien. III. Die Verminderung des Furchungsmaterials und ihre Folgen (Weiteres über Theilbildungen). IV. Experimentelle Veränderungen des Typus der Furchung und ihre Folgen (Wirkungen von Wärmezufuhr und von Druck). V. Von der Furchung doppeltbefruchteter Eier. VI. Ueber einige allgemeine Fragen der theoretischen Morphologie. *Zeitschrift für wissenschaftliche Zoologie* 55: 1–62.
Driesch, H. 1899. *Die Lokalisierung morphogenetischer Vorgänge: Ein Beweis vitalistischen Geschehens*. Leipzig: Engelmann.
Driesch, H. 1908. *The Science and Philosophy of the Organism*. London: Black.
Driesch, H. 1914. *The Problem of Individuality*. London: Macmillan and Co.
Dürken, B. 1936. *Entwicklungsbiologie und Ganzheit*. Leipzig: Teubner.
Ebeling, A.H. 1913. The Permanent Life of Connective Tissue Outside of the Organism. *Journal of Experimental Medicine* 17: 273–285.
Emerson, A.E. 1939. Social Coordination and the Superorganism. *American Midland Naturalist* 21: 182–209.
Freyhofer, H.H. 1982. *The Vitalism of Hans Driesch*. Frankfurt: Lang.
Gibson, A.H., C.L. Kwapich, and M. Lang. 2013. The Roots of Multilevel Selection: Concepts of Biological Individuality in the Early Twentieth Century. *History and Philosophy of the Life Sciences* 35: 505–532.
Gilbert, S.F. 2014. A Holobiont Birth Narrative: The Epigenetic Transmission of the Human Microbiome. *Frontiers in Genetics* 5: 282. https://doi.org/10.3389/fgene.2014.00282.
Gilbert, S.F., J. Sapp, and A.I. Tauber. 2012. A Symbiotic View of Life: We Have Never Been Individuals. *The Quarterly Review of Biology* 87: 325–341.
Goldstein, K. 1934. *Der Aufbau des Organismus*. The Hague: Nijhoff.
Goodwin, B. 1999. Reclaiming a Life of Quality. *Journal of Consciousness Studies* 6: 229–235.
Graham, L.R. 1987. *Science, Philosophy, and Human Behavior in the Soviet Union*. New York: Columbia University Press.
Griffiths, P.E., and R.D. Gray. 2001. Darwinism and Developmental Systems. In *Cycles of Contingency*, eds. S. Oyama, P.E. Griffiths, and R.D. Gray, 195–218. Cambridge, MA: MIT.
Haeckel, E. 1866. *Generelle Morphologie der Organismen*. 2 vols. Berlin: Reimer.
Haldane, J.B.S. 1947. *What is Life?*. New York: Boni and Gaer.
Haldane, J.S. 1884. Life and Mechanism. *Mind* 9: 27–47.
Haldane, J.S. 1917. *Organism and Environment as Illustrated by the Physiology of Breathing*. New Haven, CT: Yale University Press.
Haldane, J.S. 1931. *The Philosophical Basis of Biology*. London: Hodder and Stoughton.
Haldane, J.S. 1935. *The Philosophy of a Biologist*. Oxford: Claredon.
Hein, H. 1972. The Endurance of the Mechanism—Vitalism Controversy. *Journal of the History of Biology* 5: 159–188.
Henderson, L.J. 1913. *The Fitness of the Environment*. New York: Macmillan.
Henderson, L.J. 1917. *The Order of Nature*. Cambridge, MA: Harvard University Press.
Hertwig, O. 1906. *Allgemeine Biologie*. Jena: Fischer.
Hertwig, O. 1922. *Der Staat als Organismus*. Jena: Fischer.
Hopkins, F.G. 1913. An Address on the Dynamic Side of Biochemistry. *British Medical Journal* 2: 713–717.
Hopwood, N. 1997. Biology Between University and Proletariat: The Making of a Red Professor. *History of Science* 35: 367–424.
Huneman, P. 2010. Assessing the Prospects for a Return of Organisms in Evolutionary Biology. *History and Philosophy of the Life Sciences* 32: 341–371.
Huxley, J.S. 1912. *The Individual in the Animal Kingdom*. Cambridge: Cambridge University Press.
Huxley, J.S. 1926. The Biological Basis of Individuality. *Journal of Philosophical Studies* 1: 305–319.
Jablonka, E., and M.J. Lamb. 2005. *Evolution in Four Dimensions*. Cambridge, MA: MIT.
Joravsky, D. 1963. Soviet Marxism and Biology. *American Journal of Jurisprudence* 8: 35–50.
Kammerer, P. 1907. Die Nachkommen der spaetgeborenen *Salamandra maculosa* und der fruehgeborenen *Salamandra atra*. *Archiv für Entwicklungsmechanik der Organismen* 25: 7–51.

Kant, I. 1902. *Kritik der Urteilskraft. Kants gesammelte Schriften*, vol. 5, Academy Edition, ed. Königlich Preußische Akademie der Wissenschaften. Berlin: Reimer. [Original: 1790/1793].
Koestler, A. 1971. *The Case of the Midwife Toad*. London: Hutchinson.
Laland, K., and G. Brown. 2018. The Social Construction of Human Nature. In *Why We Disagree About Human Nature*, eds. T. Lewens and E. Hannon, 127–144. Oxford: Oxford University Press.
Laland, K., B. Matthews, and M.F. Feldman. 2016. An Introduction to Niche Construction Theory. *Evolutionary Ecology* 30: 191–202.
Laland, K., T. Uller, M. Feldman, K. Sterelny, G.B. Müller, A. Moczek, E. Jablonka, and J. Odling-Smee. 2014. Does Evolutionary Theory Need a Rethink? Yes, Urgently. *Nature News* 514: 161–164.
Laland, K., T. Uller, M. Feldman, K. Sterelny, G.B. Müller, A. Moczek, E. Jablonka, and J. Odling-Smee. 2015. The Extended Evolutionary Synthesis: Its Structure, Assumptions and Predictions. *Proceedings of the Royal Society B* 282: 20151019. https://doi.org/10.1098/rspb.2015.1019.
Laubichler, M. 2001. Mit oder ohne Darwin? Die Bedeutung der darwinschen Selektionstheorie in der Konzeption der Theoretischen Biologie in Deutschland von 1900 bis zum Zweiten Weltkrieg. In *Darwinismus und/als Ideologie*, eds. U. Hoßfeld and R. Brömer, 229–262. Berlin: VWB.
Levins, R., and R.C. Lewontin. 1985. *The Dialectical Biologist*. Cambridge, MA: Harvard University Press.
Lewens, Tim. 2017. Human Nature, Human Culture: The Case of Cultural Evolution. *Interface Focus* 7: 20170018. https://doi.org/10.1098/rsfs.2017.0018.
Lidgard, S., and L.K. Nyhart. 2017. The Work of Biological Individuality: Concepts and Contexts. In *Biological Individuality*, eds. S. Lidgard and L.K. Nyhart, 17–62. Chicago:University of Chicago Press.
Lillie, R.S. 1945. *General Biology and Philosophy of Organism*. Chicago: University of Chicago Press.
Linsbauer, K. 1934. Individuum—System—Organismus: Ein Beitrag zum Mechanismus-Vitalismus-Problem. *Mitteilungen des naturwissenschaftlichen Vereins für Steiermark* 71: 63–77.
Lloyd Morgan, C. 1926. The Concept of the Organism, Emergent and Resultant. *Proceedings of the Aristotelian Society* 27: 141–176.
Meyer, A. 1935. *Krisenepochen und Wendepunkte des biologischen Denkens*. Jena:Fischer.
Meyer-Abich, A. 1940. Hauptgedanken des Holismus. *Acta Biotheoretica* 5: 85–116.
Meyer-Abich, A. 1942. Kant und das biologische Denken. *Acta Biotheoretica* 6: 185–211.
Meyer-Abich, A. 1948. *Naturphilosophie auf neuen Wegen*. Stuttgart: Hippokrates.
Meyer-Abich, A. 1956. Organismen als Holismen. *Acta Biotheoretica* 11: 85–106.
Minelli, A., and G. Fusco (eds.). 2008. *Evolving Pathways*. Cambridge: Cambridge University Press.
Needham, J. 1928. Recent Developments in the Philosophy of Biology. *The Quarterly Review of Biology* 3: 77–91.
Needham, J. 1929. *The Skeptical Biologist*. London: Chatto and Windus.
Needham, J. 1936. *Order and Life*. New Haven, CN: Yale University Press.
Needham, J. 1937. *Integrative Levels*. Oxford: Clarendon Press.
Nicholson, D.J. 2014. The Return of the Organism as a Fundamental Explanatory Concept in Biology. *Philosophy Compass* 9: 347–359.
Nicholson, D.J. 2018. Reconceptualizing the Organism: From Complex Machine to Flowing Stream. In *Everything Flows*, eds. D.J. Nicholson and J. Dupré, 139–166. Oxford: Oxford University Press.
Nicholson, D.J., and R. Gawne. 2014. Rethinking Woodger's Legacy in the Philosophy of Biology. *Journal of the History of Biology* 47: 243–292.
Nicholson, D.J., and R. Gawne. 2015. Neither Logical Empiricism nor Vitalism, but Organicism: What the Philosophy of Biology Was. *History and Philosophy of the Life Sciences* 37: 345–381.
Niewöhner, J. 2011. Epigenetics: Embedded Bodies and the Molecularisation of Biography and Milieu. *BioSocieties* 6: 279–298.
Pepper, J.W., and M.D. Herron. 2008. Does Biology Need an Organism Concept?' *Biological Reviews* 84: 627–628.
Peterson, E.L. 2011. The Excluded Philosophy of Evo-Devo? Revisiting C. H. Waddington's Failed Attempt to Embed Alfred North Whitehead's 'Organicism' in Evolutionary Biology. *History and Philosophy of the Life Sciences* 33: 301–320.
Peterson, E.L. 2016. *The Life Organic*. Pittsburgh, PA: University of Pittsburgh Press.
Pigliucci, M., and G.B. Müller (eds.). 2010. *Evolution: The Extended Synthesis*. Cambridge, MA: MIT Press.
Pouvreau, D. 2009. *The Dialectical Tragedy of the Concept of Wholeness: Ludwig von Bertalanffy's Biography Revisited*. Marblehead, MA: ISCE Publishing.

Prenant, M. 1938. *Biology and Marxism*. London: Lawrence and Wishart.
Reiß, C. 2007. No Evolution, No Heredity, Just Development—Julius Schaxel and the End of the Evo-Devo Agenda in Jena, 1906–1933: A Case Study. *Theory in Biosciences* 126: 155–164.
Reydon, T.A.C., Dullemeijer, P., and Hemerik, L. 2005. The History of Acta Biotheoretica and the Nature of Theoretical Biology. In *Current Themes in Theoretical Biology*, eds. T.A.C. Reydon and L. Hemerik, 1–8. Dordrecht: Springer.
Rieppel, O. 2016. *Phylogenetic Systematics*. Boca Raton: CRC Press.
Ritter, W.E. 1919. *The Unity of the Organism, or the Organismal Conception of Life*. 2 vols. Boston: Gorham Press.
Roux, W. 1881. *Der Kampf der Teile im Organismus*. Leipzig: Engelmann.
Russell, E.S. 1924. *The Study of Living Things*. London: Methuen.
Russell, E.S. 1930. *The Interpretation of Development and Heredity*. Oxford: Clarendon Press.
Russell, E.S. 1950. The 'Drive' Element in Life. *British Journal for the Philosophy of Science* 1: 108–116.
Sarkar, S. 1992. Science, Philosophy, and Politics in the Work of J. B. S. Haldane, 1922–1937. *Biology and Philosophy* 7: 385–409.
Schaxel, J. 1917. Mechanismus, Vitalismus und kritische Biologie. *Biologisches Centralblatt* 37: 188–196.
Schaxel, J. 1919. *Grundzüge der Theoriebildung in der Biologie*. Jena: Fischer.
Schaxel, J. 1931. Das biologische Individuum. *Erkenntnis* 1: 467–492.
Schrödinger, E. 1944. *What is Life?*. New York: Macmillan.
Sershantow, W.F. 1978. *Einführung in die Methodologie der modernen Biologie*. Jena:Fischer.
Sheehan, H.M. 2007. J. D. Bernal: Philosophy, Politics and the Science of Science. *Journal of Physics* 57: 29–39.
Smuts, J. 1926. *Holism and Evolution*. London: Macmillan.
Sölch, D. 2016. Wheeler and Whitehead: Process Biology and Process Philosophy in the Early Twentieth Century. *Journal of the History of Ideas* 77: 489–507.
Spemann, H., and Schotté, O.E. 1932. Über xenoplastische Transplantation als Mittel zur Analyse der embryonalen Induktion. *Naturwissenschaften* 20: 463–467.
Stahl, G.E. 1684. *Dissertatio Medica Inauguralis De Intestinis…*. Jena.
Stockard, C.R. 1921. Developmental Rate and Structural Expression: An Experimental Study of Twins, 'Double Monsters' and Single Deformities, and the Interaction among Embryonic Organs during Their Origin and Development. *American Journal of Anatomy* 28: 115–277.
Sultan, S.E. 2015. *Organism and Environment*. New York: Oxford University Press.
Svensson, E.I. 2018. On Reciprocal Causation in the Evolutionary Process. *Evolutionary Biology* 45: 11–14. https://doi.org/10.1007/s11692-017-9431-x.
Toepfer, G. 2011. Organismus. In *Historisches Wörterbuch der Biologie*, vol. 2, ed. G. Toepfer, 777–842. Stuttgart: Metzler.
Turner, J.S. 2000. *The Extended Organism*. Cambridge: Harvard University Press.
Uexküll, J.v. 1909. *Umwelt und Innenwelt der Tiere*. Berlin: Springer.
Uexküll, J.v. 1928. *Theoretische Biologie*. 2nd ed. Berlin: Springer.
Ungerer, E. 1926. *Die Regulationen der Pflanzen*. Berlin: Springer.
Ungerer, E. 1965. Die Erkenntnisgrundlagen der Biologie. Ihre Geschichte und ihr gegenwärtiger Stand. In *Handbuch der Biologie*, vol. 1, ed. F. Gessner, 1–94. Konstanz: Athenaion.
Vargas, A.O., Q. Krabichler, and C. Guerrero-Bosagna. 2016. An Epigenetic Perspective on the Midwife Toad Experiments of Paul Kammerer (1880–1926). *Journal of Experimental Zoology Part B* 328: 179–192.
Waddington, C.H. 1940. *Organisers & Genes*. Cambridge: Cambridge University Press.
Waddington, C.H. 1942. The Epigenotype. *Endeavour* 1: 18–20.
Waddington, C.H. 1957. *The Strategy of the Genes*. London: Allen and Unwin.
Waggoner, M.R., and T. Uller. 2015. Epigenetic Determinism in Science and Society. *New Genetics and Society* 34: 177–195.
Walsh, D.M. 2015. *Organisms, Agency, and Evolution*. Cambridge: Cambridge University Press.
Weiss, P.A. 1940. The Problem of Cell Individuality in Development. *American Naturalist* 74: 34–46.
Wheeler, W.M. 1911. The Ant Colony as an Organism. *Journal of Morphology* 22: 307–325.
Wheeler, W.M. 1920. The Termitodoxa, or Biology and Society. *The Scientific Monthly* 10: 113–124.
Wheeler, W.M. 1928. *The Social Insects*. New York: Harcourt.
Whitehead, A.N. 1925. *Science and the Modern World*. Cambridge: Cambridge University Press.

Willmer, E.N. 1965. *Cells and Tissues in Culture*. London: Academic Press.

Woltereck, R. 1909. Weitere experimentelle Untersuchungen über Artveränderung, speziel über das Wesen quantitativer Artunterschiede bei Daphniden. *Verhandlungen der deutschen zoologischen Gesellschaft* 19: 110–173.

Woodger, J.H. 1929. *Biological Principles*. London: Routledge and Kegan Paul.

Woodger, J.H. 1930–1931. The 'Concept of Organism' and the Relation between Embryology and Genetics. Part I–III. *The Quarterly Review of Biology* 5: 1–22, 438–463; 6: 178–207.

Zavadovsky, B. 1931. The 'Physical' and 'Biological' in the Process of Organic Evolution. In *Science at the Cross Roads*, ed. N.I. Bukharin, 69–80. London: Kniga.