The Explanatory Role of *Umwelt* in Evolutionary Theory: Introducing von Baer's Reflections on Teleological Development

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Abstract: This paper argues that a central explanatory role for the concept of *Umwelt* in theoretical biology is to be found in developmental biology, in particular in the effort to understand development as a goal-directed and adaptive process that is controlled by the organism itself. I will reach this conclusion in two (interrelated) ways. The first is purely theoretical and relates to the current scenario in the philosophy of biology. Challenging neo-Darwinism requires a new understanding of the various components involved in natural selection processes. An important prerequisite for the explanation is the ability to understand development in a teleological way. Here, the concept of *Umwelt* plays a crucial role: if organisms are responsible for generating adaptive variation in specific environments, we need a theory that explains the context-dependent nature of adaptively oriented processes. The *Umwelt* is thus a central element in determining the goal that an adaptive process pursues. The second path in my analysis also has a historical dimension. I will present Karl Ernst von Baer's reflections on teleological development and his influence on von Uexküll's thinking. I will present various ideas developed by von Baer, such as the distinction between *Ziel* and *Zweck* and the use of musical metaphors, which can help to understand development teleologically and give von Uexküll's theory a central place in this framework.

Keywords: Umwelt; *Ziel-Zweck*; Musical Metaphors; Teleological Development; Karl Ernst von Baer; Jakob von Uexküll

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The highest law of life, which connects all plans in time, has been named 'directedness' by K. E. v. Baer.

J. von Uexküll (1936: 144)

Natural forces which are not directed to an end cannot produce order.

K. E. von Baer (1886b: 88)=

Introducción

The last decades of theoretical biology are crossed by disputes about the status of the Modern Synthesis. The aim to reframe biological theory beyond the gene-center stance becomes noticeable once developmental processes emerge as highly complex phenomena. A new understanding of development is required to construct an alternative evolutionary theory and explain how its central components -inheritance, variation, and fitness-are produced by developmental processes. As this paper intends, philosophers and biologists are nowadays trying to fulfill this requirement. The view of genes as the unit of control and organization in development is substituted by a picture where the whole developing system self-regulates its developmental trajectory. This introduces a special kind of vocabulary involved in the explanation of inheritance, variation, and fitness, such as the notions of agency, norms, action, and other concepts that belong to a specific kind of (historically despised) scientific explanation: teleology.

The aims of this paper are twofold. First, to argue that the notion of *Umwelt* plays a crucial role in the understanding of teleological development, and hence *Umwelt*'s theory is explanatory and useful in the context of evolutionary theory. This would mean also connecting *Umwelt*'s theory with other similar conceptions in biological theory employed nowadays, and taking biosemiotics as an important theory in the construction of an alternative biological theory. The second aim is rather historical. I will present some of von Baer's ideas on his teleological view of development. This is a motivation to acknowledge the direct influence of von Baer on von Uexküll, but also because von Baer's reflections on teleological development can help to elaborate the explanatory role of Umwelt's theory for our understanding of development.

1. Teleology and Development

1.1 The Role of Organismal Development in Evolutionary Theory

The role of organismal development in evolutionary theory is a central area of dispute in the contemporary philosophy of evolutionary biology (Bateson, 2005; Baedke, 2018; Nicholson, 2014; Huneman, 2010). As might be expected, rivalries and tensions arise between the various positions within this area. To understand the theories that advocate that organismal development plays a central explanatory role in evolutionary theory, it is also important to understand the theory that has neglected such an explanatory role, namely the Modern Synthesis or neo-Darwinism.

On the foundations of Darwin's natural selection, Mendelian inheritance, and mathematical models of populational change, the Modern Synthesis built its enterprise: the genetic theory of evolution. The central insight was to explain the core components of natural selection in genetic terms, without addressing developmental processes. Natural selection requires heritable fitness differences among

members of a population (Lewontin, 1974; Godfrey-Smith, 2009). In other words, the individuals in a population must differ, these differences must carry with them different fitness values, and finally, the differences must be heritable. Darwin, of course, did not have a complete theory of natural selection, for he still needed a solid theory of how variation is generated and how traits are inherited. In this sense, the construction of the Modern Synthesis is only one way of understanding the components of natural selection.

The genetic theory of inheritance, shaped primarily by the work of Weissmann and Mendel, reduced the processes of inheritance to what was passed on through the germline at conception and rejected the influence of developmental processes in inheritance. In other words, the variations that arise from epigenetic motifs cannot be transmitted (there can be no somatic inheritance), nor can they influence what is inherited through the germline (somatic changes do not influence the germline). Although heredity and development were united in pre-Weismann times, developmental processes are displaced from the theory of heredity (Amundson, 2005). The genetic theory of heredity is linked to the genetic theory of variation. If variation must be inherited for evolution to occur, the source of variation must be linked to the source of inheritance: genes. Genetic mutation and genetic drift are the main sources of variation and both phenomena take place at the genetic level. Since selection is a process that affects phenotypes, the fitness of phenotypes must be closely related to the fitness of heritable variations. In other words, what is inherited at conception must explain the construction of traits, i.e., it must explain development. When traits are constructed by genotypic inheritance, selection can detect the fitness of the inherited variations (genes) by examining the fitness of the phenotypes. Development is a transparent process (Walsh, 2003): phenotypes reveal genotypes to natural selection. In this way inheritance, variation, and fitness, can be understood as a property of genes and populations of genes; thus, "changes in the frequencies of alleles by natural selection *are* evolution" (Campbell, 1994: 86; emphasis added). Originally, genes were not understood in molecular terms. Mendelian inheritance was cellular inheritance. With the discovery of DNA in 1953, the material nature of genes changed. However, the theoretical role of genes remains intact: Whatever piece of matter genes are, they are responsible for explaining the components of natural selection (Å gren, 2021). This way of understanding natural selection leads aside organismal development. Development is just the consequence of genetic information and thus it does not pertain to evolutionary theory: "One consequence of Weismann's separation of the germline and the soma was to make it possible to understand genetics, and hence evolution, without understanding development" (Maynard Smith, 1982: 6).

Challenges against the genetic theory of evolution are directed primarily against neo-Darwinism, not Darwin. In other words, the claim that the development of organisms is relevant to evolutionary theory implies that development plays a role in explaining the core components of natural selection. Indeed, this is what various theoretical and experimental advances suggest. Extended inheritance systems and epigenetic modification of genes have been discovered and used to challenge Weisemann's genetic theory of inheritance (cf. Jablonka and Lamb (2020) for a review). Several sources of variation are not based on genetic change, such as phenotypic plasticity, self-organization, or niche construction (e.g. West-Eberhard, 2003; Gilbert and Epel, 2015; Müller and Newman, 2003; Wagner, 2014). And crucially, since the post-genomic era, the role of DNA as the sole source of developmental information has been replaced by a distributed view of development, where different resources are involved in trait construction, such as genomic, intracellular, extracellular, and exogenous causes (Griffiths and Stotz, 2013; Oyama et.al., 2001; Keller, 2002; Lewontin, 2000). In other words, the Genotype-Phenotype Map does not represent a straight and visible route between genes and phenotypes; rather, the road for constructing traits is complex, with different routes, forks, and variables. The link between genes and phenotypes is not transparent but opaque. Therefore, the fitness of organisms cannot be directly linked to their genetic basis. In summary, evolutionary processes cannot be described by looking only at genes. Developmental processes are part of evolutionary theory.

Certainly, this is a cartoonish depiction of the scenario, but it reflects the core idea of the so-called *developmental or epigenetic turn* in theoretical biology. Moreover, it is not the intention of this paper to challenge the Modern Synthesis but to contribute with some theoretical insights to the emergence of the developmental turn. In this sense, it is important to keep in mind what is at stake in the debates about the role of organismal development in evolution, i.e., the capacity of organismal development to produce heritable variation in fitness.

1.2 The Need for a Goal-Directed View of Change

Most debates in the contemporary philosophy of biology revolve around the developmental turn. Many theories and controversies have arisen to discuss what and how to deviate from the Modern Synthesis. This essay will analyze a specific but central issue for the foundations of the developmental turn that is a source of intense debate today: a *teleological theory of development*.

The need to construct a goal-directed view of development departs from the purported explanatory role of organismic development. A crucial element that the developmental turn adds to evolution theory is the existence of adaptively directed phenotypic variation. This can be understood in contrast to the genetic theory of variation advocated by the Modern Synthesis. In this framework, the main source of variation arises at the genetic level. As is generally known, genetic variations (according to MS) are random. Random merely means that the origin of the variation is not causally linked to its adaptive significance. Genetic variation occurs independently of its effect on the phenotypic level. *Random* means that they are not adaptively oriented (even if they finally are adaptive). The distributed and context-sensitive view of organismal development advocated by the developmental turn pursues the idea of adaptively directed (phenotypic) variation: variations that arise to increase the fitness of the organism.

This leads to a different understanding of variation and novelty. In the Modern Synthesis, a population confronted with a particular environmental problem must wait for a random variation that fits with the problem -an adaptive solution; as George Williams (1992: 484) wrote, “adaptation is always asymmetrical; organisms adapt to their environment, never vice versa.” Somehow, nature must provide solutions to unknown problems. In this way, the developmental turn calls for the introduction of organismal development as an adaptive force, while the MS treats natural selection as the unique source of adaptive evolution, treating organisms as “*vehicles* in which replicators travel about” (Dawkins, 1982: 82; emphasis in the original), as “merely the *medium* by which the external forces of the environment confront the internal forces that produce variation” (Levins and Lewontin, 1985: 88; emphasis added), as the “*arena* in which this interaction [genome variations and natural selection] is played” (Michel and Moore, 1995: 127; emphasis added), or as “the *superficial face* that genes show to the world” (Sober, 1984: 228; emphasis added). On the contrary, the developmental turn ties the origin of variations to their adaptive role in an organism embedded in the environment; organisms provide solutions to problems that they confront during their lifespan. Theorists of the developmental turn, therefore, must construct a theory of agency and goal-directedness in development. Understanding how organisms can adaptively regulate their conditions of existence is a central scientific goal if we are to replace the gene-centered view of evolution with a sound and coherent theory. In other words, understanding goal-directed developmental processes is not just a topic in itself, but an essential requirement of the developmental turn, a crucial piece in an incomplete puzzle (Rama, 2023).

There are various proposals for understanding agency and teleology beyond gene-centered and reductive approaches (the most detailed one is proposed by Denis Walsh (2015)). In this paper, I will attempt to contribute to the development of a teleological theory of development. However, I will make a preliminary remark on this topic. The point is that not all theories of agency and teleology based on organismic biology are suitable for our purpose and our need to explain teleology in development. The main problem is that a teleological view of

development should not be confused with a *teleological view of physiology*. There are several reasons why teleological physiology should not be confused with developmental teleology. Crucially, the goal of physiological processes seems to be different from the goal of development. In short, teleological physiology -as espoused, for example, by Autonomous Systems Theory (e.g. Moreno and Mossio, 2015)- is about self-maintenance. Teleological views of physiology take an organismic standpoint to see how the different parts of an agent contribute to maintaining itself under viable conditions (e.g. Barandiaran et.al., 2009). Agency in physiological processes is about regulating the coupling with the environment and the internal organization to *maintain* the system. Teleological physiology emerges from a holistic view of living systems, where different parts play a significant functional role in the achievement of a specific goal related to maintenance (e.g. Kauffman, 2019; Christensen and Bickhard, 2003; McLaughlin, 2000). Development, however, is not about preservation, but about change, an opposite phenomenon. Certainly, the organism is maintained while it changes. But development is not about the maintenance of an internal structure, a set of elements that are in certain functional relationships (as in teleological physiology), but about the construction of elements and relationships. Organisms go through different internal configurations and different couplings with their environment. This cannot be explained solely from a physiological perspective, which only looks at how an organism maintains its life. The difference between developmental goals and physiological goals is crucial and reveals the inadequacy of some agential perspectives on our aims. A similar point was recently noted by Nuño de la Rosa (2023), who claims that the processes of reproduction require specific goals that cannot be adequately accounted for from a physiological perspective (i.e., the goals of reproduction are not about maintenance).

As long as we are not able to separate the different goals that an organism pursues (Rama, 2022), our *explanandum* remains without *explanans*. That is, we need to understand how ontogenetic changes are adaptively oriented and how organisms construct themselves in an adaptively oriented way. Pointing out that an organism is capable of orienting its processes towards maintenance is correct, but it does not explain how this system was constructed. Teleological physiology is not suitable for explaining development, because the system that is maintained by physiological processes was constructed by developmental processes. In this sense, teleological physiology says nothing about how organisms produce themselves. It is about how organisms maintain themselves. If we keep in mind the place that teleological development occupies within the evolutionary approach to the developmental turn, we cannot be satisfied with these accounts of teleology and agency. Of course, this does not mean that these theories of teleological physiology are wrong. It just means that they are not appropriate for our explanatory aims. Nor am I claiming that teleological development has not been explored in the current literature. I am trying to clarify the scope of our analysis to understand what we need: a theory of how an agent deploys its developmental resources at a particular stage of ontogenesis to bring about an appropriate change.

I am not going to put forward a theory of teleological development here. I merely want to point out some of the problems associated with teleological development and suggest some ways of dealing with them. The concept of *Umwelt* developed by Jakob von Uexküll is the pivotal point of my analysis (cf. Tønnessen et.al., (2015) for a recent introduction). Here I offer both a historical and a theoretical investigation. In section 2, I will first emphasize the central explanatory role of the *Umwelt* in the contemporary context of the developmental turn. This means that the concept of *Umwelt* should be used in goal-directed explanations of development (section 2.1) and that the theory of *Umwelt* should be linked to different areas within current theoretical biology (Brentari, 2018). In section 3, I move on to the historical side of my analysis. I will present von Baer's view on teleological development and its influence on von Uexkuell's work. First, I will outline some of von Baer's reflections on the nature of teleology within natural science, then I will present his distinction between *Ziel* and *Zweck* as an appropriate strategy for naturalizing teleology, and finally, I will argue that his use of *musical metaphors* represents a heuristic device that has been replaced in contemporary biology by various fields within the developmental turn. In the conclusion, I will bring together the ideas from Section 2 and Section 3 by emphasizing how von Baer's ideas specify the explanatory role of *Umwelt* within the developmental turn.

2: The *Umwelt* in Evolutionary Theory

2.1 Healing the Blindness

The adaptability of living systems is generated by evolved genetic information, according to the MS. The teleonomic view of development presented by Mayr (1961, 1974) explains how the adaptability of an organism arises on the basis of its genetic blueprint. The blindness of organisms arises from this view: the genetic program represents - in informational terms - the traits to be constructed, and no representative abilities are ascribed to the developing organisms. The organism does not seem to be able to construct traits according to what it "sees" of its environmental conditions. However, once genes lose control over development, developmental control is provided by the developing system itself. Genetic blueprints, then, cannot be the whole story about the construction of adaptability during development. If the whole developing system is responsible for order in living systems, then we must replace the genetic view of development. In other words, if we think of development as a goal-directed, context-sensitive process driven by the whole developmental system, we should explain how an organism "sees" its context in order to guide its development into an adaptive harbor; we need to cure the blindness of organisms.

The theory of Umewlt might be a suitable candidate for such a healing. The ability of developing systems to perceive their developmental context must be recognized in order to view development as a goal-directed process. Most of the developmental phenomena at the heart of the developmental turn – e.g. plasticity, self-organization, niche construction, epigenetic regulation - give organisms the ability to "see" their external (and internal) context in order to regulate the course of development.

More specifically, the Umwlet becomes crucial in the directedness of development. It is an answer to the question: directed towards what? In teleological explanations, directedness is oriented towards goal states. In the teleonomic view of MS, the goal states are represented in the genetic program. But in an organismic view of development, the target states must be represented differently. This is where the concept of *Umwelt* comes into play. The thesis here is that *goal states of development are defined on the Umwelt (and the Innenwelt) of the developing systems.* The *Umwelt* comes to replace the metaphor of the genetic blueprint in our understanding of teleological development.

Furthermore, the phenomenological and subjective nature of *Umwelt* emphasizes the fact that it is the organism itself that constructs its own "points of view" of the world. Understanding development as an agent-driven process introduces a set of vocabularies that refer to the phenomenological - e.g. sensitiveness, perception - and cognitive - e.g., memory, learning - capacities of developmental systems. While there is an ongoing debate about which phenomenological, cognitive or mental terms should be extended to the realm of the living (Rama, forthcomingb; cf. section 3), the notion of *Umwelt* is an empirically grounded and philosophically robust notion for dealing with the vicissitudes of development.

The active role of organisms in development is linked to the process of interpretation - the process of constructing an Umwelt. Gene-based accounts of development employ the word "read" to explain how developmental information is expressed during ontogenies; developmental systems read genetic information in a way that leaves no room for the active and agentive participation of organisms: Inherited information is an instruction (Shea 2013). In contrast to this view, the notion of interpretation suggests a transfer of the unit of organization in development from inherited information to the organism that interprets that information. The construction of the Umwelt as a central element in goal-directed activities is a process that is controlled and produced by the agent itself - not the passivity of reading an inherited text, but the active manipulation and utilization of the inherited information.

2.2 *Umwelt*'s Theory in the Developmental Turn

The epistemological relevance of the concept of *Umwelt* in evolutionary theory becomes clear when one realizes that various approaches in the context of the developmental turn have appealed to concepts similar to that of *Umwelt*. A first approximation shows relevant similarities between the constructivist ideas of Richard Lewnotin (2000) and the concept of *Umwelt*. It would not be unimaginable to attribute to Lewointin von Uexkull's words (1923: 266): "Nobody is a product of their environment — everybody is the master of one's *Umwelt*". Lewontin's critique of the externalism of neo-Darwinism is deeply motivated by the active role of organisms in creating their environmental conditions, emphasizing, like von Uexküll, the subjective character of organism-environment relations.

In this context, we can find, for example, the use of the concept of affordance (Heras-Escribano, 2019) in evolutionary biology. The concept of *affordance* refers to the possibilities of action an organism has in a particular environment -or as von Uexküll (1992: 323) said, referring to similar idea, "[e]xternal stimuli [...] approach the animal in the form of questions." Both concepts are understood particularly in terms of relationships between organisms and the environment. In both cases, they confer context-sensitivity on organisms. Moreover, both affordances and *Umwlet* are not created externally but by the result of the inner, active participation of organisms -interpretation; the organism is an agent capable of constructing its coupling with the environment. Certainly, the relationship between *Umwelt* and affordances deserves proper and detailed investigation.[1] Apart from the similarities between the two terms outlined earlier, they play a similar role in explaining the direction of development. Affordances have often been used in an organismic view of evolution. The clearest example, which also draws on Lewntonin's insights, is Denis Walsh's notion of *Affordance Landscape*, as part of his *Situated Darwinism* (Walsh, 2012, 2013, 2015). The claimed explanatory role coincides with the explanatory role of *Umwelt* outlined above: the attribution of a goal-directed and context-sensitive capacity to organismic activity.

Another case, also related to Lewntoin's work (Lewontin, 2000), can be found in niche construction theory, specifically in the notion of *experiential niche construction* introduced by Sonia Sultan (2015). Here it is important to make some conceptual clarifications. It is useful to distinguish between two concepts of niche construction: the individual and the population concept (Rama, forthcominga). The concept used by Odeeign-Smee et.al. (2003) in their well-known book refers to the ability of a population to change its fitness by altering the external environment; allegedly, populational niche construction is said to be an important variable within populational biology. Individual niche construction, in contrast, is a part of developmental biology (Stotz, 2017). It concerns the processes by which an organism constructs its niche during development. Broadly speaking, there are two types of processes within individual niche construction: the processes that physically construct the environment in which an organism lives, and the processes that experientially construct the environment. In the first case, the construction is about changing the material nature of the environment. In the second case, however, there are no external changes, but the construction has an epistemic connotation. Accordingly, organisms construct the way they experience their niche. The sensitiveness of an organism is not predetermined from the outside but is constructed by the organisms themselves. In this context, once again, we observe that the notion of experiential niche construction comes into play to perform a similar explanatory role to the notion of Ummwet. The experienced niche becomes a central element in the explanation of agency and adaptiveness. As already emphasized in relation to the notion of *Umwelt*, various developmental studies (in the

[1] The similarities between affordances and the concept of *Umwelt* are contested (see Fultot and Turvey, 2019; Feiten, 2020; Heras-Escribano and DeJesus, 2018). While the concept of affordances emphasizes the unmediated character of the relationship between organism and environment (affordances are not internal, representational constructs), the concept of *Umwelt* states that "the relationship that binds an organism to its environment is never immediate or automatic: between the reception of stimuli and the response of the organism, there is room for an activity of interpretation or elaboration of the stimuli themselves" (Brentari, 2018: 157). In this sense, the anti-representationalist spirit of affordances is not (necessarily) present in the concept of *Umwelt*. Be that as it may, this debate does not invalidate my point: that beyond the differences there are relevant commonalities that have exploded in the philosophy of biology.

context of niche construction theory, eco-devo, or epigenetics) require the notion of experience to understand how developmental responses can be context-sensitive and goal-directed to the external conditions of organisms.

In this section, I have emphasized the importance of *Umwelt* in evolutionary theory by linking it to other interrelated approaches. These conceptual and interdisciplinary relationships illustrate the importance of biosemiotics in the developmental turn (Rama, 2021). An important step in biosemiotics is to understand that the *Umwelt* exists due to the manifold semiotic processes that every living system undergoes. The picture that emerges depicts the organism as a complex system interconnected by many semiotic processes that create a context-dependent capacity and the opportunity to act adaptively in an environment. The decisive factor is that a similar picture is drawn of different areas in the developmental turn. Ecological developmental biology (eco-devo) is mainly devoted to understanding how developing systems use different signaling systems to adapt their developmental trajectories to their ecological contexts where "[c]ascades of inductive events (signal-resopnse dynamics) are responsible for organ formation." (Gilbert and Barresim, 2010: 106). Or Sultan (2015: 20) states, "ecological development, or 'eco-devo,' seeks to explicitly include the organism's particular environment in studying both the signaling pathways and the ecological and fitness consequences of phenotypic expression." As a semiotically grounded representation of the *Umwelt*, the signalling-based account of development becomes a key to understanding the adaptively directed nature of living activities in terms of "semiotic agency" (Sharov and Tønnessen, 2021). A biosemiotic view of development also has important similarities with the post-genomic stance of Developmental Systems Theory (Oyama et.al., 2001). The distributed view of biological information in development points in the same direction as the semiotic and signaling accounts of development (Griffiths and Stotz, 2013). The connection between biosemiotic and biological information can provide a salient unifying framework and a strong empirical and theoretical foundation for introducing biosemiotic within the developmental turn (Deacon, 2015, 2021), and "connecting the concepts of theoretical biology with the concepts of semiotics is a programmatic task for furthering both fields" (Kull, 2022: 129).

So far, in section 2.1, I have emphasized the explanatory role of *Umwelt* in the developmental turn. In addition, in section 2.2 I have shown some links between *Umwelt*'s theory and specific proposals within the developmental turn. On the one hand, the concept of *Umwelt* is related to other scientific concepts that are used by the developmental turn and have a similar explanatory function, such as the concept of affordances or experiential niche construction. On the other hand, the biosemiotic theory of the *Umwelt* also deserves to be considered as a discipline within the developmental turn, and its similarities with other theories, such as eco-devo and DST, need to be exploited. If the developmental turn is the foundational niche for contemporary approaches to *Umwelt* theory, the connections highlighted here may allow for future investigation and further theorizing.

3. Karl Ernst von Baer on Teleological Development

In this section, I will present Karl Ernst von Baer's view of teleological development. There are several reasons for introducing this historical contribution. One of them is that von Baer has a direct influence on von Uexküll's work. I will present various Baerian ideas that were later also taken up by von Uexküll. In addition, von Baer's reflections will shed light on important questions of teleological development. Consequently, the conclusion of this paper is devoted to understanding how von Baer´s ideas on teleology contribute to the role that the concept of *Umwelt* plays in explaining development.

3.1 Teleology in Nature: Goals and Necessities

To provide historical insight, Kant's view of teleology is an appropriate starting point. It also partly explains the fundamental ideas in science that neo-Darwinism embarrasses to render organisms explanationless. In this sense, Kant's view was profoundly influenced by the scientific revolution and the assumption of a only acceptable

mode of explanation: mechanistic explanation (a stance is named the Newtonian paradigm (Smolin, 2013)). The so-called Kant's Puzzle arises from the assumption of another principle: that teleological explanations are unavoidable in order to understand nature. Natural purposes (*Naturzwecke*) are needed to explain various intrinsic and distinctive properties of living things. Kant's Puzzle, thus, is an epistemic tension between what is explanatorily useful (teleological explanations) and explanatorily valid (mechanistic explanations), between the Newtonian paradigm and the teleological paradigm. The causal structure of teleological explanation, in which future events (ends-states) appear to have some kind of causal influence on present activities (means), does not fit with the temporal structure of mechanistic explanation, in which causes always precede their effects. Under this scenario, Kant argued, there can be no science that introduces teleological explanations into its toolkit.

Kant's ideas influenced most of German biology in the 18th and 19th centuries. An entire enterprise - known as Teleomechanicism (Lenoir, 1989) - was constructed to analyze and ultimately solve Kant's Puzzle, to achieve a "teleology without regrets" (Lenoir, 1981). Within Teleomechanicism, according to Lenoir (1989: 16), von Baer could be seen as the last and most important figure whose attempts to approach teleology came closer to a naturalistic position. Moreover, von Baer's reflections, as most Teloemcancists, are mainly concerned with developmental processes. Here I will draw on two posthumously published works (1886a, 1886b) based on a series of lectures he gave in Berlin in 1866. These works are extremely useful in that they summarise most of von Baer's ideas on teleological development. He also provides a rich historical analysis of how "teleophobia" (1886a: 72) arose in natural science. He also deals with other interesting topics such as free will, the philosophy of mind, and cosmology. When contemporary philosophers of biology attempt to reconstruct an alternative, non-neo-Darwinian biological foundation, they usually draw on the organicist movement in the first half of the century, to which von Uexküll also belongs (cf. Nicholson and Gawne, 2015). In this sense, von Baer and the traditions to which he belonged represent a further source of inspiration and reflection.

Von Baer's historical analysis shows how teleological explanations came into conflict with the foundations of science. The only supposedly justifiable explanation of nature is based on "absolute necessities": the application of physico-chemical, mechanical laws. All natural beings are a necessary result of the action of these laws. The same explanatory model that Newton applied to the movement of inert objects was introduced into the realm of living beings (in particular, he discusses Heackel's interpretation of Darwin's theory, i.e. the first step of neo-Darwinism). According to this view, living beings are created exclusively by mechanical effects on the material substrate of living beings. No goals - no teleological explanation - are needed to explain how living beings are constructed. It is sufficient to establish laws that necessarily produce adult organisms.

He does not accept this position, however, because "if you deny all goals or purposes in nature in this triumphant feeling [explaining nature only through absolute necessity], in my opinion, you go too far, far too far" (1886a: 65); the rejection of gaols in development is more "a scientific superstition" (1886a: 73) than a justified fundamental idea. For him, there should be no tension between mechanistic and teleological explanation: "Do purpose and "absolute necessities" always exclude each other? […] Doesn't purpose have to look for means?" (1886a: 68). His criticism of this view, then, is precisely that he does not recognise that the necessities in living organisms (the structure of an organic body) are the means that regulate organisms in order to achieve goals, as this quote shows: "now it is announced loudly and confidently: Ends do not exist in nature, there are in it only necessities; and it is not even recognized that precisely these necessities are the means for reaching certain goals. Becoming without a goal is simply unintelligible" (1886b: 231). He gives many examples of developmental processes to demonstrate the future-oriented character of development. The organs of the body which are formed in the egg are so constructed that they may be used in later stages; body parts s are constructed long before they are used: "The caterpillar bites or cuts its food into pieces; - for this purpose, the tools are formed before they are needed, on the embryo within the egg (1886a: 4) […] It is absolutely impossible to ignore that all these changing states are set up in such a way as to achieve the ultimate goal, the development of the butterfly" (1886a: 55).

In this sense, the neglect of teleological explanation ignores not only the future-oriented nature of development - which is extremely evident - but also that goals are responsible for the construction of the order we find in nature, insofar as "natural forces which are not directed to an end cannot produce order" (1886a: 88). It is the goals of development that *orchestrate* the means of constructing traits. While Darwinists see development as a blind process guided by absolute necessities, von Baer sees these absolute necessities as the result of organizations pursuing goals, an idea also defended by current views of goal-directedness, that defines goal-directedness as "the capacity of a system as a whole to enlist the causal capacities of its parts and direct them toward the attainment of a robustly stable end-point" (Walsh, 2015, 195). The blindness of developmental processes, which can be cured by the concept of Umwelt, was constructed in direct opposition to teleological explanations.

Development is a stage-by-stage process in which "the present state is only possible through the preceding ones" (1866a: 52). Von Baer advocates a processual view of development (Nicholson and Dupre 2018). According to this view, "the essence of life can only be the process of life itself or the course of life, that is, the series of states following each other." Development is therefore a continuous accumulation of changes in form and function. In every ontogenetic change, the organism pursues a goal: the regulation of its environmental connection and its internal structure in order to achieve the goal of producing an apt characteristic. The goals are thus present at every ontogenetic stage in the regulatory mechanism - the way in which an organism controls its means - in such a way that "every organism in the process of coming into being has a goal. Without goals how could anything subject to regulation come about?" (1886b: 180).[2]

3.2 *Ziel* and *Zweck*

Certainly, von Baer did not propose a teleological theory of development, mainly because many developmental phenomena were unknown. Nevertheless, he provides some interesting insights that help us intending to construct a teleological theory of development. I will present two important ideas that were mainly embarrassed by von Uexküll. First, the distinction between *Ziel* and *Zweck*, and second, the use of the musical metaphor as a heuristic device to deal with the regulatory capacities of developmental systems.

For von Baer, most criticisms of teleological explanations arise from "a confusion of terms" (1886a: 72) and that natural languages are "extremely poor for everything spiritual [meaning the intentional concepts associated with teleological languages]" (1886a: 74). Part of the reason for teleophobia lies in the subtle semantic nuance between the German words *Zweck* (roughly translatable as 'purpose') and *Ziel* (typically rendered in English as 'goal'), a distinction which is not clearly grasped in "Western languages" (Lenoir, 1989: 272). Once this distinction is noted, he calls for a defense of goals and a rejection of purposes, mainly because "we should not picture the primordial source of existence too human-like, and must consider distance and diversity unattainable […] A large part of the attacks [to teleology] on the essence of the matter seems to me to lie in the inadequacy of this word and concept [Zweck]" (1886: 79-80).

In this sense, the word purposes has an anthropomorphic character that may not be sufficient to explain living systems. Moreover, the notion of purposes seems to be linked to inference or the explicit intention to do something, such as intelligent design. It is therefore a good strategy for anti-teleologists to be careful with the chosen world. Von Uexküll adopted von Baer´s terminology (Kull, 2001: 6) and rejected the notion of purpose for practically similar reasons: "Instead of seeing in it [teleology] merely a rule stretching across time and space,

[2] The idea that the final stages of development are adult stages is controversial, as adulthood seems difficult to define (Minelli, 2011; Balari and Lorenzo, 2016). Even if a certain stability is reached at a certain point in life, this does not mean that no further changes can occur. Moreover, stability (i.e., the cease of ontogenetic change) is relative to each trait (morphological stability is reached earlier than cognitive stability), and changeability at further stages is also relative to each trait. For our purposes, it is sufficient to understand developmental processes as future-oriented, i.e. as an open-ended state or as a stage of phenotypic stability.

men have spoken of ‘purpose’ and ‘purposefulness’ in Nature as a sort of human being […] it is advisable therefore to dismiss from biology, for all time, expressions such as ‘purpose’ and ‘purposefulness’” (von Uexküll, 1926: 270). In particular, Kant’s expression for the teleological character of living systems was "natural purpose" (*Naturezweck*). While this semantic conundrum is not the only problem, part of Kant’s conclusion about the non-scientific character of teleology may derive from his conception of teleology itself.

Goals, on the other hand, seem more appropriate and explanatorily sufficient for the treatment of developmental phenomena. Goals, stripped of any anthropomorphic or “spiritual” connotation, refer to the targetability (*Zielstrebigkeit*) of a particular action; the direction an organic process takes in order to reach a certain stable end state. In the course of development, while passing through ontogenetic stages, the organism constructs itself in order to acquire new properties. The directionality of this process and the way it affects the means of constructing traits is what von Baer understands as *Ziel*.

3.3 Musical Metaphors

The regulation of the various developmental pathways towards the target state at each ontogenetic stage is thus the starting point for teleological explanations of development. As already mentioned, this gives the developing organisms a relevant degree of explanatory power (beyond their genetic bases; cf. section 1). How did von Baer explain these regulatory abilities? The most important explanatory aid provided by von Baer is that of a metaphor: the musical metaphor. This is another element that von Uexküll adopted from von Baer. The work of both thinkers is full of metaphors that refer to musical phenomena.

There are various metaphors based on musical phenomena - such as rhythm, tones, or melodies. The most interesting, however, is that of *harmony*. As von Baer points out, “the reciprocal interconnections of organisms with one another and their relationship to the universal materials that offer them the means for sustaining life, is what has been called the *harmony* of nature, that is a relationship of mutual *regulation*” (1886b: 228–229; emphasis added). The harmony of living beings arises from the mutual regulation of the various parts of the system and its environment. The other musical metaphors are therefore subordinate to the metaphors of musical harmony. Just as musical harmony consists of the relationship between the elements (notes, chords) of a harmonic arrangement, harmony in living beings is based on the connection between the different elements of a living system and its environment.

It is important to understand the explanatory role of a metaphor. Metaphors are heuristic devices that guide our knowledge and investigation. They help us to think about things and to search for a scientific explanation. In the context of our analysis, von Baer’s use of metaphors is closely linked to the restriction imposed by Kant that there can be no science that explains teleological phenomena. If we think of teleological physiology (cf. section 1), the scientific disciplines that deal with it were built up in the twentieth century (dynamic systems theory, cybernetics, artificial intelligence, complex systems theory, etc.). Certainly, these fields did not exist when Kant was thinking about teleology. If we look at the development of teleology, it seems that von Baer is in a similar situation. He did not have the explanatory weapons to deal with teleological development. That is one of the reasons why he uses a metaphor. So the question is whether or not there are scientific disciplines that deal with teleological development.

This question has already been answered in section 1. The developmental turn aims to construct development as a goal-oriented theory. In this sense, several scientific disciplines attempt to explain development teleologically - e.g. post-genomics, eco-devo, niche construction theory or development systems theory. Certainly, this does not mean that we already have a complete and solid theory of teleological development, but new areas of research and theoretical approaches have been developed in recent decades that were certainly not available from Bser’s knowledge. This does not mean that musical metaphors must become devoid of explanation as the sciences develop. Metaphors still retain many heuristic values that are independent of the development of science

(Haraway, 1976). Indeed, musical metaphors are frequently used today in the context of the developmental turn (e.g. Noble, 2006; Oyama, 2001; Robert, 2004).

Importantly, the above areas of research are dedicated to understanding the regulatory capacities of developmental systems, that is, what musical metaphors attempt to illuminate. Analyzing phenomena such as phenotypic plasticity or niche construction is precisely about how developmental systems are able to regulate their relationship with their environment during ontogeny. At the cellular level, molecular epigenetics, anchored in a post-genomic view of genetics, seeks to discover the different ways in which cells integrate the various information resources to regulate cellular development.

4. Conclusion

The connections between section 2 and section 3 are related to the influence of von Baer on von Uexküll's career. In section 2, I argued that the concept of *Umwelt* is a central explanatory component for our goal of developing an alternative, non-neo-Darwinian evolutionary theory. This explanatory role plays in explaining development beyond the gene-centre paradigm, i.e., in conceiving of development as a context-dependent, agent-driven process - as a goal-directed natural phenomenon. In section 3 we saw von Baer's critique of the Darwinian view of his time; the critique is precisely that it is impossible to avoid the goal-directededness of development. By tracing this historical connections, and taking von Uexküll as a founder of modern biosemiotics, it is not unexpected that "it can be concluded that the majority of biosemioticians have been quite critical toward the neo-Darwinian school of thought, appreciating considerably higher the views of the followers of Karl Ernst von Baer" (Kull, 2004: 103).

Von Baer's conception of teleological development is based on the idea that the developmental system is capable of regulating its means towards goals. Development is a continuous sequence of stages in which changes take place; at each stage, a corresponding change in form and function is mediated by the organism itself. If we combine this view with the concept of *Umwelt* and its place in developmental theory, we come to the conclusion that the construction of the *Umwelt* is a central precondition for the regulatory processes in each ontogenetic stage, in each ontogenetic change.

Another observation that emerges from our analysis concerns the connection between von Baer's distinction between *Ziel* and *Zweck* and the notion of *Umwelt* itself. As already mentioned, the adherence to the word *Ziel* is meant to avoid any non-natural connotation to teleology. The concept of *Umwelt* might suffer from a similar scenario, insofar as one may understand that the *Umwelt* in a human-like conception of the world. If we are to ascribe an explanatory role to *Umwelt* in development - e.g. in cell development or morphogenesis - a different, less antrphomorphic interpretation is required, just as one should avoid the notion of *Zweck* in biology. The *Umwelt*, therefore, should not have to be understood in this way in order to be explanatorily useful. If we understand it in signalling terms where different information is exchanged in different physico-chemical processes - as suggested in section 2.2 - then the *Umwelt* is the construction of a context-dependent ability to act on the environment and regulate the organism's own structure and functionality; i.e. as the construction of organism's phnoemonology that allows organic systems to be treated as agents in their own right.

This article is also about the foundations of telological explanations. By looking at this issue from a historical perspective, I argue that developmental biology is now building its own theoretical and experimental foundations for dealing with teleological development. While Kant neglected this possibility and von Baer relied on a metaphor, the biological sciences now provide the correct answer to the old puzzle. This article contributes to constructing a teleological view of development that is necessary for a new evolutionary paradigm. On the way to realising the developmental turn, it is necessary to understand various interdisciplinary, historical and theoretical contexts; in aiming to understand the adaptive nature of life or, as Darwin said, endless forms most beautiful, it is not possible to avoid the beauty of the complexity of developmental processes, insofar as "it is

precisely the recognition of the mutual interrelation of all the processes in nature and the harmony in their institutions that gives them the greatest pleasure" (von Baer 1886a: 51).

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References

Ågren, J. A. (2021). *The Gene's-Eye View of Evolution.* Oxford: Oxford University Press.

Amundson, R. (2005). *The Changing Role of the Embryo in Evolutionary Thought: Roots of Evo-Devo.* Cambridge: Cambridge University Press.

Baedke, J. (2018). O organism, where art thou? Old and new challenges for organism-centered biology. *Journal of the History of Biology,* 52(2), 293– 324. doi: 10.1007/s10739-018-9549-4

von Baer, K. E. (1886a). *Uber den Zweck in den Vorgängen der Natur — Erste Hälfte. Uber Zweckmäßigkeit oder Zielstrebigkeit überhaupt.* In Reden gehalten in wissenschaftlichen Versammlungen und kleinere Aufsätze vermischten Inhalts. Zweiter Theil. Studien aus dem Gebiete der Naturwissenschaften (pp. 49–106). Braunschweig: Friedrich Vieweg und Sohn.

von Baer, K. E. (1886b). *Uber Zielstrebigkeit in den organischen Körpern insbesondere.* In Reden gehalten in wissenschaftlichen Versammlungen und kleinere Aufsätze vermischten Inhalts. Zweiter Theil. Studien aus dem Gebiete der Naturwissenschaften (pp. 170–234). Braunschweig: Friedrich Vieweg und Sohn.

Balari, S., & Lorenzo, G. (2014b). The end of development. *Biological Theory*, 10(1), 60–72. doi: 10.1007/s13752-014-0180-0

Barandiaran, X., Di Paolo, E., & Rohde, M. (2009). Defining agency: Individuality, normativity, asymmetry, and spatio-temporality in action. *Adaptive Behavior,* 17(5), 367–386. doi: 10.1177/105971230934381

Bateson, P. (2005). The return of the whole organism. *Journal of Biosciences,* 30(1), 31–39. doi: 10.1007/bf02705148

Brentari, C. (2015). *Jakob von Uexkull: the discovery of the umwelt between biosemiotics and theoretical biology*. Dordrecht. Springer

Campbell, J. H. (1994). Organisms create evolution. In J. H. Campbell & J. W. Schopf (Eds.), *Creative Evolution?!* (pp. 85–102). Boston, MA: Jones & Bartlett.

Christensen, W., & Bickhard, M. H. (2002). The process dynamics of normative function. *The Monist*, 85(1), 3–28. doi: 10.2307/27903755

Dawkins, R. (1982*). The Extended Phenotype*. Oxford: Oxford University Press.

Deacon, T. W. (2015). Steps to a science of biosemiotics. *Green Letters*, *19*(3), 293-311.

Deacon, T. W. (2021). How molecules became signs. *Biosemiotics*, *14*(3), 537-559.

Feiten, T. E. (2020). Mind after Uexküll: A foray into the worlds of ecological psychologists and enactivists. *Frontiers in Psychology*, *11*, 480.

Fultot, M., & Turvey, M. T. (2019). Von Uexküll's theory of meaning and Gibson's organism–environment reciprocity. *Ecological Psychology*, *31*(4), 289-315.

Gilbert, S. F., & Barresi, M. J. F. (2010). *Developmental Biology* (11th ed.). Sunderland, MA: Sinauer.

Gilbert, S. F., & Epel, D. (2015). *Ecological Developmental Biology: The Environmental Regulation of Development, Health, and Evolution.* Sunderland, MA: Sinauer.

Godfrey-Smith, P. (2009). *Darwinian Populations and Natural Selection*. Oxford: Oxford University Press.

Griffiths, P. E., & Stotz, K. (2013). *Genetics and Philosophy. An Introduction.* Cambridge: Cambridge University Press.

Heras-Escribano, M. (2019). *The Philosophy of Affordances.* Cham: Palgrave Macmillan.

Heras-Escribano, M., & De Jesus, P. (2018). Biosemiotics, the extended synthesis, and ecological information: Making sense of the organism-environment relation at the cognitive level. *Biosemiotics*, 11(2), 245–262. doi: 10.1007/ s12304-018-9322-2

Haraway, D. J. (1976). *Crystals, fabrics, and fields: Metaphors that shape embryos*. Yale University Press.

Huneman, P. (2010). Assessing the prospects for a return of organisms in evolutionary biology. *History and Philosophy of the Life Sciences,* 32(2-3), 341–371. doi: 10.2307/23335078

Jablonka, E., & Lamb, M. J. (2020). *Inheritance Systems and the Extended Evolutionary Synthesis.* Cambridge: Cambridge University Press.

Kauffman, S. (2019). *A World Beyond Physics: The Emergence and Evolution of Life.* Oxford: Oxford University Press.

Keller, E. F. (2002). *The Century of the Gene.* Cambridge, MA: Harvard University Press.

Kull, K. (1999). Biosemiotics in the twentieth century: A view from biology. *Semiotica*, 127(1-4), 385–414. doi: 10.1515/semi.1999.127.1-4.385

Kull, K. (2001). Jakob von Uexküll: An introduction. *Semiotica*, 2001(134), 1–59. doi: 10.1515/semi.2001.013

Kull, K. (2004). Uexküll and the post-modern evolutionism. *Σημειωτκή-Sign Systems Studies*, *32*(1-2), 99-114.

Kull, K. (2021). The aim of extended synthesis is to include semiosis. *Theoretical Biological Forum,* 119-132.

Lenoir, T. (1981). Teleology without regrets. The transformation of physiology in Germany: 1790–1847. *Studies in History and Philosophy of Science Part A, 1*2(4), 293–354. doi: 10.1016/0039-3681(81)90019-4

Lenoir, T. (1989). *The Strategy of Life: Teleology and Mechanics in Nineteenth-Century German Biology*. Chicago: The University of Chicago Press.

Levins, R., & Lewontin, R. C. (1985). *The Dialectical Biologist.* Cambridge, MA: Harvard University Press.

Lewontin, R. C. (1974). *The Genetic Basis of Evolutionary Change.* New York: Columbia University Press.

Lewontin, R. C. (2000). *The Triple Helix: Gene, Organism, and Environment.* Cambridge, MA: Harvard University Press.

Maynard Smith, J. (1982). *Evolution and the theory of games*. Cambridge, UK: Cambridge University Press

Mayr, E. (1961). Cause and effect in biology: Kinds of causes, predictability, and teleology are viewed by a practicing biologist. *Science*, 134(3489), 1501–1506. doi: 10.1126/science.134.3489.1501.

Mayr, E. (1974). Teleological and teleonomic, a new analysis. In R. S. Cohen & M. W. Wartofsky (Eds.), *Methodological and Historical Essays in the Natural and Social Sciences* (pp. 91–117). Dordrecht: Reidel.

McLaughlin, P. (2000). *What Functions Explain: Functional Explanation and Self-Reproducing Systems.* Cambridge: Cambridge University Press.

Michel, G. F., & Moore, C. L. (1995). Developmental Psychobiology: An Interdisciplinary Science. Cambridge, MA: MIT Press.

Minelli, A. (2011). Animal Development, an Open-Ended Segment of Life. *Biological Theory,* 6(1), 4–15. doi: 10.1007/s13752-011-0002-6

Moreno, A., & Mossio, M. (2015). Biological Autonomy. A Philosophical and Theoretical Inquiry. Dordrecht: Springer.

Müller, G. B., & Newman, S. A. (Eds.). (2003). *Origination of Organismal Form: Beyond the Gene in Developmental and Evolutionary Biology.* Cambridge, MA: The MIT Press.

Nicholson, D. J. (2014). The return of the organism as a fundamental explanatory concept in biology. *Philosophy Compass,* 9(5), 347–359. doi: 10.1111/phc3 .12128

Nicholson, D. J., & Gawne, R. (2015). Neither logical empiricism nor vitalism, but organicism: What the philosophy of biology was. *History and Philosophy of the Life Sciences*, 37(4), 345–381. doi: 10.1007/s40656-015-0085-7

Nicholson, D. J., & Dupré, J. (Eds.) (2018). *Everything flows: towards a processual philosophy of biology*. Oxford University Press.

Noble, D. (2006). *The Music of Life: Biology Beyond Genes.* Oxford: Oxford University Press.

Nuño de la Rosa, L. (2023). Agency in Reproduction. *Evolution & Development*. (25) 418-429.

Odling-Smee, J., Laland, K. N., & Feldman, M. W. (2003). *Niche Construction: The Neglected Process in Evolution.* Princeton, NJ: Princeton University Press.

Oyama, S. (2001). Terms in tension: What do you do when all the good words are taken? In S. Oyama, R. Gray, & P. E. Griffiths (Eds.), *Cycles of Contingency: Developmental Systems and Evolution* (pp. 177–193). Cambridge, MA: The MIT Press.

Oyama, S., Gray, R., & Griffiths, P. E. (Eds.). (2001). *Cycles of Contingency: Developmental Systems and Evolution.* Cambridge, MA: The MIT Press.

Rama, T. (2021). Biosemiotics at the bridge between Eco-Devo and representational theories of mind. *Rivista Italiana di Filosofia del Linguaggio*, 15(2), 59–92. doi: 10.4396/2021203

Rama, T. (2022). Agential Teleosemantics. PhD Thesis. Autonomous University of Barcelona.

Rama, T. (2023). Evolutionary causation and teleosemantics. In *Life and Mind: New Directions in the Philosophy of Biology and Cognitive Sciences* (pp. 301-329). Cham: Springer International Publishing.

Rama, T. (Forthcominga). Populational and Invidual Niche Construction: a Critical Analysis

Rama. T. (Forthcomingb). A Cognitive Revolution in Theoretical Biology?

Robert, J. S. (2004). *Embryology, Epigenesis and Evolution: Taking Development Seriously.* Cambridge: Cambridge University Press.

Sharov, A., & Tønnessen, M. (2021). *Semiotic agency*. Springer International Publishing.

Shea, N. (2013). Inherited representations are read in development. *The British Journal for the Philosophy of Science*, 64(1), 1–31. doi: https://doi.org/10.1093/bjps/axr050

Smolin, L. (2013). *Time reborn: From the crisis in physics to the future of the universe*. HMH.

Sober, E. (1984). *The Nature of Selection. Evolutionary Theory in Philosophical Focus.* Chicago, IL: The University of Chicago Press.

Stotz, K. (2017). Why developmental niche construction is not selective niche construction: And why it matters. *Interface Focus,* 7(5), 20160157. doi: 10.1098/rsfs.2016.0157

Sultan, S. E. (2015). *Organism & Environment: Ecological Development, Niche Construction, and Adaption.* Oxford: Oxford University Press.

Tønnessen, M., Magnus, R., & Brentari, C. (2016). The biosemiotic glossary project: Umwelt. *Biosemiotics*, *9*, 129-149.

von Uexkull, J. (1923). *Weltanschauung und Gewissen. Deutsche Rundschau*, 197, 253–266.

von Uexkull, J. (1926). *Theoretical Biology.* London: Kegan Paul, Trench, Trubner & Co.

von Uexkull, J. (1936). *Niegeschaute Welten. Die Umwelte meiner Freunde*. Berlin: S. Fischer Verlag.

von Uexküll, J. (1992). A stroll through the worlds of animals and men: A picture book of invisible worlds. *Semiotica*, 89(4), 319-391.

Wagner, G. P. (2014). *Homology, Genes, and Evolutionary Innovation.* Princeton, NJ: Princeton University Press.

Walsh, D. M. (2003). Fit and diversity: Explaining adaptive evolution. *Philosophy of Science,* 70(2), 280–301. doi: 10.1086/375468

Walsh, D. M. (2012b). Situated adaptationism. In W. P. Kabasenche, M. O'Rourke, & M. H. Slater (Eds.), *The Environment: Philosophy, Science, and Ethics* (pp. 89–116). Cambridge, MA: The MIT Press.

Walsh, D. M. (2013). The affordance landscape: The spatial metaphors of evolution. In G. Barker, E. Desjardins, & T. Pearce (Eds.), *Entangled Life. Organism and Environment in the Biological and Social Sciences* (pp. 213– 236). Dordrecht: Springer.

Walsh, D. M. (2015). *Organisms, Agency, and Evolution.* Cambridge: Cambridge University Press.

West-Eberhard, M. J. (2003). *Developmental Plasticity and Evolution.* Oxford: Oxford University Press.

Williams, G. C. (1992). *Natural selection: Domains, levels, and challenges*. Oxford University Press.