

Philosophical Dimensions of Individuality

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Abstract

Although natural philosophers have long been interested in individuality, it has been of interest to contemporary philosophers of biology because of its role in different aspects of evolutionary biology. These debates include whether species are individuals or classes, what counts as a unit of selection, and how transitions in individuality occur evolutionarily. Philosophical analyses are often conducted in terms of metaphysics (“what is an individual?”), rather than epistemology (“how can and do researchers conceptualize individuals *so as to address some of their scientific goals?*”). We review several philosophical distinctions in order to shift attention from metaphysics to epistemology. Many controversies involve epistemological differences rather than metaphysical disagreement. This implies that a pluralist stance about individuality in biology is warranted and has metaphysical consequences because the pluralism emerges from the diversity of scientific interests that investigate the complexity of living phenomena.

Keywords: individuality, individuation, monism, parts, pluralism, wholes

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<A>Introduction

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Natural philosophers have long been interested in individuality and the relationship between parts and wholes. A key source for this interest has been empirical examples from animals and plants where intuitive notions of individuality seem to break down, such as in cases of colonial marine invertebrates or insect metamorphosis. In the early modern period, Leibniz offered a novel view of nested individuality in which genuine individuals could be compositional elements or parts of larger individuals *ad infinitum* (Smith 2011). This view was inspired by microscopical discoveries of Leeuwenhoek and his contemporaries and provided strong persistence conditions for individuals through major life history transformations, such as metamorphosis and even death. Increased attention to complex life cycles of terrestrial and marine invertebrates in the 19th century led to an explosion of competing perspectives on how to conceptualize individuality (Elwick 2007). For example, Rudolf Leuckart tried to articulate general laws about biological individuals and their part-whole relations by interpreting the alternation of generations as an instantiation of the division of labor, where the different parts of a colonial organism were individuals in their own right (Nyhart and Lidgard 2011).

More recently, individuality has been of primary interest to contemporary philosophers because of its crucial role in different aspects of evolutionary biology. These debates include whether species are individuals or classes, what counts as a unit of selection, and how transitions in individuality occur evolutionarily. These discussions often rely on prior accounts of individuality to determine *whether* the concept is applicable, such as in the case of species, and *when* the concept is applicable, such as in cases where there is a question about whether a group

can exhibit properties that are not simply an aggregate sum of its individual member organisms. For example, Ellen Clarke reviews thirteen distinct conceptions of individuality and argues that the situation demands a solution: “there is a real problem of biological individuality, and an urgent need to arbitrate among the current plethora of solutions to it ... there is a choice to be made about which definition, or how many definitions to accept” (Clarke 2010, 312 & 314). One reason for the urgency derives from the needs of evolutionary theory, which must be able to identify individuals in order to measure reproductive fitness: “counting the units enables us to predict and explain how the traits of such units are changing over time, under the action of natural selection” (Clarke 2013, 429). Clarke offers “a monistic account of organismality” to solve the problem of individuality (2013, 429); her unified account says what a biological individual is in all circumstances.

We will return to Clarke’s particular proposal below (in the subsection on Evolutionary Individuality), but here it serves as an introductory illustration of how philosophical analyses are often conducted in terms of metaphysics (“what is an individual?”), rather than epistemology (“how can and do researchers conceptualize individuals to address different scientific goals?”).¹ As Clarke reminds us, a “plethora of solutions” are on offer—different ways that researchers conceptualize individuals. These include displaying the capacity of reproduction, having a single-cell bottleneck during the life cycle, or exhibiting a separation of germ and soma. A metaphysical framing of the issue suggests that one property or a combination of several can be used to univocally answer the question of what an individual is. This metaphysical orientation often takes the shape of fundamental theorizing. Many philosophers of science assume that our best fundamental theories inform us about the basic furniture of the world. The necessary and sufficient conditions for individuality are ascertained from abstract theorizing that is fundamental

to all of biology; in this case, evolutionary theory adopts the mantle of fundamentality.² Once formulated, the fundamental theory of what an individual is governs scientific practice; i.e., it tells scientists what to count when measuring fitness and drawing evolutionary inferences. The metaphysics of what an individual is determines how biologists do their epistemology or go about the practice of individuation.

In this chapter we review and characterize several philosophical distinctions pertinent to individuality, such as metaphysics versus epistemology, individuals versus classes, and monism versus pluralism, in light of the diverse contributions to the volume. We pay special attention to the way metaphysical assumptions have animated controversies, past and present. Both biological and philosophical researchers have frequently assumed that they were engaged in fundamental theorizing to determine what an individual is, but this assumption is often unnecessary and unwarranted. Indeed, our aim is to shift attention in discussions of individuality from metaphysics to epistemology. We argue that some of these controversies involve epistemological differences rather than metaphysical disagreement. In addition to shedding light on several cases explored in the contributions, this reorientation implies that a pluralist stance about biological individuality is warranted. The epistemological conclusion resulting from this reorientation yields consequences for metaphysics because the pluralism arises out of different scientific interests that produce distinct approaches to the complexity of living phenomena in the world.

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<A>**Individuality and the Return of Metaphysics**

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Despite a predisposition against metaphysics in early and mid-20th century philosophy,

where epistemology and the analysis of language were favored in the study of the sciences, the past twenty-five years have been marked by a revival of metaphysical theorizing as a central area of analytic philosophy of science.³ This renaissance of metaphysical theorizing has run in parallel with analyses from a variety of philosophers interested in questions about the identity of objects, parts and wholes, the persistence of objects through time and across change, and accidental versus essential properties of individuals. For example, mereology—the logic of parts and wholes—has been pursued as an alternative to set theory, where parts and wholes are concrete objects unlike a set, which is an abstract entity even when having concrete objects as its members (Varzi 2014). However, mereological theory does not put empirical constraints on what objects can count as a whole (e.g., a *biological* individual), and instead offers a general logical characterization of the relationship between a part and the whole or among different parts of a whole.

One prominent metaphysical task is to articulate a coherent framework of change that recovers how an object can be the same entity at two different time points. To this end, some metaphysicians conceptualize a material object as a four-dimensional entity composed of three spatial dimensions and one temporal dimension or extended region of time during which it exists. On this type of account, objects have temporal parts in addition to spatial parts (Hawley 2010).⁴ One paradox of this view is that an object cannot (technically speaking) change because two of the four-dimensional object's temporal parts—no matter how different they are—are still two existing parts of one overall object. Finally, metaphysicians often distinguish between an individual's accidental and essential properties (Robertson and Atkins 2013). An accidental property is one an individual happens to have but which it could lack. Thus, an individual could change any of its accidental properties and still remain the same individual. In contrast, the

individual must possess its essential properties because they are what it is to be this individual. If any of these essential properties were absent then the object would not exist (any longer). This is about the defining properties of a *particular* individual, but it does not address the properties that define the category “individual,” in particular which objects qualify as biological individuals (e.g., organisms).

These debates about mereology, temporal parthood, and essential properties in analytic metaphysics are disconnected from the sciences and biology in particular. They are conducted in full abstraction from concrete details and pertain to questions that are not specifically biological (e.g., the very possibility of change, in general). As we observed, philosophical discussions were not always disconnected from empirical cases and philosophers’ reflections on individuality have been motivated by intriguing biological and other material examples. In contrast to contemporary analytic metaphysicians, philosophers of biology have addressed some of these examples when treating biological individuality, such as whether physiologically linked and genetically identical stands of quaking aspen are a group of individual trees or a single individual. However, many of these philosophers of biology share a methodological assumption with analytic metaphysicians; namely, that there is a single correct account of what an individual is or how we should understand individuality. Just as an account of temporal parthood in analytic metaphysics is intended to cover all cases of parts through time, so also a fundamental theory of individuality in philosophy of biology is usually intended to cover all cases of biological individuals. This monist impulse—there is a single correct account—derives from a type of metaphysical orientation that assumes a univocal parsing of the world into individuals that can be counted and non-individuals that must be treated otherwise.⁵ Although we favor an emphasis on biological examples that provoke questions about what counts as an individual, we resist the monist impulse by

reorienting analyses of individuality epistemologically. In order to achieve this reorientation, we first need to see the contours of some discussions in contemporary philosophy of biology.

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<A>**Philosophical Interest in Biological Individuality**

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Species as Individuals

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A classic debate in biology concerns how to conceptualize species, especially given their mutability. Biologists and philosophers jointly effected a major transformation in this debate with the idea that a species is an individual. Proposed by Michael Ghiselin (1974) and elaborated by David Hull (1978), this conceptualization challenged a traditional and predominant idea that a particular species is a natural kind. On the natural kind view, organisms are *members* of a species; on the individual view, organisms are *parts* of a species-individual, just like cells are parts of an individual organism. Implicit in the natural kind view is a commitment to some form of similarity among species members, possibly even essential properties shared by all members. An individuality thesis has no such commitment; cells can be quite different and still be parts of one individual (e.g., mammalian blood cells that lack a nucleus). Likewise, the variation among organisms within a species-individual need not be circumscribed by a morphological similarity metric or any presumption about shared genetic composition.

More generally, the species-as-individuals thesis was meant to accommodate the fact that a species taxon: (i) is denoted by a proper name; (ii) is a particular object that occupies a certain region of space and exists during some period of time; and, (iii) exhibits variation at any time and can be subject to significant (evolutionary) change across time, while still being the same

species. An individual has these three basic properties, whereas a natural kind is often understood not to have them, especially spatiotemporal boundedness and mutability. This same line of argument has been extended to higher taxa and homologues. Thus, the higher taxon “mammals” is considered an individual, and homologous structures in different organisms, such as kidneys, are not members of a natural kind but parts of a homologue-individual (Ereshefsky 2009; Wagner 2014; see also Brigandt this volume).⁶

The notion of “individual” at work in these arguments is relatively generic because it was typically assumed that the important difference is marked by distinct ontological categories: individuals *versus* natural kinds. This notion does not provide more specific conditions on individuality, which might be desirable for distinguishing particular species of microorganisms as individuals from an individual organism containing interacting microorganisms from different taxa. This highlights a lacuna in discussions of species as individuals: even though there have to be criteria for determining which organisms constitute a species-individual (and which do not), most proponents of the species-as-individuals thesis have not explicitly addressed those criteria. A key reason for this lacuna is that species-as-individuals proponents associate such criteria with the membership conditions for natural kinds (Ereshefsky 2010).

Although the species-as-individuals thesis has become near orthodoxy among both biologists and philosophers, Richard Boyd (1999a) introduced a revised conceptualization of natural kinds—the *homeostatic property cluster* (HPC) account—that does not involve traditional assumptions (e.g., natural kinds are spatiotemporally unrestricted), and therefore permits species and other biological entities to be natural kinds. A key element of the HPC account is that a whole cluster of properties, which are merely correlated, can characterize a kind. As a consequence, a particular member of a kind need not have all of these properties, and

any one property need not be found in all kind members (e.g., members of a species). While this element makes room for diversity within a kind (i.e., for a species taxon to exhibit variation), another element severs the commitment to these characteristic properties of a kind being intrinsic (e.g., genetic composition or morphological similarity). Instead, relational properties, such as “having the same ancestor as [another organism]” or “being able to interbreed with [another organism],” which explicitly include criteria used in species concepts, are part of the homeostatic cluster of properties characterizing the kind. These types of relational properties are fully compatible with phenotypic diversity and evolutionary change.⁷

One positive feature of the HPC approach is that it is a general account of kinds in biology and other special sciences. An HPC approach goes beyond a narrow focus on species and attempts to capture other kinds, such as stem cells and genes, which exhibit considerable internal diversity (Wilson et al. 2007).⁸ Another significant feature, especially in the present context, is that the HPC approach introduces *epistemic* considerations into a discussion about species as individuals that has tended to focus exclusively on *ontological* issues about the nature of species. By asking what classificatory, explanatory, and other scientific purposes are addressed by grouping different objects together, regardless of whether they are viewed as forming a kind or an individual (Brigandt 2009; Boyd 1999a), the strategy of the HPC account moves away from the metaphysically framed question—*what are species*—to epistemologically framed questions—*how and why are biologists grouping organisms into species*.

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Evolutionary Individuality

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Recent conceptual reflection has concentrated on the issue of biological individuality in

evolutionary theory, where there has been renewed attention to how individuality originates evolutionarily (e.g., see the contributions in Bouchard and Huneman 2013). Philosophical accounts of individuality often try to capture two kinds of challenging phenomena. The *first set of phenomena* involves cases where individuality is difficult to assess across the diversity of life forms. An aspen tree, for instance, is connected underground to other trees within a whole grove of aspen. These interlinked aspen trees are genetically identical so that the spatially circumscribed boundedness and genetic uniqueness often used to define paradigmatic individuals do not hold. There are many different examples of colonies of organisms with highly integrated causal linkages and specialized roles among their constituent organisms. Sometimes, as in the case of an ant colony, most organisms cannot even reproduce—resulting in something analogous to the separation of germ-line cells from somatic cells and a bottleneck across generations, which are observed in many (though not all) metazoans. Such a “superorganism” colony raises the question of whether it is a biological individual. The constituent organisms comprising a Portuguese man-of-war (*Physalia physalis*) exhibit a functional division of labor, spatial contiguity, and form a spatially bounded whole—like a paradigmatic multicellular individual. Since these constituent organisms cannot survive in isolation, one could argue that they are not individuals, unlike the whole Portuguese man-of-war, even though the latter is often conceptualized as a colony *composed of* multiple individuals.

The widespread phenomenon of symbiosis complicates these issues further, given that a putative individual can include organisms from very different taxa. Many of these seemingly strange cases involve multicellular organisms, but philosophers have increasingly scrutinized the realm of microbes (O’Malley 2014). Microbial communities can involve the same kind of close interactions and functional specialization observed in paradigmatic individuals, but they also

exhibit lateral gene transfer, all of which can provide evolutionary coherence without genetic identity (Ereshefsky and Pedroso 2013, 2015; Clarke 2016).

Theories of individuality typically seek necessary and sufficient conditions for ascertaining when biological objects are individuals (e.g., Clarke 2013) or offer dimensional analyses that return judgments in terms of degrees of individuality (e.g., Godfrey-Smith 2009). The properties often associated with individuality go together in many metazoans: being internally contiguous and having a spatial boundary, having specialized and physiologically integrated parts, being able to reproduce, bearing adaptations, and having mechanisms that reduce internal evolutionary conflict, such as germ-soma separation (Clarke 2010). However, the various non-standard cases demonstrate that across all taxa, different criteria of individuality do not always align.⁹ One philosophical response is to use an HPC approach (introduced above in the subsection on Species as Individuals) because it is intended to make room for diversity within a complex kind. Rob Wilson and Matt Barker (2013) argue that the ontological category of “biological individual” is characterized by several different properties. These properties are correlated, but only imperfectly, so that many organisms do not possess all of the characteristic properties and some non-organisms turn out to be biological individuals.

A more nuanced strategy is to treat some branches of the tree of life differently. For each taxon or lineage, the goal would be to offer some precise criteria of individuality that should be met in this circumscribed context. Ellen Clarke (2012) adopts this approach by looking for criteria in plants that have biological effects analogous to situations known from animals. For example, instead of using the animal-specific separation of germ and soma as a criterion for plants as well, Clarke encourages us to concentrate on mechanisms that contribute to the effect of producing heritable variance in fitness. Even though plants do not have the reproductive division

of labor found in animals, they exhibit other mechanisms that have the same effect, such as apomictic reproduction or meristem stratification. Thus, while such criteria were originally derived from abstract considerations about individuality (i.e., having the effect of producing heritable variance in fitness), the particular account is plant-specific. More recently, Clarke (2013) has offered an account that relies on the concept of multiple realization. The individuating mechanisms that underlie individuality can be instantiated in many ways; the particular way in which a mechanism is instantiated in a taxon is not as crucial. The two abstract mechanisms on this account are: (a) policing mechanisms that prevent an object's constituents from being subject to differential selection; and, (b) demarcating mechanisms that facilitate an object's integrity so that it can undergo selection. There are many ways to police or demarcate, hence multiple realization, but the mechanisms must be present. According to Clarke, a biological individual is any object that exhibits both types of mechanisms simultaneously.

The *second set of phenomena* that philosophical accounts of individuality attempt to capture is major evolutionary transitions and the evolution of individuality. How did unicellular organisms give rise to multicellular organisms? How did some multicellular animals come to form superorganisms? In addition to providing a characterization of what a biological individual is, these questions require an account of how individuals emerge at new levels of organization. For this second set of phenomena, the explanatory focus is on natural selection and the concomitant notions of fitness, conflict, and cooperation (Sterner this volume). Once a "genuine" individual at a higher level has arisen, mechanisms must be in place to eliminate (or minimize) fitness differences among its constituent parts. For example, germ-soma separation can eliminate evolutionary conflict among constituent cells so that the multicellular animal is the level at which selection operates. Under these conditions, any fitness difference and selection at the level of

constituent cells—though potentially beneficial (e.g., clonal selection in lymphocytes) or harmful (e.g., cancer)—would be evolutionarily inert. This encourages a theoretical orientation that highlights the capacity to eliminate fitness differences among constituent parts as a critical prerequisite to stabilizing new types of individuality. By implication, mechanisms that suppress conflict at sub-organismal levels become criteria for individuality, and entities that do not exhibit these mechanisms can be considered suspect as individuals.

In addition to the elimination of conflict and facilitation of cooperation *after* an individuality transition, the transition process itself must be explained. During a transition in individuality, there are still potential evolutionary conflicts among the lower-level individuals; some have the opportunity to cheat on and exploit the cooperation within the colony. To the extent that natural selection favors cooperation in the transition process, it is an instance of group selection because the colony is still a group of lower-level individuals and not yet a higher-level individual. For this reason, philosophers invoke multilevel selection theory (Okasha 2006). Moreover, even in highly derived organisms, the formation of chimeras that have genetically heterogeneous cellular constituents regularly occurs. Slime molds (dictyostelids and myxomycetes) have a life cycle where unicellular conspecifics aggregate to form a multicellular “organism.” In many sponges, cnidarians, bryozoans, and ascidians, two or more multicellular organisms—which are conspecific, yet genetically distinct—fuse to form a chimera (“intergenotypic fusion”). Apart from creating problems for criteria of individuality that insist on genetic homogeneity, genetic chimeras raise questions for selection-based explanations given that some cheaters can be horizontally transmitted (Grosberg and Strathmann 2007).

Inspired by the role that individuals play in evolutionary theory and the difficult questions raised by the evolution of individuality, most contemporary philosophical accounts of

individuality are evolutionary in orientation (Clarke 2012). These accounts construe a biological individual as the bearer of fitness and the entity on which natural selection operates. The notion of fitness presupposes a conception of how many offspring a parent has, so one must define which biological object qualifies as a parent individual, and which one counts as a separate offspring individual. Peter Godfrey-Smith (2009) approaches these questions by starting from populations (rather than individuals), which he terms “Darwinian populations” if they are able to undergo evolution by natural selection. Any member of such a population is, derivatively, a “Darwinian individual,” which can be an entity from genes to superorganisms. Godfrey-Smith conceptualizes individuality using five quantitative properties that describe how Darwinian populations can differ: (1) heritability (i.e., the degree of parent-offspring similarity), (2) the abundance of variation, (3) the degree of competition within the population (i.e., the extent to which a fitness gain in one individual lowers the fitness of others), (4) the smoothness of the fitness landscape (i.e., the extent to which a small change in an individual’s traits results in a small change in fitness), and (5) the degree to which reproductive fitness is determined by an individual’s internal character (as opposed to the influences from external features). This yields a five-dimensional space in which populations from different taxa occupy different positions. If all values for the properties are high, cumulative selection is possible and we are dealing with a paradigmatic Darwinian population. Other populations can exhibit different combinations of values for these properties and thereby exhibit different degrees of individuality for its members. An interesting feature of this account is that one individual may score higher than another individual in one dimension, but score lower (i.e., be less like a paradigmatic individual) with respect to a different dimension.¹⁰

In the history of biology, discussions of individuality tended to focus on physiological

features, especially prior to the advent of evolutionary theory. Diverging from the philosophical trend of focusing on evolutionary construals of individuality, Thomas Pradeu (2012) reinvigorates the earlier physiological perspective.¹¹ Pradeu's account of biological individuality and identity concentrates on having an immune system, which establishes and maintains an individual's boundaries. He claims that all known organisms have an immune system, including invertebrates, plants, and prokaryotes, and thereby possess the required basis for individuality. In addition to highlighting the physiological properties of the immune system, Pradeu argues that his approach captures the issues addressed by evolutionary accounts of individuality. Apart from preventing fitness conflicts at lower levels by mechanisms such as a separation between the germ-line and somatic cells, there also is the need to eliminate new variants by policing mechanisms, and the immune system is instrumental in this task.

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<A>**Shifting Attention from Metaphysics to Epistemology**

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Whether it is species construed as individuals or HPC kinds, or biological individuals defined evolutionarily or physiologically, these discussions are frequently conducted in terms of metaphysics ("what are species? what is an individual?"), rather than epistemology ("how can and do researchers conceptualize species or individuals to address different scientific goals?"). This is especially noticeable in the widespread assumption that historical construals of individuality in terms of physiology are false or subsidiary because biological individuals are primarily entities on which natural selection acts. From a metaphysical standpoint, it is not sufficient to provide characterizations of different criteria for individuality in the context of scientific practice; the situation calls for adjudicative action: "there is an urgent need for the

concept to be cleaned up” (Clarke 2010, 323). Thus it is not surprising that Ellen Clarke offers “a monistic account of organismality” (2013, 429). This urgent need derives from an assumption that there is a single correct or monistic account of what species or individuals are (metaphysics), regardless of the diverse and incompatible ways that scientists designate species and individuals (epistemology). We recommend reversing the orientation and starting from the vantage point of epistemology, then (if desired) proceeding to metaphysics.

How would one effect this reorientation? A first step is to explore answers to questions surrounding investigations into or reliant on a notion of biological individuality: how does a biologist decide to count individuals? how does a biologist decompose an individual into (meaningful) parts? What criteria *are* used and *should be* used depends on the underlying goals of inquiry (see also Lidgard and Nyhart this volume). This leads to a second step that explores answers to questions about *epistemic goals*: why does a biologist use a particular conceptualization of individuality? what methodological or explanatory purpose do certain decomposition criteria serve? In evolutionary inquiry, measurements of fitness are important for explaining changes in populations. With respect to this aim, a well-defined fitness value is a criterion of adequacy for an account of what an individual is. Similarly, some considerations for decomposing individuals into parts are motivated and constrained by the need to account for evolutionary transitions, which require the suppression of selective dynamics among constituent parts. In developmental inquiry, in contrast, spatial boundaries of parts are important for understanding changes during ontogeny. Therefore, a way of counting individuals or decomposing individuals into parts and tracking them through time has spatial separation as a criterion of adequacy (Love forthcoming). In physiological inquiry, functional interconnections are central to tracking activity in different systems. In such an epistemic context, counting

individuals may require taking into account mutualistic relationships and decomposing individuals into parts that transgress spatial boundaries and diverge from what is relevant to selective dynamics. In systematic inquiry, a robust operationalization of characters and character states, including the absence of features, is a criterion of adequacy for classification and building phylogenies. Therefore, criteria for counting individuals and decomposing them into parts can be heterogeneous, including both structural and functional features, as long as reliable and robust character codings are achieved.

This coarse-grained way of distinguishing how different goals constrain the epistemology of individuality or individuation can be traced out further to show that within evolutionary, developmental, physiological, or systematic inquiry (*inter alia*), there are additional constraints that operate during scientific inquiry. Although there are thematic differences in the conceptualization of individuals and their parts across disciplines, a more fine-grained tracing of the goals of inquiry within a discipline can reveal these additional constraints and suggests that there are not simply independent concepts of individuality across disciplines (e.g., developmental individuals, physiological individuals, evolutionary individuals, etc.). While one cannot exclude *a priori* the possibility of there being a unique definition of individuality that meets all relevant epistemic goals in all disciplines, the complexity of the biological world generally means that all-purpose concepts will not be useful even if they can be formulated. Given this, the diversity of goals in scientific research generates an expectation that there will always be many extant approaches to individuation and decomposition in biological inquiry, even within the same discipline. Importantly, when the presence of these different investigative and explanatory goals is explicitly acknowledged and their details are characterized, we can gain philosophical insights into how different approaches to what counts as individuals and their meaningful parts fruitfully

coexist in biological sciences.

Philosophers have drawn attention to this feature of biological epistemology for more than four decades (Kauffman 1971; Wimsatt 1974; Winther 2011). This raises the question of how most philosophical accounts of individuality could not have such a central element of scientific reasoning in view. *Fundamental theorizing* is one reason. Particular accounts advance specific properties as defining of individuality by treating one area of inquiry as the most fundamental. This then governs how individuals are understood in all areas of inquiry and is commensurate with a metaphysical orientation aiming to determine the single correct (monistic) account of what individuals are. The strategy of fundamental theorizing is most frequently observed with respect to individuality and evolutionary processes (see the above subsection on Evolutionary Individuality). A common justification is that the connection between individuality and fitness considerations is somehow primary or basic:

It is in an evolutionary context that the notion of the individual really does a lot of work. ... The notion of the biological individual is inextricably bound up with the notion of fitness. (Clarke 2010, 313)

Clarke's claim that biological individuals are "inextricably bound up" with concerns about survival and reproduction implies that the evolutionary perspective is somehow fundamental for all of biology when evaluating the nature of individuality. Although fundamental theorizing can be reductionist in character, focusing on lower levels of organization (e.g., molecular biology, chemistry, or physics), the present situation shows that "fundamental" is not always the lowest level of size and spatial parthood. In Clarke's claim, the notion of fitness from evolutionary biology is deemed to be most basic. Peter Godfrey-Smith holds a similar view: "The link between 'individuality' and reproduction is in some ways inevitable.

Reproduction involves the creation of a new entity, and this will be a countable individual” (Godfrey-Smith 2009, 86). Although his notion of individuality is more multifaceted than the one offered by Clarke, the underlying methodology of fundamental theorizing is shared. Even Thomas Pradeu (2012), who offers a physiological, immune system construal of biological individuality instead of an evolutionary definition, views his account as picking out the most fundamental feature of individuality because he maintains that evolutionary aspects of individuality are *derivatively* captured by the immunological properties he singles out.

The strategy of fundamental theorizing requires discounting individuation practices from areas of inquiry that lead to conflicts with the resulting account of individuality. Divergent characterizations used by biologists are seen as something to be eliminated or reinterpreted because the metaphysical account of individuality is meant to govern how biologists do their theorizing—it says *what individuals really are*. At best, different individuation practices can be subsumed within the fundamental account; at worst, they are mere tools that aid inquiry but lack correspondence to the structure of the world. While developmental or physiological inquiry speaks of individuals, these are “real” only if they map onto the account of individuality drawn from fundamental theorizing in the context of evolution.

Although the strategy of fundamental theorizing about evolutionary individuality has some benefits, its commitment to a monistic account and discounting of successful individuation practices that diverge from it are problematic and leave opaque the forms of reasoning we find among biologists engaged in individuation and decomposition. If we shift from metaphysics to epistemology in discussions of individuality by foregrounding the diverse goals of inquiry that shape and constrain what counts as individuals and their meaningful parts, then we are in a position to achieve at least three significant philosophical aims (see also Brigandt 2013; Sterner

2015; Lidgard and Nyhard this volume). First, we are able to comprehend why diverse individuation practices within disciplines successfully function in the sense of leading to fecund investigative approaches and increasing explanatory depth. If we can make explicit how definitions of individuality match the underlying epistemic goals of biologists, then we better comprehend why these practices work (and conversely, if there is some form of mismatch). Second, we gain tools for identifying sources of conflict within and across disciplines, such as the existence of different criteria of adequacy (e.g., functional versus structural) due to different goals of inquiry. When conflict arises, scrutinizing these criteria and underlying goals can help in evaluation without assuming that one approach to individuality is wrong. Third, we can discriminate more finely among philosophical approaches to individuality by explicitly distinguishing between definitions of individuality and epistemic goals of inquiry.¹² For example, the HPC account endorsed by Wilson and Barker (2013), which views many imperfectly correlated properties as constitutive of individuality, does not inherently favor any particular property or biological domain as fundamental. At the same time, their approach is monistic given its unique HPC definition of individuality, as opposed to acknowledging that there are multiple concepts of individuality, each answering to different epistemic goals of inquiry (something only acknowledged by some other HPC approaches).

In the next section we explore how contributions to this volume can be understood to fulfill these three aims: comprehending successful matching of characterizations of individuality and epistemic goals, diagnosing conflicts between characterizations of individuality resulting from different goals, and discriminating more precisely among philosophical perspectives on individuality.

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<A>Illuminating Case Studies of Individuality in Biological Inquiry

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The historical, philosophical, and scientific analyses in this volume offer a treasure trove of materials for illustrating the value of shifting from metaphysics to epistemology in the context of discussions of biological individuality. This value has at least two dimensions in the context of comprehending distinct but successful practices of individuation, diagnosing conflicts about individuality, and discriminating among philosophical perspectives: (1) *interpretive*, providing new and helpful perspectives on historical and contemporary scientific situations; and (2) *explanatory*, offering accounts of why biologists reason the way they do in different contexts of inquiry where distinct aspects of complex biological phenomena are in view. We highlight examples from both dimensions drawn from the chapters herein and take up their implications for formulating novel perspectives on the metaphysics of individuality in the final section. Our aim is not to be exhaustive but illustrative. This means individual chapters may be germane to both dimensions, but we concentrate attention on only one. The hope is that others would see the various benefits of an epistemological reorientation, which investigates the different epistemic goals underlying accounts of individuality as well as their metaphysical implications, and follow suit.

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Interpretive

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Michael Osborne (this volume) takes us back to the context of parasitology in relation to social theory in late 19th and early 20th century France. This was a fertile period for cross-pollination between approaches because parasitology, as a labeled field, was coalescing as a

medical specialization in schools of tropical medicine that might supersede bacteriological pathology. What ensued was an interweaving of different understandings of individuality, which our reorientation interprets as arising from distinct epistemic goals of inquiry. For example, if the aim was to understand the origins of human disease, then individuality was conceptualized immunologically as a relationship of host to pathogen, where the pathogen was of a different species than the host and the causal dynamics of significance pertained to the host's functional integrity. But if the aim was to understand the parasite and its life cycle, then individuality was understood physiologically in terms of whether the parasite was able to live on its own apart from one or more hosts (i.e., functional autonomy). Whether the parasite was autonomous from the host is bracketed when studying medical pathology; whether the host's functional integrity was compromised in a particular way was relegated to the background when studying the natural history of the parasite. Some researchers adhered to both epistemic aims as they moved between natural history and medical pathology, even though these aims generated distinct conceptualizations of individuality. This engendered unexpected friction as the matching relationship between aim and conceptualization sometimes exhibited slippage.

In addition to this interweaving of individuality notions germane to investigating parasitism, socioeconomic relations between France and its African colonies nurtured the application of biological concepts like parasitism to describe societal relationships. As a consequence, different conceptualizations of individuality, which were not always explicitly articulated, ended up being invested with commitments of social ideology. The inclusion of social-political aims added a layer of complexity to the multiple scientific goals in play, which in this case actually encouraged the scientists involved to understand their conceptual differences monistically—society could not be organized in more than one way at a time. If the focus was on

an African colony drawing a benefit from France (another individual) which bore the cost, then understanding the colony as a distinct individual, negatively valenced (i.e., as a parasite), seemed intuitive. If the focus was on the health of France in light of its component parts, then the autonomy of the colony was less salient than the integrity of the nation's physiological functioning. Thus, the distinct conceptualizations of individuality, motivated by different epistemic goals of inquiry, became reified as competitors as they trafficked through social discourse in a way that did not occur when moving between the contexts of natural history and medical pathology. At the same time, the movement through social discourse led to reciprocal effects, such as using a supposed developmental trajectory for a category of humans to model a common evolutionary trajectory for parasitic species.

A different historical episode surrounding biological individuality comes to us in early 20th century German idealistic morphology through the work of Martin Heidenhain and his notions of "enkapsis" and enkaptic hierarchy, which Olivier Rieppel (this volume) investigates. These notions were meant to capture an integrated structural and functional organization of organisms composed of multiple levels and could be extrapolated to other levels (e.g., ecosystems and human societies). This complex, integrated understanding of individuality grew out of an organicist perspective, which rejected approaches to living systems that treated them as nothing but physicochemical parts. Thus, we can note that a particular epistemic goal constrained what counted as an individual and as meaningful parts; individuality had to be conceptualized in a way that supported a reciprocal dynamic of causal relations between the components acting to produce the complex whole and the complex whole influencing the behavior of the parts. But the epistemic goal also contributed to a monistic orientation because the enkaptic hierarchy literally encompasses all of the causal relations relevant to individuals as such.

Heidenhain was engaged in a form of fundamental theorizing and this is evident in the fact that enkapsis extended far beyond the organism. As noted earlier, “fundamental” does not necessarily mean lowest level of spatial parthood, so Heidenhain could eschew reduction to the physicochemical level and at the same time engage in fundamental theorizing by construing enkapsis as *the* basis for various biological as well as societal phenomena. Enkapsis applied to ecology as much as evolution and moved across boundaries between zoology and social theory where it was used to justify aspects of Nazi ideology (e.g., “the individual will sacrifice his life if this is required for the survival of the whole,” August Thienemann, cited in Rieppel, this volume). Apart from this export of biological ideas into political ideology, it is intriguing to hypothesize that Heidenhain’s monistic interpretation of enkapsis potentially contributed to its methodological sterility. If enkapsis was understood in the context of investigating a specific type of individual, such as a metazoan organism, then it could be more successful in engendering a fruitful line of research about relationships between parts and wholes, especially if seen as one strategy among many for dissecting the causal architecture of complex living systems. Rieppel sees value of this kind in applying the idea of enkapsis within contemporary biological investigations, and others have argued that it is distinctively helpful in going beyond standard part-whole relationships when conceptualizing hierarchically organized biological individuals (Zylstra 1992).

That monism might be associated with methodological sterility—that the complexity of the biological world generally means that all-purpose concepts will not be useful even if they can be formulated—is further supported in the work of Herbert Spencer. Snaith Gissis (this volume) explicitly recognizes this: “perceiving any living entity as an individual for some purposes and as a collectivity for others would have greatly simplified his work.” But Spencer was undaunted

and advocated the methodological principle that the simple should be understood in terms of the complex and not *vice versa*. A hybrid notion of “collective individuality” was needed to capture the totality of intricate interplay and fundamental entanglement of organism-environment couplings. The distinctive epistemic goal of inquiring into the properties of interaction was so paramount that Spencer emphasized incessant relations occurring between individuals conceptualized as a joint array or system, not how to individuate them from one another or decompose them into meaningful parts. Individuality is not constitutive of interactive processes but the result or outcome of those processes. These processes accomplish individuation by finding temporary but stable equilibrium points of individual-environment interactions.

It is difficult to operationalize Spencer’s fundamental theorizing that took complex interactions and relations, such as organism-environment couplings, as the foundation for understanding everything else. Identifying the single correct view of individuality involves treating relationships between parts, wholes, and their environments at a high degree of abstraction. This is a key reason why general all-purpose concepts are less useful in the investigation of complex biological phenomena. While it is in some sense true that nature exhibits “spatiotemporal bounding,” biologists require more specific conceptualizations of individuality to meet epistemic goals of inquiry (e.g., spatiotemporal bounding that seals off internal physiological activities, as illustrated by an epithelium occluding the passage of ions). Both Heidenhain and Spencer recognized the complexity of biological individuality (multilevel and interacting with external conditions), but lost their grip on it by trying to capture individuality with a single concept lacking operational traction. An important lesson is that the most fruitful matchings of individuality conceptions and epistemic goals typically derive from more circumscribed epistemic goals that carve off a portion of biological complexity rather than

embracing it in full.

The alternation of generations is a striking biological phenomenon that puts direct pressure on conceptualizations of individuality, as Lynn Nyhart and Scott Lidgard (this volume) indicate. Organisms sexually reproduce to beget offspring that develop into adults that do not resemble their parents and reproduce asexually to beget offspring that develop differently but resemble the sexually reproducing, initial generation. Steenstrup concentrated on the radically different morphologies exhibited in these reproductive transitions and interpreted them as shifts in the nature of individuality (“something more than a metamorphosis is concerned,” cited in Nyhart and Lidgard this volume). Others tried to find a single conception of the individual that would account for the material continuity of an alternating, successive pattern across generations. Depending on the epistemic goal—whether to account for a change in the strategy of sexual reproduction (since reproduction was often taken as defining of individuality), or to account for the stable succession of alternating patterns of sexual reproduction across generations—different conceptualizations of individuality seemed better suited to the task. And when Steenstrup focused his attention across generations, he treated sexual reproduction as the higher form of individuality, defined in terms of increasing autonomy over time, which progressively succeeds the asexual form of individuality.

More generally, the phenomenon of a life cycle (illustrated dramatically by the alternation of generations) shows that goals of inquiry involve commitments to temporality that affect suitable characterizations of individuality. Richard Owen’s epistemic goal of providing an explanation of diverse types of development in terms of a causal law of nature encouraged an emphasis on processes where hierarchical levels of individuals are cumulatively built up and propagated asexually and sexually in different ways. Huxley, in contrast, focused his epistemic

attention on the “independent existence” or autonomy seen in vertebrates, and thus anchored individuality across time in sexual reproduction from the single egg in one generation to a single egg in the next generation. Asexual budding and other forms of propagation were renamed and relegated as subsidiaries, transformations of parts rather than changes in what counted as the whole. Plant phenomena introduced distinctive wrinkles since there was no paradigmatic part to fix the temporal origination or achievement of “autonomous” individuality, and yet these accented novel developmental processes in hierarchically structured systems relevant to the stability and propagation of organization characteristic of individuals. Both Owen and Huxley understood their accounts of individuality monistically, but from an epistemological perspective we can interpret their value in terms of distinctive goals of inquiry with different criteria of adequacy that are helpful in particular contexts for investigating and explaining the temporal origins and the maintenance of biological individuality.

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Explanatory

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Several of the interpretations above are suggestive of the explanatory dimension of our epistemic approach to individuality, which consists in investigating why biologists reason the way they do in different contexts of inquiry. Treating cells as individuals is one locus where we gain such traction. Biologists routinely shift their perspective on cellular individuality as a means to investigating biological systems. Conceptualizing cells in relationships of reciprocal regulation stresses their parthood, but focusing—as Andrew Reynolds (this volume) does—on cell-cell communication or cell sociology stresses their role as wholes or individuals.¹³ The switch in focus makes additional conceptual resources accessible, such as reaching for a notion

of the division of labor in modern nation states as a model for cell-organism relations when cells are understood as components, or resisting a machine metaphor for describing biological systems (e.g., cells as building blocks) by accenting joint cellular agency; appealing to cell sociology flags this because machine parts do not exist in community.

The ability to switch between different conceptualizations of individuality for cells (parts versus a whole) provides researchers with increased reasoning capacity to achieve different goals of inquiry surrounding individuality. If the aim is to comprehend the cellular level as functionally autonomous, then characterizing cells as individuals is warranted. For example, cellular sociobiology, in contrast to cell sociology, literally treats cells as independent agents. If the aim is to comprehend aggregate properties, such as are observed during development, then cellular independence is replaced by how a cell is affected and transformed by its “social” environment, and the agency of individual cells is muted to emphasize their joint contribution to a greater whole. These “group level” and genuinely social effects are best captured through definitions of individuality above the cellular level; and structural relationships, such as adhesion, emphasize the contribution of the cell to a larger whole. In each of these cases, what counts as the internal and external environment changes, thereby drawing attention to different causal relations that would otherwise be obscured. Conceptualizing cells as parts and wholes in different contexts of inquiry is a powerful analytical tool for dissecting complex biological phenomena that would be unavailable if individuality was fixed at a particular level.

Switching perspectives between cells as individuals and cells as parts of individuals is on full display for transitions of individuality, which Matthew Herron (this volume) empirically investigates. In these cases biologists need to understand why a particular direction of change has taken place, which means tracking the fitness costs and benefits related to different arrangements

of and interactions among cells. Thus, individuality is typically conceptualized in terms of genetic and evolutionary criteria (see the above subsection on Evolutionary Individuality). Herron uses the volvocine algae as a model taxon because of the diversity exhibited for between-cell organization and evolutionary trajectories towards higher-level individuality. He shows the epistemological value of analyzing evolutionary individuality from multiple vantage points by zooming in on developmental and ecological changes during the life cycle. This offers insight into what sequence of steps is most plausible for the transition from cells as individuals to cells as components of a multicellular individual. By implication, Herron is open to the evolutionary reversibility of different between-cell organizational features, which goes beyond the unidirectional explanatory focus taken by standard studies of transitions in individuality. This epistemic perspective makes it possible to experimentally explore changes in individuality that occur due to short-term ecological changes affecting population organization and thereby enrich our understanding of long-term evolutionary modification.

As opposed to answering whether a given *Volvox* spheroid is an individual, based on a monistic definition of individuality, Herron's epistemic goal of inquiry is to investigate *how much* individuality is present *at each* of the different levels: cells, colonies, and clones (genets). He lays out thirteen derived traits relevant to multicellularity, such as the conversion of the cell wall into extracellular matrix, an incomplete cytokinesis, and the retention of cytoplasmic bridges in adults. This sounds similar to Wilson and Barker's (2013) HPC construal of individuality, which views a cluster of properties as metaphysically defining of individuality even though not every individual needs to possess all of these properties. Yet Herron is not aiming for *the* definition of individuality; instead, he is trying to tease apart which of his derived traits is present in a certain taxon of the volvocine algae, and what sequence of steps occurred in

a particular lineage. This empirical approach makes it possible to mechanistically dissect transitions in a way that relying only on evolutionary individuality at an abstract level, as we have seen in some instances of fundamental theorizing, does not.

Beckett Sterner (this volume) can be understood as making a similar point about the explanatory potential of more concrete perspectives on individuality. He argues that the standard view of an evolutionary individual deriving from fundamental theorizing with fitness as the most basic feature is inadequate to meet the epistemic goal of mechanistically explaining evolutionary transitions in individuality. Instead, he introduces a new concept—the “demarcator”—to refer to both developmental and ecological structures or processes occurring during a life cycle that are necessary (though not sufficient) to circumscribe individuals as such. This strategy involves examining concrete mechanisms that fulfill the role of demarcator, specifically through the control of inheritance, and thereby provide conditions of individuation in biological systems. Including concrete examples of scaffolding, these mechanisms are instantiations of the abstract properties appealed to when characterizing individuality (e.g., establishing a boundary by policing), and add what is missing when only fitness is utilized to mark out individuals. These mechanisms provide the conditions for individuality through change and multiplication during reproduction and criteria for what counts as a genuine part of the whole. Working out the detail of these concrete mechanisms also provides insight into why particular events, such as a unicellular bottleneck, occur *when* they do within a life cycle and why those events exhibit specific ranges of variation.

Although the concept of a demarcator needs to be fleshed out more thoroughly in empirical research, we can see that it could assist in fulfilling the aim of explaining evolutionary transitions more adequately, as well as aiding the investigation of how much individuality is

present at different levels of organization and what sequences of steps are most plausible for transitions in different multicellular lineages. Here we have the explanatory dimension *in potentia*: if biologists aim to mechanistically explain evolutionary transitions in individuality, then additional conceptualizations of individuality beyond those based on an abstract construal of fitness in multilevel selection theory are required. Additionally, other epistemic goals, such as explaining why particular events occur within a life cycle, can be pursued with a characterization of individuality in terms of demarcators, which are otherwise opaque on the standard view of an evolutionary individual. Overall, these possibilities offer a rationale for why biologists could or should reason about biological individuality with different definitions, rather than a single all-purpose conception, in different contexts of inquiry given their specific epistemic aims (see also Sterner 2015).

Cells are not the only or primary meaningful conceptualization of parts in organisms. Biologists have a variety of reasons for decomposing an individual into parts (Winther 2011). Ingo Brigandt (this volume) focuses his attention on organismal parts in the context of one of the most perennial axes of debate: structure versus function. Each of these is manifest in different suites of epistemic goals, reflected in venerable terminology: anatomy versus physiology, comparative morphology versus functional morphology. Brigandt's central claim is that structure and function are on par in the context of decomposing individuals into parts; neither is more fundamental than the other. The key move in his argument is the isolation of a particular sense of function (function as *activity*), which permits the conceptualization of a functional body part that has equal standing to structural body parts by abstracting away from the contribution that the activity-function makes to the larger system or whole organism (Wouters 2003). His hierarchical approach, according to which a bodily part (structure as well as activity-function) is composed of

both lower-level structures and activity-functions, heightens the parity between structure and function by using them in combination. Conceptual abstraction also permits biologists to use structure and function separately as principles of decomposition for the parts of biological wholes in different contexts of inquiry, thereby accounting for why biologists reason the way they do in different contexts of inquiry.

Although Brigandt focuses on how structure and function can work together to generate a more robust ontology of parts, he is fully aware that functional and structural characterizations of parts match different epistemic goals. Many structures have their identity by virtue of some activity, which might play multiple roles in different biological contexts. The practices of individuation for parts adopted by biologists are geared toward apprehending the different types of individuals that result from distinct contextual situations. The epistemological reorientation we advocate makes more salient those research programs that look specifically at what structures do and how that changes through time, such as during development. By analogy, the ability to work with multiple concepts of individuality not only serves different epistemic goals of inquiry but also makes possible their *joint* use to serve the *same* epistemic goal. This option is not visible to fundamental theorizing premised on monism and motivated by the metaphysical question of what a part is. And the value of our reorientation extends beyond the parts of organisms on which Brigandt's chapter focuses, as it holds from the molecular to the supraorganismal level, and thereby highlights why keeping multiple characterizations of individuality in the toolbox of scientific reasoning contributes to the achievement of diverse epistemic goals.

Even though it has receded to the background in most philosophical analyses, Hannah Landecker (this volume) reminds us in her contribution of the aim of explaining physiological autonomy and thereby considerably broadens the array of diverse epistemic goals. Her emphasis

on conversions of agency in biological systems indicates that there is a different kind of transition in individuality that is of interest to biologists—metabolic transitions. If having the capacity to metabolize is one way of characterizing individuality physiologically, how do we understand the dynamics of causal agency in situations where individuals are consuming and transforming other individuals (a “logic of conversion”)? Akin to Sterner’s emphasis on concrete mechanisms controlling features of inheritance that are a necessary condition for individuality, Landecker’s historical argument traces the emergence of a concept of metabolism that is a necessary condition for individuality: “metabolism is intrinsic to concepts of the process of individuation: how an organism becomes an individual, set off from the world, that becomes the unit of analysis for those who study locomotion, perception, and desire – physiology, neurology, psychology, etc.” (Landecker this volume).

Here it is clear that characterizations of individuality in terms of fundamental theorizing from evolutionary biology are not in the foreground. Those studying physiology, neurology, and psychology simply have different epistemic aims and came to them through a very different historical path. Landecker highlights this tension in two ways. First, she notes that Hans Jonas exhibited a monist impulse to fundamentally theorize that metabolism is the *sina qua non* of individuality: “Jonas, as is the case with most philosophers, was trying to generate a universally applicable analysis of what *is*.” The complicated historical stage of actors conceptualizing and investigating metabolism that Landecker details, alongside of contemporary research, destabilizes this monism dramatically. Second, she mentions that definitions of life have often been cast as a choice between two fundamental viewpoints: the capacity to form lineages and the capacity to be metabolically self-sustaining (Dupré and O’Malley 2009). Our epistemological reorientation encourages a rejection of this dichotomy because it is insensitive to the different

epistemic aims at play in biological investigation. If the goal is to explain the persistent agency for an individual that has been consumed, then the capacity to form a lineage (of some sort) may be extremely useful given that the metabolic sustaining capacity is gone. If the goal is to account for a logic of conversion where the capacity to form a lineage is destroyed (in the eaten) in the service of preserving or maintaining another individual (the eater), then a capacity for self-sustaining metabolism necessarily moves to the foreground.

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<A>Implications and Conclusions

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The epistemological reorientation for discussions of biological individuality that we have argued for does not require returning to metaphysical questions, but we believe the implications are worth exploring, if only briefly. As we have seen, most recent analyses of biological individuality have assumed that there is one correct account of the nature of individuality. For many philosophers, this monism is motivated by what we labeled “fundamental theorizing,” which involves singling out one or more features as the most basic for being an individual (e.g., being a bearer of fitness). Competing accounts of individuality based on different features or combinations thereof (e.g., spatiotemporal boundedness or physiological autonomy) must either be rejected or demonstrated to derive from the fundamental feature. In contrast, both the interpretive and explanatory dimensions of our epistemological reorientation described in the previous section provide fodder for formulating novel perspectives on the metaphysics of individuality. One of these themes is that multiple concepts of individuality matched to different epistemic goals give us a better understanding of the complexity of biological individuality. Our analysis of this complexity goes beyond previous acknowledgements by some philosophers that

different criteria of individuality may have to be used for different taxa (Clarke 2012, 2013; Wilson and Barker 2013). First, it includes and articulates scientists' epistemic goals in addition to biological entities and phenomena (e.g., taxa and lineages). Second, it makes room for the possibility that different construals of individuality may be needed for the same biological entity (or taxon), especially when biologists differ with respect to their epistemic goals (see also Lidgard and Nyhart this volume).

If individuality is pursued monistically within a highly abstract framework intended to cover all levels and contexts where individuality is present, as observed in the historical cases of Heidenhain and Spencer (Rieppel this volume; Gissis this volume), then the project seems more resistant to concrete empirical characterization. This is problematic given that one philosophical task is to discern metaphysical implications of biological phenomena, scrutinized and explained scientifically. Part of this resistance may derive from a decoupling of concepts of individuality and epistemic goals. Using the abstract framework of information theory, David Krakauer and colleagues (2014) offer a complete theory of individuality for identifying biologically significant individuals and their meaningful parts at any level of organization—but with little to no discussion of what epistemic aims this would fulfill. Their claim that biologists are using the informational concept of an individual even though they are not aware of it does not illuminate scientists' epistemic motivations either.¹⁴ And even if a specific epistemic goal underlying the approach by Krakauer et al. was articulated (e.g., elucidating common features of stable configurations of individuality in different biological systems), then the value of their information-theoretic conception of individuality would be keyed to that goal. Rather than providing a monistic definition, their account would be *another* conceptualization of individuality in the toolkit of biologists available for pursuing different goals of inquiry.

What then might we learn metaphysically from our epistemological reorientation in contexts where biological individuality is in view? Negatively, the biological complexity investigated with multiple conceptions of individuality in conjunction with diverse epistemic goals is not susceptible to a monist characterization. In direct opposition to the fundamental theorist who seeks to identify a single, complete, and comprehensive account of individuality, a pluralist stance towards the metaphysics of individuality seems warranted (see also Brigandt 2013; Kellert et al. 2006).¹⁵ There are multiple correct, empirically substantiated answers to the metaphysical question of what an individual is. Pluralism, in this context, is not only epistemological but also metaphysical. That there is more than one correct way to account for individuality means that there is more than one way to be an individual. The successful pairing of different characterizations of individuality with the diverse investigative and explanatory aims of biologists is an indicator of the structure of reality *qua* biological individuals (see also Boyd 1999b; Dupré 1993).

Once a pluralist stance has been adopted, deriving metaphysical implications is less of an exercise in sorting out competing conceptions of individuality and more about identifying successful matches of particular definitions of individuality with particular epistemic goals. Examining these scientific successes, which are related to how a specific definition's use has value *vis-à-vis* some epistemic goal, tells us something about the way the world is. Conceptualizing evolutionary individuals in terms of fitness considerations is well suited to the epistemic aim of explaining changes in the relative frequency of individuals exhibiting differing traits in populations over time because there are evolutionary individuals of this type in nature. If a mechanistic account of reproduction and differential persistence of individuals is sought, additional empirical facts beyond a mathematically abstract construal of individuality have to be

adduced (Sterner this volume). Conceptualizing physiological individuals in terms of metabolic autonomy is well suited to the epistemic aim of explaining how an individual maintains its distinctness over the course of a lifetime because there are physiological individuals of this type in nature. The physical features underlying the “autonomy” and possibly “agency” seen in these contexts (Landecker this volume; Reynolds this volume) are not captured by an evolutionary characterization. While our epistemic reorientation does not preclude the possibility that we will subsequently identify commonalities in matches between definitions and epistemic goals that permit us to combine them into more abstract pairings, there is no prerequisite that it occur. Many types of definition-goal matches are possible. In some cases, there may be a single best conception of individuality for a particular epistemic goal. Sometimes one conception of individuality may be conducive to multiple epistemic goals. In other cases, multiple conceptions of individuality may be required to address particular epistemic goals, as seems to be the case in explaining evolutionary transitions of individuality.

The metaphysical picture that emerges from our epistemological reorientation is messy but has a solid grounding: successful science. That there are many types of biological individuals is something that we have empirically discovered about the biological world; this complexity is not susceptible to a unified characterization of individuality (see also Mitchell 2003). The warrant for this is empirical and derived from the successful practices of individuation and decomposition observed in actual scientific inquiry (Kellert et al. 2006). In our view, the only way to recover a systematic, monist account of biological individuality is to neglect, discount, or actively reject the manifold ways that scientists successfully mark out individuals and carve them up into meaningful parts. The rationale for this rejection would have to come from another source, such as a distinctive commitment to unification not derived from scientific practice: “to

pursue the task of seeing how everything hangs together” (Godfrey-Smith 2014, 4). The pluralist stance starts with the task of seeing *whether* everything hangs together. With respect to whether there is an adequate, all-purpose concept of biological individuality, the answer appears to be “no” (see also Lidgard and Nyhart this volume).

In this introductory overview we have reviewed and characterized a variety of philosophical distinctions that are relevant to discussions of biological individuality (e.g., individuals versus classes) with the ultimate aim of advocating for an epistemological reorientation of these discussions. Metaphysical assumptions have animated controversies about individuality, both in the past of biology and in the present for philosophy. We have encouraged a rejection of fundamental theorizing to determine what an individual really is as unnecessary and unwarranted. Our argument for a shift in attention from metaphysics to epistemology is motivated by successful biological practices of individuation and decomposition in the context of different epistemic goals, and is amply illustrated in the contributions to this volume. The resulting metaphysical project of elucidating the implications of a pluralist perspective on biological individuality diverges from other approaches in contemporary philosophy of biology but has the advantage of taking seriously the array of empirical successes that biologists have had in investigating the complex nature of individuality in living phenomena.

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Acknowledgements

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¹ This same point can be illustrated with discussions about the metaphysical nature of species, in particular whether they are individuals rather than classes (covered below in the subsection on Species as Individuals; see also Brigandt 2009; Love 2009).

² “Fundamental theorizing” should not be confused with reduction to the molecular or microphysical level. Although the two can sometimes coincide, in this particular case they do not.

³ A prominent exemplification is the Society for the Metaphysics of Science (<https://sites.google.com/site/socmetsci/>).

⁴ An analogous conception in the context of organisms as biological individuals is Willi Hennig’s account of the relation between a semaphoront, which is his notion for a time-slice of an organism during a very short period, and an individual across its entire lifetime (see Havstad et al. 2015).

⁵ Our use of the term “monism” does not refer to the philosophical position—much discussed in late 19th and early 20th century philosophy—that matter and mind are both manifestations of a united, underlying substance (Weir 2012). Instead, in our analysis, monism refers to a rejection of the possibility that there is more than one legitimate definition of what a biological individual is.

⁶ Commenting on the question of whether homologues are natural kinds or individuals, Havstad et al. (2015) extend Hennig’s notion of a semaphoront from species to homologues by distinguishing between a bodily part across an organism’s whole lifetime, which undergoes substantial ontogenetic change, and an ontogenetic stage of this bodily part.

⁷ Although nearly all proponents of the HPC account of kinds are philosophers, a few biologists agree that species can be seen as HPC kinds (Rieppel 2007, 2009, 2013; Assis 2011).

⁸ Whether it should capture all or only scientific kinds are additional questions. Some philosophers have worried that an HPC account does not hold for some classifications of particular successful sciences and includes classifications that are explicitly rejected by some sciences (Ereshefsky and Reydon 2015).

⁹ This might be expected given the number and diversity of criteria that have been put forward: (1) displaying the capacity of reproduction; (2) exhibiting a life cycle; (3) having a unique genotype; (4) engaging in sex; (5) having a single-cell bottleneck during the life cycle; (6) exhibiting a separation of germ and soma; (7) displaying mechanisms that police for cheaters; (8) having identifiable spatial boundaries and contiguity or physiological integrity; (9) exhibiting histocompatibility or an immune self identity; (10) being under selection as a unit of fitness maximization; (11) having cooperation among but not conflict between parts; (12) exhibiting a common evolutionary fate or co-dispersal; and, (13) being an entity that bears adaptations (Clarke 2010). Clarke and Okasha (2013) discuss the diversity of criteria for individuality in comparison to the plurality of species concepts.

¹⁰ Though it is generally assumed that evolutionary theory requires individuals to be the entities bearing fitness, Frédéric Bouchard (2011) has argued that the notion of an individual (and an individual's reproductive fitness) may be dispensable. On his account, evolutionary explanations only require a concept of lineage and the differential persistence of lineages; these concepts apply to the full range of difficult cases, from colonial species to multi-species symbioses, which

is a major motivation for his approach.

¹¹ Godfrey-Smith (2013) recognizes a difference between the evolutionary and physiological approach by distinguishing between his “Darwinian individual” and an “organism.”

¹² This is analogous to distinguishing a definition of “evolutionary novelty” and the epistemic goal of explaining the evolutionary origin of novelty (Brigandt and Love 2012). For other examples illustrating the benefits of paying attention to the epistemic goals of inquiry in addition to the definitions of concepts, see Brigandt (2012).

¹³ Similar themes emerge when talking of “molecular ecosystems” (Nathan 2014).

¹⁴ “It is our belief that when biologists speak of individuals they are often invoking informational individuals without always making this assumption explicit.” (Krakauer et al. 2014, 7)

¹⁵ Lidgard and Nyhart (this volume) articulate the diverse uses of biological individuality concepts in terms of changing “problem spaces,” and explicitly view epistemic goals to be ingredients of such problem spaces. Given that a particular construal of biological individuality may serve some epistemic goals while excluding features that would be relevant for others, Lidgard and Nyhart see the need for multiple concepts of individuality. Beckett Sterner (2015) likewise argues for a pluralism about biological individuality on the basis of the presence of multiple epistemic goals (which he calls “epistemic roles” the concept of individuality must satisfy). He claims that even when evolutionary goals are at stake, the monistic evolutionary accounts of individuality by Clarke and Godfrey-Smith are insufficient.