ArtefaCToS. Revista de estudios de la ciencia y la tecnología
eISSN: 1989-3612
Vol. 12, No. 1 (2023), 2.ª Época, 27-54
DOI: https://doi.org/10.14201/art20231212754

'Organism' *Versus* 'Biological Individual': The Missing Demarcation

'*Organismo*' *versus* '*individuo biológico*': *la demarcación faltante*

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Received: 27/10/2022. Reviewed: 08/02/2023. Accepted: 08/03/2023

Abstract

The demarcation of organisms from other biological individuals has received relatively little attention. In this paper, I extricate and systematize the different ways in which the organism–biological individual relationship has been construed: (1) coalescence of the two concepts, (2) biological individual eliminativism, (3) organism eliminativism, (4) organism as a 'paradigmatic' biological individual, (5) organism as a limit state towards which biological individuals tend in evolution and development, (6) organism as instantiating the whole in a part-whole hierarchy of biological individuals, (7) organism as equivalent to physiological individual, and (8) organism as a special kind of physiological individual. I show that, in most of these stances, the organism concept is too imprecise to be demarcated from other biological individuals, which fosters some form of eliminativism. I also argue that the comparisons between organisms and biological individuals are performed in two different modes: 'horizontally' (i.e., between individuals not related hierarchically) or 'vertically' (i.e., between individuals belonging to different levels within the same hierarchy). Finally, I explain the challenges that each of these comparison modes face and suggest that the 'vertical' mode adumbrates a potential way forward.

Keywords: biological individuality; organismality; organism; paradigmatic individual; part-whole relationship; agency; major transitions in evolution; autonomy.

Resumen

El problema de la demarcación entre el organismo y otros tipos de individuos biológicos ha recibido relativamente poca atención. En este artículo desgloso y sistematizo las diferentes formas en las que se ha interpretado la relación 'organismo'-'individuo biológico': (1) coalescencia de estos dos términos, (2) eliminativismo del individuo biológico, (3) eliminativismo del organismo, (4) organismo como individuo biológico 'paradigmático', (5) organismo como estado límite al que tienden los individuos biológicos durante la evolución y el desarrollo, (6) organismo como instanciación del todo en una jerarquía parte-todo de individuos biológicos, (7) organismo como equivalente a individuo fisiológico y (8) organismo como un tipo especial de individuo fisiológico. Muestro que, en la mayoría de estas posturas, el concepto de organismo es demasiado impreciso como para ser demarcado de otros individuos biológicos, lo cual promueve alguna forma de eliminativismo. También argumento que las comparaciones entre organismos e individuos biológicos son llevadas a cabo de dos modos: 'horizontalmente' (i.e., entre individuos no relacionados jerárquicamente) o 'verticalmente' (i.e., entre individuos pertenecientes a diferentes niveles de la misma jerarquía). Finalmente, explico los desafíos que enfrentan cada una de estas formas de comparar y sugiero que el modo de comparación 'vertical' deja entrever un posible camino a seguir.

Palabras clave: individualidad biológica; organismalidad; organismo; individuo paradigmático; relación parte-todo; agencia; grandes transiciones evolutivas.

1. Introduction

The organism concept is widely debated both in biology and its philosophy because organism-centered perspectives are currently making a comeback (Gilbert & Sarkar, 2000; Ruiz-Mirazo *et al.*, 2000; Etxeberria & Umerez, 2006; Huneman, 2010; Nicholson, 2014; Baedke, 2019). It should be kept in mind, however, that organism-centered stances have been jeopardized not only by reductionist, gene- and population-centered perspectives but also by their problems in satisfactorily articulating the very organism concept which they have sought to build (on the waxing and waning of the importance attributed to 'organisms' throughout the history of biology and the challenges that organism-centered perspectives have faced, see Benson, 1989; Baedke, 2019). So, if the organism concept is to be advanced as the centerfold conceptual and explanatory unit in the life sciences, it needs to be spelled out. And this customarily entails demarcation work.

Organisms—if nothing else—are living beings embedded in their environments. Correspondingly, attempts have been made to demarcate them from (i) non-living things and (ii) the environment. The former demarcation was central

to the vitalism-mechanism debates and the rise of the organicist tradition in the early 20th century (Nicholson & Gawne, 2015). The latter has received attention especially in recent debates (e.g., on niche construction and agency) that stress the active role of the organism in modifying its environment and thus participating in the creation of the conditions for its persistence and the modulation of its evolutionary trajectory (Baedke *et al.*, 2021). In this article, I will focus on a less probed project: (iii) the *organism–biological individual demarcation*.

Now, when the organism concept collides with cognate concepts in the aforementioned dyads, the result lies somewhere between two antithetical perspectives that may be called *essentialism* and *eliminativism*. Sometimes the organism emerges as bearing essential properties that make it stand out as an irreducible special unit. Other times, in turn, continuity between the organism and its neighboring notions is emphasized to the point that their boundaries disappear and typically one of the two concepts in each coupling vanishes altogether. In the demarcation of organisms from non-living systems, essentialism takes the form of vitalism and eliminativism that of reductionist physicalism. Apropos organism-environment segregation, those who disavow the reciprocity between organism and environment and seek for definitive boundaries between the two stick to an essentialist viewpoint, whereas those who claim that there is no boundary between organism and environment vouch for an eliminativist stance. When demarcating the organism from other biological individuals, some authors are committed to finding those properties that are essential to organisms and no other kind of biological individual has, while others utterly blur the distinction between those two concepts to the detriment of one of them. Fortunately, there is enough room between those extremes. Most positions in all of these debates try to recover the organism as a unit worth singling out whilst staying mindful of the fact that sharp distinctions are often artificial and do not make justice to the complexities of the biological world—witness organicism and the nuanced stances on the organism-environment relationship. The real challenge in these cases is finding a good balance between conceptual *narrowness* and *imprecision*.

Why does the organism–biological individual distinction matter? To begin with, this demarcation is not a mere definitional quibble or a matter of terminological taste, but has far-reaching theoretical and practical consequences of which examples abound. For instance, Gawne & Boomsma (2022) suggest that the lack of consistency and conceptual clarity in the way 'organismality', 'individuality', and related terms have been used to describe the so-called 'major transitions in evolution' is to be blamed for the repeated independent "discovery" of those phenomena and the fragmentation of the literature on that topic into parallel traditions. According to Haber (2013), the debates on eusociality have been misguided by the use of the organism concept as a parameter of the extent to which

colonies can be regarded as individuals—i.e., 'superorganisms'. Haber argues that the concept is too vague to be able to do any useful work in these debates and that 'individual' should be preferred instead. Finally, Baedke *et al.* (2021) assert that how organisms are marked off from other biological individuals makes a strong difference in how niche construction is conceptualized and ultimately modeled. Niche construction emanates from the reciprocal interaction between organisms and their environments wherein organisms bring about and react to environmental changes most of the times in agential ways. Baedke *et al.* (2021) discuss the interplay between microbiota and host in the transition to herbivory in ruminant holobionts (Chiu & Gilbert, 2020) and show that, depending on which entities are regarded as organisms (i.e., the host, the microbes, or the holobiont as a whole), this case of niche construction can be understood and classified in disparate ways. Thence, adjudicating organismal status dictates who the agent is, what counts as the environment, and what kind of niche-constructing activity is enacted between the two.

More generally, demarcating the organism from other biological individuals is indispensable in every instance where the organism is invoked as a special, autonomous, active, and causally efficacious unit in the biosciences. Without such delineation, we simply do not know to which entities organismal properties and processes such as agency, niche construction, and developmental plasticity refer, and it is not clear whether these properties and processes are exclusive to the organism or can be predicated on other biological individuals as well. This is, I submit, the main reason why this demarcation is warranted and badly needed. All the more so when considering that both the organism-*qua*-living-system and the organism-environment demarcation projects fall short of offering a thorough understanding of what organisms are. The former, because it equates 'organism' with 'living system', overlooking the fact that the category 'organism' conceivably does not exhaust all kinds of living systems that there are (i.e., organisms are living systems, but likely not all living systems are organisms). The latter, because it takes the organism for granted and leaves it unexplained. These projects, though legitimate and sound, can hardly provide answers to questions such as: What is the organismal status of a tissue-forming cell? How is it different from that of a free-living unicellular protist? Or, what is the organism in a siphonophoran—each cell, each zooid, or the whole colony?

In this paper, I aim at fleshing out the problem of the demarcation between 'organism' and 'biological individual'. I start by charting the manifold positions at stake in the relationship between these two concepts. This has not been attempted before and therefore constitutes an important philosophical contribution of this article. I assort the stances into two groups labeled, for the sake of simplicity, 'organism = biological individual' (section 2) and 'organism ≠ biological individual'

(section 3). Then, I discuss some of the main topics that stem from the preceding systematization, such as the relationship between evolutionary individuality and the organism concept, and conclude with some suggestions for potential paths through which an organism–biological individual demarcation could be achieved (section 4). A handful of caveats are due at this point. First, I focus solely on those theoretical developments that explicitly pertain to the relationship between 'organism' and 'biological individual', abstaining from comprehensively discussing the countless notions of 'biological individual' and 'organism' that have been put forward (see instead, e.g., Cheung, 2006; 2010; Pepper & Herron, 2008; Wolfe, 2010; Toepfer, 2011; Lidgard & Nyhart, 2017; Bueno *et al.*, 2018). Second, even pursuing this more modest project, I do not claim my list to be complete or definitive. Yet, I believe that, due to its systematic character, it may straightforwardly accommodate additional examples—hopefully without the need for further categories. Third, the stances I compile are not mutually exclusive. Still, they are conceptually distinct, and thus it is worth keeping them separate. Last but not least, I favor breadth over depth for reasons of space. In largely uncharted territories such as this, a map painted with broad brushstrokes is better than having none.

2. Organism = biological individual

When equating 'organism' with 'biological individual', scholars simply use the terms interchangeably (section 2.1) or argue for the elimination of one concept or the other (sections 2.2 and 2.3). Let's briefly unravel the rationale for these positions.

2.1 Coalescence of the terms

It has been noticed several times (e.g., Prévot, 2014; Lidgard & Nyhart, 2017; Okasha, 2022) that 'organism' and 'biological individual' are generally used interchangeably in the literature, without this coalescence being properly argued for or problematized. Presumably, in most cases, it is assumed that the issue is unimportant or merely a semantical issue (e.g., in Kingma, 2020; Kaiser & Trappes, 2021). However, it seems that at least some authors use the term 'organism' as a shortcut for 'biological individual' on the assumption that the debate on individuality is primarily concerned with organisms, which are taken to be the 'paradigmatic' individuals. In this vein, Bueno *et al.* (2018, 5) state that much of the work on biological individuality "focuses on organisms, the paradigmatic biological individuals, and the difficulty of formulating criteria of organismality and, accordingly, biological individuality". Some scholars go a step further and claim that the biological individuality debate has been *de facto* motivated by the

question of what organisms are or which entities count as organisms. Pepper & Herron (2008, 622), for instance, affirm that "the question of what constitutes an individual is usually identical with the question of what constitutes an individual organism". As I shall expand in section 4, this position is typical of many evolutionary accounts of individuality (e.g., Gardner & Grafen, 2009; Queller & Strassmann, 2009; Folse & Roughgarden, 2010; Clarke, 2010; 2013; 2016; Bouchard, 2013).

2.2 Biological individual eliminativism

The position according to which the whole debate on biological individuality (or, at least, a substantial part of it) is in fact about organismality, has recently been expounded by Samir Okasha. His main argument reads as follows:

> [T]he expression "biological individual", as used in the literature on biological individuality, really means "individual entity of a certain (biological) sort", where the sort is implicitly determined by the context. And the sort in question, most though not all the time, is "organism". (Okasha, 2022, 11)

The main idea here is that the problem of biological individuality and most of the vast literature around it rest on a category mistake, which consists in the utilization of the expression 'biological individual' as a sortal[1]. Okasha demonstrates that neither 'individual' nor 'biological individual' is a sortal, since questions about counting and persistence—i.e., those that, by the way, figure most prominently in the debates on biological individuality—cannot be answered unless they are specified in terms of a true sortal concept, for they invite the reply "Biological individuals of what sort?." He rightly notices that even though there is a myriad of true sortal terms in biology that refer to *bona fide* biological individuals (i.e., individuals that are biological, such as organs, cellular parts, etc.), in the debates on biological individuality many of them are *a priori* ruled out as candidates. He submits that "[t]he grounds for excluding those entities from the extension of ' biological individual' are obscure, until it is realized that the biological individuality debate is (mostly) about what an organism is" (Okasha, 2022, 11). That is, the sortal term that is customarily implied in the debates on biological individuality is 'organism'. Consequently, Okasha suggests that the term 'organism' be preferred over 'biological individual'.

[1] Roughly, a sortal is a term—typically a count noun—for which there exist criteria for counting and determining the persistence conditions of the entity it refers to, however vague those criteria might be.

A different approach to biological individuality eliminativism is advanced by Hermida (2021). She starts by defining organisms by the property of 'being alive'. Simple organisms are those that are not composed of other organisms (e.g., bacteria), whereas composite organisms are those composed of other organisms hierarchically. Even though she does not speak of biological individuality, her notion of organism clearly covers living entities that are usually considered biological individuals and not clear-cut organisms (e.g., cells, slime molds, and symbiotic associations).

2.3 Organism eliminativism

In a previous article, Okasha (2011) advanced another interesting argument for the use of the term 'organism' as a synonym of 'biological individual' that draws on the notion of rank freedom from phylogenetic systematics. He analogizes the Linnaean view of fixed ranks with the intuition that organisms are located at a specific level (i.e., constituting a rank) in the hierarchy of nested biological individuals, and that the individuals below and above them are parts and groups of organisms, respectively. He contends that the idea of rank freedom should be applied here, since "[i]t makes no more sense to ask whether a particular biological entity (e.g., an ant colony), occupies the rank of 'organism' than it does to ask whether a particular monophyletic taxon occupies the rank of 'family'" (Okasha, 2011, 59). Adopting this view on the individuality hierarchy implies that all the individuals in the hierarchy are on par, and thus the term 'organism', according to him, "doesn't denote a rank in the ecological hierarchy; rather, *all* entities in that hierarchy, at all levels of inclusiveness, are organisms, or at least approximate that status" (Okasha, 2011, 59).[2]

Okasha's discussions on sortals (section 2.2) and rank freedom (this section) converge on the same outcome: organisms and biological individuals are indistinguishable. But, whereas in the former he concludes that 'organism' should be preferred over 'biological individual', here he remains agnostic as regards which term is to be favored. However, I label his 2011 approach 'organism eliminativism' because, even though he does not propose eliminating the term 'organism' altogether—but rather expanding it to all biological individuals—in practice he turns it inconsequential by stripping it away from any special significance, thus leaving its elimination only a step reach. That extra step is made by Matt Haber:

> Like Okasha (2011), this is a rejection of the rank of organism, but goes one step further … to recognize that *organism* is not simply not doing any work, but instead is obfuscating matters. Rather than worrying about

[2] Throughout this article no emphasis has been added to quotes.

> whether a particular grouping, be it of cells, multicellular individuals, or cellular parts, constitutes an organism or not, the goal is instead to focus on individuals and features of those individuals. (Haber, 2013, 211-212)

The obfuscated matters Haber refers to are the discussions on the individual or organismal status of animal eusocial colonies. After reviewing the different positions at stake, Haber pinpoints that the concept of 'superorganism' is problematic because it translates the problem of individuality of colonies to the question of whether they are organisms and ultimately to what an organism is, for which there are no good answers. That is why he embraces and extends Okasha's perspective and advances the elimination of the concept of organism in favor of the biological individual.

3. Organism ≠ biological individual

In this section, I cover different positions on how the organism–biological individual distinction has been drawn. These include the claims that organisms are paradigmatic exemplars of biological individuals (section 3.1), limit cases towards which biological individuals tend in evolution and development (section 3.2), or wholes in part-whole hierarchies of biological individuals (section 3.3). They also include the idea that organisms are only a subset of biological individuals writ large, namely physiological individuals (section 3.4), or even a subset of physiological individuals (section 3.5).

3.1 Organism as a 'paradigmatic' biological individual

Organisms are often said to be 'paradigmatic' individuals. But what does it mean? I submit that there are at least three ways of interpreting it. Firstly, one can interpret this statement as implying that the debate on biological individuality is in fact about organismality—which would bring us back to Okasha's argument in section 2.2. In other words, the debate would revolve around the organismal status of biological entities that show certain properties intuitively ascribed to organisms (e.g., cohesiveness, functional integration, reproductive capacity, fitness, etc.) but that are neither clear-cut examples of ('paradigmatic') organisms nor clear-cut examples of non-organisms. Under this interpretation, the idea of 'paradigmatic individuals' would simply mean 'clear-cut examples of organisms' against which "problematic" cases are contrasted.

Secondly, it could mean that the entities traditionally called organisms usually display a high degree of individuality in light of the criteria of biological

individuality that have been put forward.[3] A key idea here, which has gained widespread acceptance (Pradeu, 2016a), is that individuality is not an either/or property but comes in degrees. In contrast to the previous interpretation, biological individuality and organismality should not necessarily be understood as synonymous notions in this context. Rather, organisms are a kind of biological individual that rank higher than others, thus epitomizing biological individuality. For instance, Clarke (2010) compares six candidates of biological individuals for six criteria of individuality. Her results perfectly reflect our intuitions about the individuality of those examples. She finds that a puppy—the 'paradigmatic higher metazoan' in her assessment—matches all six criteria followed by the man-o'-war, the bacterium, the bee colony, the aspen grove, and finally the lobster claw. Similarly, Santelices (1999) places metazoans as the best representatives of individuality in terms of genetic homogeneity, genetic uniqueness, and autonomy; Pepper & Herron (2008) locate paradigmatic individuals at the extreme of a continuum of genetic homogeneity and physiological integration; and Godfrey-Smith (2009; 2013) takes humans as paradigmatic Darwinian individuals (i.e., units of selection).

Thirdly, 'paradigmatic' individuals can be interpreted as standards of individuality that suggest what properties define individuality and help characterize other individuals in terms of how closely they approach the paradigm state. Wilson (1999) takes this approach and proposes that the following individuality criteria can be extracted from, and are exemplified by, an adult higher animal: being a particular; spatial-temporal continuity and boundedness; indivisibility; nervous system; allorecognition and immune response; genetic homogeneity; development from a single cell; sexual reproduction; and identity. Whereas in the previous interpretation the paradigmatic cases were purportedly identified after evaluating many cases of biological individuals under some more or less general and objective criteria, here the paradigmatic cases are explicitly used to establish those criteria with which to perform comparisons.

3.2 Organism as a limit state towards which biological individuals tend

The idea of organisms as epitomes of individuality also comes in a diachronic version in which the paradigmatic individuality state is a limit towards which more imperfect or incomplete forms of individuality tend. For instance, Pepper & Herron (2008, 626) speculate that positive feedback loops between functional integration and natural selection lead to increasing individualization towards a paradigmatic state: "In cases where positive feedback has fully

[3] See Lidgard & Nyhart (2017) for a fairly comprehensive list of individuality criteria.

run its course without interference or complications, we expect the result to be complete functional integration and independence, or in other words, a 'unitary' or 'paradigm' organism".

This notion of progress as the build-up of the individuality hierarchy from groups of individuals to organisms or organism-like individuals during the evolutionary trajectories of multicellular lineages is a central idea of the 'major transitions in evolution' research field (Buss, 1987; Maynard Smith & Szathmáry, 1995). For example, Folse & Roughgarden (2010, 451) explain this kind of transition event, in which organisms at new levels emerge, as "a linear sequence beginning with alignment of fitness by genetic relatedness, the export of fitness by germ-soma specialization, and, finally, functional organization by adaptation at the higher level".

However, this idea has old roots. For example, Julian Huxley (1912/2022) envisions a general pattern of 'life' progressing up towards an ideal 'perfect individual' state. Also, Haeckel (1866) contends that the individuality hierarchy has accrued in the course of evolution as higher levels of individuality have sequentially emerged by aggregation of individuals from preexisting levels, thus giving rise to increasingly complex life forms. Moreover, he maintains that, throughout development, the functional whole ('biont') climbs up the hierarchy of individuality starting from the basal 'plastid' level (i.e., the zygote) to its higher-level mature state (either 'person' or 'colony') as successive levels of lower-level individuals ('morphonts') pile up. That is, development progresses from the bottom-up in the individuality hierarchy, mirroring the evolutionary trajectory—'ontogeny recapitulates phylogeny'.

von Bertalanffy's (1952) standpoint resembles Huxley's in that individuality progresses towards an unreachable ideal state. It also shares with Haeckel's the idea that the process of increasing individuality works at both the ontogenetic and phylogenetic scales. Perfect individuality cannot be attained because it would imply complete indivisibility and thus preclude reproduction, which requires the creation of a new individual out of parts of a previous one. Nonetheless, he argues that individuality is steadily approached in the course of development and evolution through the progressive centralization of biological systems (e.g., through the emergence of circulatory and nervous systems):

> Strictly speaking, there is no biological individuality, but only a progressive individualization, both phylogenetic and ontogenetic, which is based upon the progressive centralization, certain parts gaining a leading role and thus determining the behaviour of the whole. Individuality is a limit which is approached but not reached, either in development or in evolution. (von Bertalanffy, 1952, 49; see also Jeuken, 1952)

3.3 Organism as instantiating the whole in a part-whole hierarchy of biological individuals

There is a leveled and hierarchical understanding of individuality that is related to the notion of organisms as limits and is intimately entangled with the central tenets of the major transitions literature. It envisages organisms as the individuals located at the highest level in hierarchies of nested biological individuals. A way of approaching it is by contrast to Margarida Hermida's eliminativist position (section 2.2). Recall that Hermida equates 'organism' with 'living being' (~biological individual) and discriminates between simple and composite organisms depending on whether they are composed of other organisms or not. She anticipates a counterargument as follows:

> We might … deny that there are composite organisms, by requiring that only the larger living object counts as an organism. However, this seems to be an unprincipled requirement. If we deny that cells in a multicellular organism are themselves organisms, even though they are alive, we must 1) deny that organisms are a natural kind defined by the property "being alive"; and 2) specify a kind "living non-organism" to apply to living beings that are part of composite organisms. (Hermida, 2021, para. 5)

However, Mahner & Bunge (1996, 146-149) do exactly 1) and 2). They define 'biosystems' as concrete (material) systems that have the property of being alive.[4] In their account, an 'elementary biosystem' ('simple organism' *sensu* Hermida) is "any biosystem such that none of its components is a biosystem", and a 'composite biosystem' is "any biosystem composed of (at least two elementary) biosystems". These authors maintain—*contra* Hermida—that not all biosystems are organisms. Rather, an organism is specifically "a biosystem (whether elementary or composite) which is not a proper subsystem of a biosystem". Since all elementary biosystems are cells, "cell and organism are (in metaphorical terms) the smallest and largest units of life, respectively".

In evolutionary terms, some authors conceptualize the organism as the largest adaptation-bearer unit in a compositional hierarchy (Gardner & Grafen, 2009; Queller & Strassmann, 2009; Folse & Roughgarden, 2010). To quote an example, Queller & Strassmann (2009, 3144) affirm that "the organism is the largest unit of near-unanimous design … That is, the organism has adaptations and it is not much disrupted by adaptations at lower levels".

[4] I take 'biosystems' to be coextensive with 'biological individuals' since Mahner & Bunge (1996, 28, 177) conceptualize them as (biological) individuals belonging to different 'levels of individuality'.

3.4 Organism = physiological individual

Recent debates on biological individuality have focused primarily on 'evolutionary individuality', which regards individuals as units of reproduction and evolution and resorts to the theory of evolution by natural selection to ground individuality. The diverse developments grouped under this banner highlight the properties of biological entities that determine or influence their capacity to undergo natural selection (i.e., sexual reproduction, reproductive bottlenecks, germ-soma separation, etc.). More synthetic approaches either weave together several such properties (e.g., Godfrey-Smith, 2009; 2013; Griesemer, 2018), while others focus on the mechanisms that increase the capacity to undergo selection, such as policy and demarcation mechanisms (Clarke 2013; 2016) that result in low conflict and high cooperation between the parts of the individual (Queller & Strassmann, 2009) and thus in the export of fitness from the parts to the whole—i.e., the purported main unit of adaptation (Folse & Roughgarden, 2010).

Instead, 'physiological individuality' constructs individuals as cohesive and integrated wholes emerging from the interaction of functionally differentiated and causally interconnected parts. It is a broad and rather vague umbrella term that lumps together a wide variety of concepts and criteria of individuality that emphasize, among others, metabolism (e.g., Dupré & O'Malley, 2009), functional integration (e.g., Wilson 2000), autonomy (e.g., Arnellos 2018), immunology (e.g., Pradeu, 2012), or ecological interactions (e.g., Huneman, 2021) as the kernels of biological individuality, as well as those that construct individuals as 'interactors' (e.g., Hull, 1980) or 'persisters' (e.g., Godfrey-Smith, 2013; Smith, 2017).

Several authors have stressed the importance of distinguishing physiological from evolutionary individuality on the basis that the organism concept, as it is commonly used, is more akin to physiological than to evolutionary individuality (Pradeu, 2016b). In fact, in most of the viewpoints apropos the organism–biological individual relationship discussed in this paper, the concept of organism involved is essentially physiological. This may explain why the conflation between 'organism' and 'biological individual' seems plausible in the first place. As claimed by Griesemer (2018, 137), "[m]ost biologists use the term 'individual' interchangeably with 'organism' except when they are discussing questions of units and levels of evolution".

This has motivated some authors to synonymize 'organism' and 'physiological individual'. As Thomas Pradeu explains it,

> it is historically much more accurate to use the word "organism" to refer to a physiological individual than to an evolutionary individual … But, in

> addition to being at odds with history and common usage, it is misleading to refer to evolutionary individuals as "organisms", since it suggests, inadequately, that evolutionary individuality and physiological individuality always coincide, which is not true. (Pradeu, 2016b, 807)

According to these authors, the category 'biological individual' would then comprise physiological individuals (=organisms) plus evolutionary individuals (*sensu*, e.g., Pradeu, 2016b) or, equivalently, organisms plus Darwinian individuals (*sensu*, e.g., Godfrey-Smith, 2013). A problem of equating 'organism' with 'physiological individual' is that many entities that fall under the category 'physiological individual' are presumably not organisms but parts (e.g., cells) or groups (e.g., holobionts) of organisms. Thus, the equation implies either an undefined position with respect to all those cases or a restricted form of eliminativism.[5]

The first stance is exemplified by Subrena Smith and John Dupré. Smith tries to clarify the conditions that underlie Godfrey-Smith's (2013) criterion of 'persistence' that supposedly demarcates organisms from Darwinian individuals because she is cognizant that "to say that organisms persist is to say very little about them and does not distinguish organisms from parts of organisms or ecosystems" (Smith, 2017, 6). She finds that differentiation, integration, development, and constitutive embeddedness in an environment are the features that underpin persistence. But, by the end of her paper, she confesses that "[p]erhaps organismality is vague and the dividing line between organism and non-organism is more a function of the parameters of one's explanatory project than it is a fact about the structure of the biological world" (Smith, 2017, 12).

Dupré advocates for a view of living entities as processes intermingling in causal networks. Within this framework, it is humans who draw the (otherwise blurry) boundaries around these processes based on specific practical or theoretical aims. This implies what Dupré brands as 'promiscuous individualism'—there are many ways of dividing the biological word into individuals. Arnellos (2018, 201) impugns Dupré's position, for it "results in a rather vague definition of organisms, as well as in a blurred position in regard to the distinction between organisms and biological individuals". In fact, Dupré's commitment to process ontology and 'promiscuous individualism' compels him to aver that "what is an organism, and whether something is a part of an organism or not, are not questions that necessarily admit of definitive answers" (Dupré, 2012, 153).

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[5] Since there are other kinds of biological individuals besides the physiological, equating organisms with *physiological* individuals does not amount to equating them with *biological* individuals at large. This is why I keep the category 'organism = physiological individual' (this section) apart from 'organism = biological individual' (section 2).

The second alternative is best represented by Jack Wilson, who defines the 'functional individual' as a functional unit made up of causally integrated parts (Wilson, 1999). This kind encompasses, but is not exclusively composed of, organisms. Yet, telling organisms and the rest of functional individuals apart is not an easy task, for the properties that determine functional individuality vary in degree and can be ascribed to different hierarchically organized entities. As Wilson succinctly explains:

> The components of a single cell are well integrated, yet that cell may be a part of a multicellular organism in which all of the cells are also integrated into a collective functional individual. Can we determine that some of those entities are organisms and others are not? I have tried to demarcate organisms from non-organisms within the class of functionally integrated entities but have not found a satisfactory answer. (Wilson, 2000, S302)

Wilson (2000, S301) further argues that such demarcation is ultimately irrelevant for philosophers and biologists alike "because the most important questions about organisms do not depend on this concept".

3.5 Organism as a special kind of physiological individual

If the organism notion is closely linked to physiological individuality, then the problem of demarcating 'organism' and 'biological individual' translates to the organism–*physiological* individual demarcation. Accordingly, some authors have singled out properties that purportedly delineate organisms from other physiological individuals.

Johannes Martens illustrates this standpoint quite neatly:

> The difference [between 'organism' and 'biological individual'] lies in the fact that, in order to identify an entity as a biological individual, you have to decide whether the whole entity is sufficiently cohesive and functionally integrated to impose a common evolutionary fate on its parts, whereas to determine if an entity is an organism …, you must identify a certain *kind* of functional integration, namely the specialization of the parts (different tasks promoting the reproduction of the whole). So, as a consequence, one can perfectly identify in some cases an entity as a biological individual *while* refusing to recognize it as a true organism or superorganism. Such a denial should not be a matter of preference, but should be argued on a theoretical basis. (Martens, 2010, 386)

Thus, organisms constitute a particular kind of physiological individual but do not stand in continuity with other physiological individuals. Rather, they

bear certain properties that make them stand out as special units and not merely as paradigmatic cases or as limits towards which other individuals tend. Martens conceives the biological individual as a cohesive and functionally integrated whole and the organism as a biological individual whose functional integration takes a specific form: division of reproductive labor among their parts (i.e., reproductive specialization). Interestingly, Martens also points out that this structural and functional property makes the organism "a true locus of ecological action impacting directly on the causal trajectory of evolution" (Martens, 2010, 397). Thus, the particular form of functional integration and physiological wholeness that organisms display dovetail with their unique capacity to act upon the environment and ultimately bias their own evolution.

Functional integration and wholeness take on a sophisticated form in recent publications within the theoretical framework of biological autonomy.[6] Here, a central notion is 'organizational closure', which Moreno & Mossio (2015, 1) define as "a feature of biological systems by virtue of which their constitutive components and operations depend on each other for their production and maintenance and, moreover, collectively contribute to determining the conditions under which the system itself can exist". This circular, self-recursive causal regime characterizes living beings and determines their identity since it is responsible for the production of the boundary of the system, which in turn materializes the conditions of possibility for its own production. Biological individuality, Moreno & Mossio (2015, 23) suggest, "has much to do with organizational closure, to the extent that one may conjecture that closure in fact defines biological individuality". Therefore, delineating biological individuals would amount to identifying organizationally closed systems. Additionally, some authors have considered the individuality of ecosystems (Nunes-Neto *et al.*, 2014), symbiotic interactions (Bich, 2019), eusocial insect colonies (Canciani *et al.*, 2019), and collective associations of prokaryotes (Militello *et al.*, 2021) not so much in terms of the realization of higher-level closure, but as the result of the integration of organizationally closed systems through regulatory control.

However, the demarcation between organisms and other biological individuals within the organizational framework has only been explicitly addressed in the context of multicellular associations. In a nutshell, to count as an organism, a closed system must additionally be self-regulating and self-determining—i.e., it must be autonomous. In multicellular associations, self-regulation grounds functional integration. That is, the collective of cells imposes regulatory constraints that coordinate the activities and differentiation of each cell, thus making

[6] I thank an anonymous reviewer for helping me enrich the discussion on this topic and suggesting relevant literature.

the collective behave as a unitary whole (Arnellos *et al.*, 2014; see also Bich *et al.*, 2019). Functional integration through self-regulation—rooted in organizational closure—corresponds to the 'constitutive dimension' of biological autonomy. Nonetheless, there is also an 'interactive dimension' that refers to the interaction of the organism (*qua* agent) with its environment. Climactically, what defines an organism is a reciprocal relation between its constitutive and interactive dimensions (Arnellos & Moreno, 2016; Arnellos, 2018).

4. Discussion

Two patterns crop up from my systematization of the different stances on the organism–biological individual relation (Table 1). The first is that, in most cases, the concept of organism is imprecise. This means that sufficient (or even necessary) criteria for what counts as an organism are seldom offered. Consequently, many stances tend to some form of eliminativism in which organismal status is arbitrarily ascribed (i.e., organism eliminativism) or in which the organism is considered to be the (only) individual the broad notion of biological individuality refers to (i.e., biological individual eliminativism). The exception is to be found in the conceptualizations of the organism as a special kind of physiological individual (section 3.5). But, in those cases, the challenge is that the criteria for organismality seem to be too narrow. For instance, Arnellos (2018, 215) concludes that "the requirements for MC [multicellular] organisms are not satisfied in systems with a lower organizational complexity than that of eumetazoa".

Stance	Explication	Challenge	Comparison	Examples
Coalescence of the terms	'Organism' and 'biological individual' are used interchangeably	Imprecision, eliminativism	Horizontal?	10, 11, 13–15, 20, 21, 30, 32, 33
Biological individual eliminativism	Biological individuals are organisms	Eliminativism	Horizontal?	34
			Vertical	31
Organism eliminativism	There is no organism or it is indistinguishable from other biological individuals ('organism' should be replaced by 'biological individual')	Eliminativism	Vertical	17, 23
Organism as a 'paradigmatic' biological individual	'Organism' stands for (a) a clear-cut example of individual, (b) an individual displaying (the) high(est) degree of individuality, or (c) a benchmark for assessing individuality	Imprecision, eliminativism,	Horizontal	7, 8, 10, 12–14, 22
Organism as a limit state towards which biological individuals tend	Individuals progressively become more 'organismal' in the course of evolution…	Imprecision, eliminativism	Horizontal	1–5, 10
	…or development		Vertical	1, 3, 4
Organism as the whole in a part-whole hierarchy of biological individuals	The organism represents the highest level in hierarchies of biological individuals (or units)	Imprecision, elminativism	Vertical	6, 11, 13, 15, 29, 33
Organism = physiological individual	Physiological individuals are organisms (or organisms cannot be distinguished from other physiological individuals)	Imprecision, eliminativism	Horizontal?	18, 19, 22, 27
			Vertical	9
Organism as a special kind of physiological individual	Organisms are physiological individuals but of a special kind (not all physiological individuals are organisms)	Narrowness	Horizontal	16, 24–26, 28

[1]Haeckel (1866); [2]Huxley (1912/2022); [3]Jeuken (1952); [4]von Bertalanffy (1952); [5]Buss (1987); [6]Mahner & Bunge (1996); [7]Santelices (1999); [8]Wilson (1999); [9]Wilson (2000); [10]Pepper & Herron (2008); [11]Gardner & Grafen (2009); [12]Godfrey-Smith (2009); [13]Queller & Strassmann (2009); [14]Clarke (2010); [15]Folse & Roughgarden (2010); [16]Martens (2010); [17]Okasha (2011); [18]Dupré (2012); [19]Pradeu (2012; 2016b); [20]Bouchard (2013); [21]Clarke (2013; 2016); [22]Godfrey-Smith (2013); [23]Haber (2013); [24]Arnellos et al. (2014); [25]Arnellos & Moreno (2016); [26]Moreno & Mossio (2015); [27]Smith (2017); [28]Arnellos (2018); [29]Kaiser (2018); [30]Kingma (2020); [31]Hermida (2021); [32]Kaiser & Trappes (2021); [33]Oderberg (2021); [34]Okasha (2022)

Table 1. Summary of the different stances apropos organism–biological individual demarcation. See details in the text.

The second and most important pattern is that the comparisons between putative biological individuals and organisms have been performed either *horizontally* or *vertically* (Table 1). By 'horizontal' comparisons I mean that the individuals to be compared are typically taken in fully-developed or adult stage, treated as isolated wholes, and put on the same footing even though they usually belong to quite distant branches of the phylogenetic tree and starkly differ in their organizational complexity. These comparisons rely on the idea that individuality is a continuous rather than a discrete property, so different biological entities can be ranked according to their degree of individuality. Occasionally, these comparisons are performed in a principled way by resorting to general theoretical criteria (e.g., autonomy, being a unit of selection). Commonly, however, some notion of

paradigmatic individuality is explicitly or tacitly used to establish a metric with which to assess degrees of individuality. In Clarke's (2010) assessment mentioned in section 3.1, for instance, a bacterium 'has more individuality' than a bee colony because it approximates more closely a paradigmatic state.

The problem with the notion of 'paradigmatic' individuals or organisms is that it reflects a strong anthropocentric bias in our understanding of biological individuality and consequently makes horizontally-comparing approaches vulnerable to a circularity objection. Concretely, both the idea of paradigmatic exemplars as individuals displaying a high degree of individuality or as standards for assessing individuality (section 3.1),[7] as well as the notion of organisms as limits (section 3.2), rely on criteria of individuality that have been crafted on the image of our intuitive notion of what an organism is. This image is strongly conditioned by our familiarity with those biological entities we interact more closely with and that are more alike us, particularly the so-called 'higher' metazoans and, of course, humans. Then, it should not come as a surprise that "[h]igher metazoans are in general relatively easy to individuate, most tests agree on their individuation, and give or take a few worries about parthenogenesis or regenerative abilities, there aren't real problems regarding these organisms" (Clarke, 2010, 323), given that most individuality criteria have been made up by drawing inspiration from higher metazoans. More generally, I disagree with Pepper & Herron's (2008, 625) claim that the paradigm individual "is not universal, but neither is it rare, and deviations are often minor". In point of fact, the paradigmatic state falls short for the majority of life forms on Earth (Herron *et al.*, 2013) and is problematic even among mammals if pregnancy (Kingma, 2020; Morgan, 2022) and holobiosis (Dupré & O'Malley, 2009; Gilbert *et al.*, 2012) are considered. The "least problematic" individuality and organismality case, and thus the closest we could get to a 'paradigmatic' individual, would be an entity in which compositionality does not represent a challenge—e.g., a bacterium. But even bacteria perform lateral gene transfer, show collective behavior, form biofilms, etc. (see Ereshefsky & Pedroso, 2016). The moral is that there are no clear-cut, 'easy' individuality cases. The 'paradigmatic' state is a myth.

In 'vertical' comparisons, the idea of individuality as hierarchically structured bears more weight than the idea of individuality as a continuous property and it does not depend on some external, standard paradigm for its assessment. Vertical comparisons are performed between entities belonging to different levels of the same stratified or hierarchical system. Drawing on the aforementioned example,

[7] These two interpretations can be mapped onto the two variants of what Haber (2013, 199) calls 'the problem of the paradigm', namely, "presuming either that organisms are paradigmatic individuals, or that there is a paradigmatic organism". The underlying anthropocentric bias has been criticized several times (see, e.g., Pradeu, 2016a).

the comparison here would not be performed between the bacterium, the man-o'-war, and the bee colony, because they do not stand in a hierarchical relation to each other. Instead, the comparison would be carried out between each of these entities and their respective lower and higher compositional levels—e.g., between the bacterium and the biofilm it may happen to integrate, between the man-o'-war and each of its zooids, and between each bee and the whole bee colony. Here, no paradigm sets the standard of individuality and the central notion is *wholeness*.

Evidently, the 'vertical' mode of comparison is best represented by the idea of the organism as the largest unit (the whole) within a part-whole hierarchy (section 3.3). Things belonging to levels below the organism level are said to be parts (i.e., they belong to the organism as their *parts*) and things above the organism level are referred to as groups (i.e., they include the organism as a *member*). This means that every biological entity is either (a) an organism, (b) a part of an organism, or (c) a group of organisms.[8] The problem is that, excepting the organism, the *relata* of these part-whole relations are not necessarily biological individuals as they are usually discussed in the biological individuality debates. A bacterial flagellum and my teeth are genuine parts of organisms and (biological) 'individuals' in the sense of (biological) objects that can be individuated, but they are generally dismissed as proper 'biological individuals'—recall Samir Okasha's argument from section 2.2. Mahner & Bunge (1996; section 3.3) and Kaiser (2018) regard (a) and (b) as biological individuals, but not (c). In Hermida's (2021; section 2.2) terms, (a) and (b) are all organisms, but presumably not all (c). Okasha (2011, section 2.3) calls (a)–(c) biological individuals or organisms, indistinctly. And, according to Oderberg (2021), only (a) would be a biological individual.

It is appropriate at this point to explain why I do not include in my systematization a category that specifically relates 'organism' to 'evolutionary individual'. Evolutionary individuality stances are essentially hierarchical. Now, the ambiguity on how (b) and (c) relate to the notion of biological individual explains why 'organism' and 'biological individual' are coalesced in those evolutionary accounts in which the organism is defined as the largest unit that bears adaptations (section 3.3; see also Pepper & Herron, 2008). The organism is deemed not as *an* individual but as *the* individual—hence the idiom 'individual organism'—and normally it is not quite clear whether its lower-level units (e.g., cells) or upper-level units (e.g., populations) are also considered biological individuals

[8] This has been called "exclusion principle" (Godfrey-Smith, 2013; Morgan, 2022) or "tripartite distinction" (Oderberg, 2021).

in their own right, despite the fact that they may count for fitness assessments and bear adaptations. Therefore, these approaches abut biological individual eliminativism.

The coalescence between 'organism' and 'biological individual' is also pervasive in Clarke's (2013; 2016) evolutionary account, but for different reasons. She understands the evolutionary individual as "a collection of living parts which has some *capacity* for responding to selection at the between-collection level, *because* of the action of individuating mechanisms [i.e., policy and demarcation mechanisms]" (Clarke, 2016, 903). She seems to assign the term 'organism' arbitrarily since her definition bestows no special place to the organism and does not allow discrimination between organisms and other individuals. Thus, her stance adjoins organism eliminativism (see also Bouchard, 2013).

Also close to organism eliminativism is Charles Goodnight's approach, although it is rather unclassifiable. He defines individuality in terms of the level at which fitness is attributed, the lowest level at which natural selection operates, and the lowest level at which evolutionary response to selection occurs. According to Goodnight (2013, 49), individuality is relative to the observer's aims in all three cases, so "there is no one level that can clearly be called 'the individual' to the exclusion of other levels". If individuality is arbitrarily assigned, then the organismal status should *a fortiori* be also arbitrary. Nevertheless, Goodnight nuances his relativism and leaves the door open for the idea that organisms may be special after all, "[b]ecause evolution below the organism level is suppressed, and as a consequence a large amount of selection is focused on the organism".

The last evolutionary individuality approach I shall mention is Godfrey-Smith's (2009; 2013). He understands evolutionary individuals as units of selection but, unlike Ellen Clarke and Charles Goodnight, he thinks that the organism concept cannot be reduced to being a unit of selection. He explains that "[o]ne way to exist, to operate in the world, is as an organism, and physiological unity is relevant to whether an entity has that status. But not all Darwinian individuals have physiological unity—some do not have much in the way of physiology at all". In fact, Darwinian individuals as he defines them "need not even be close to being organisms. Genes, chromosomes, and other fragments of organisms can all form Darwinian populations" (Godfrey-Smith, 2009, 85-86). That is why he prefers to keep evolutionary and physiological individuality apart and define the organism in physiological terms (section 3.4).

Although proposing a solution to the organism–biological individual demarcation problem is beyond the scope of this article, I shall offer in closing some hints on what I think such a solution would require. Assuming, by hypothesis, that there is a special unit at a certain level that deserves the label 'organism', a

crucial question needs to be asked: Is that unit present in every *token* hierarchy of biological individuals? I think that, in general, the answer is assumed to be affirmative—"life comes in the form of organisms" (Goodwin & Dawkins, 1995, 47)[9]. If that is the case, then horizontal comparisons are uninformative regarding the organism–biological individual distinction, since differences in the degree of individuality of entities belonging to different *token* hierarchies or the extent to which putative organisms belonging to different hierarchies approximate more or less closely a certain standard of individuality or organismality are irrelevant. Organisms come in extremely diverse forms—some are more 'colony-like', some are more 'paradigm-like'. However, *organismal status is not dictated by the degree of individuality organisms show or by the extent to which organisms resemble a paradigmatic state, but by how they relate to the units above and below in the hierarchy they partake in*. Therefore, the organism–biological individual demarcation problem can be narrowed down to the question: "How do we demarcate organisms from other functionally integrated systems above and below that level of organization?" (Wilson, 2000, S305). In this sense, demarcating the organism amounts to having criteria to decide, when confronted with a living system, at which level the organism is located and thus what counts as its parts and with what entities it groups into higher levels. Or, in evolutionary (or developmental) transitions in individuality, having criteria to decide when an aggregating collective of organisms stops being a group and becomes a new organism or, conversely, when a disaggregating organism stops being an organism and gives rise to a group.

The notion of the organism as a whole in a part-whole hierarchy (section 3.3) is the only one among those I compiled that explicitly deals with the organism–biological individual demarcation problem thus formulated. However, I think the requirement of the whole being the largest unit in the hierarchy is unwarranted. I do not see a clear reason why the organism could not partake in higher-level *biological individuals*, although I am skeptical that an organism can be a part of other *organisms*, as Hermida (2021) contends.

5. Conclusions

The 'organism' and 'biological individual' concepts are central to biology, have an illustrious pedigree and have been among the most intensively discussed notions in the philosophy of biology in the last couple of decades. Moreover, they are so inextricably comingled that they could hardly be spelled out independently from one another. Still, their demarcation has not been sufficiently

[9] Although there might be cases of biological individuals that are neither organisms nor parts or groups of organisms (e.g., spawned gametes, cells in tissue cultures, or flowers kept alive in a vase).

discussed and, as far as my knowledge goes, the relatively few discussions that explicitly engage with it start from an incomplete view of how these concepts have actually been related.

Here, I reviewed and systematized the different perspectives on this demarcation, and identified eight ways 'organism' and 'biological individual' have been coupled together in the literature. Each one of them faces conceptual challenges when it comes to demarcating the organism from other biological individuals. Most commonly, they fail in offering precise enough criteria—if any—of what makes organisms a special unit and most of them leave the door open for organism eliminativism.

I also observed that organism–biological individual comparisons have been carried out in two different ways that I labeled 'horizontally' and 'vertically'. I argued that some horizontal comparisons face the problem of relying on an untenable anthropocentric notion of paradigm or limit case individual. More generally, the horizontal comparison mode does not help to demarcate the organism from other biological individuals, for ranking different putative organisms and individuals according to their degree of individuality or how closely they approach a paradigmatic or limit state does not help decide which of the compared entities is an organism and which is not. I also argued that the drawback of the vertical comparison mode is that it is not clear which hierarchically-arranged entities that purportedly are parts and groups of organisms are biological individuals, and thus the organism–biological individual distinction remains obscure.

Finally, I contented that the organism–biological individual demarcation problem requires vertical comparisons to determine at which level in the hierarchy the organism is located—irrespective of how closely it resembles some paradigmatic benchmark. Thus reformulated, I believe the problem becomes tractable, and its solution could yield insights into the notoriously elusive question of what the organism is.

Acknowledgments

I thank Alejandro Fábregas-Tejeda and Mariano Martín-Villuendas, guest editors of this special issue, for the invitation and support. Constructive criticism from Jan Baedke, Daniel S. Brooks, Saana Jukola, Alejandra Petino Zappala, and two anonymous reviewers substantially improved earlier versions of the manuscript—any remaining flaws are mine. I also thank the valuable input from the participants of the workshop "The Place of the Organism in Biology and Medicine" (Ruhr University Bochum, 16-18 November 2022), especially Giuseppe Fusco, Daniel W. McShea, and Matteo Mossio. I am grateful to the German Research

Foundation for financially supporting my research (DFG; project no. BA 5808/2-1). I dedicate this paper to Mario Bunge (1919-2020) who, unawarely, was my first philosophy teacher.

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