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Individuating Part-Whole Relations in the Biological World

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Abstract

What are the conditions under which one biological object is a part of another biological object? This paper answers this question by developing a general, systematic account of biological parthood. I specify two criteria for biological parthood. *Substantial Spatial Inclusion* requires biological parts to be spatially located inside or in the region that the natural boundary of the biological whole occupies. *Compositional Relevance* captures the fact that a biological part engages in a biological process that must make a necessary contribution to a condition that is minimally sufficient to one or more of the characteristic behaviors of the biological whole. Instead of emphasizing the diversity of part-whole relations in the biological world, this paper asks what biological part-whole relations have in common and what constrains their existence, in general. After presenting the two criteria for biological parthood I discuss in how far my account can cope with hard cases (e.g., redundant parts) and I reveal the merits and limits of monism.

1 Introduction

The view that nature is divided into part-whole hierarchies is deeply embedded in the sciences, for instance, in the biological sciences. Biologists represent objects (e.g., cells) as being constituted of a certain collection of organized parts (e.g., DNA, mitochondria, proteins, etc.). Assumptions about part-whole relations are involved in classifications of biological objects into kinds (e.g., the assumption that fish have gills as parts, whereas mammals have lungs as parts). Moreover, the methodological principle that one can understand the behavior of a whole by decomposing it into its parts and studying the behavior of the parts is central to generating knowledge in the biological sciences (for the limitations of reductive methods see Kaiser 2011, 2015). The importance of part-whole relations to the biological sciences raises the question under which conditions something is a part of a biological whole and what it means that the parts constitute the whole. For instance, when does a vesicle that is transported from the endoplasmic reticulum to the Golgi apparatus in a eukaryotic cell cease to be a part of the endoplasmic reticulum and become a part of the Golgi apparatus? Is the case that is attached to the body of a Caddisfly larva and that promotes the larva's survival a part of the larva or does it belong to the larva's environment? Under which conditions is a particular species or abiotic factor (e.g., nitrogen) a part of an ecosystem? Does a virus that enters a host cell and uses the cell's machinery and metabolism to replicate itself become a part of the host cell?

The goal of this paper is to answer questions like these by developing a general, systematic account of biological parthood. Such an account specifies general criteria that guide the individuation of wholes and parts in the biological sciences, and it reveals the conditions under which biological objects stand in a part-whole relation to each other. The central question of the paper is under which conditions is one biological object x a part of another biological object y .¹ If two biological objects stand in a part-whole relation to each other, I will speak of one being a *biological part* of the other. Hence, biological parthood applies to biological objects only.² The question under which conditions x is a biological part of y is a special version of what van Inwagen has called the "special composition question" (1990, 21). It is a special version because it concerns only part-whole relations in the biological world, rather than the concept of a part in general (which is the object of mereology). This paper is about biological parthood, not about parthood simpliciter.³

Questions about biological parts are intertwined with questions about biological individuality. Typically, the concept of a biological individual is centered on but not confined to organisms. Besides organisms, also parts of organisms (e.g., genes and cells) and groups of

¹ I take biological objects to be those objects that belong to the domain of the biological sciences.

² For reasons of simplicity, I will often speak of one object being a *biological part* of another object. This must be read synonymously with the claim that one biological object is a part of another biological object.

³ My focus on biological parthood is not driven by the conviction that biological part-whole relations are fundamentally different from other kinds of part-whole relations. In fact, my analysis yields parthood criteria that might be applied also to non-biological objects, for instance, in the chemical realm.

organisms (e.g., populations) are discussed as being biological individuals (e.g., Clarke 2011; Wilson and Barker 2017). Accordingly, the relata of many part-whole relations in the biological realm will be biological individuals. Rather than focusing on the question what biological individuals are and how they are individuated, this paper examines how biological individuals *relate* to each other, in particular, which conditions must be satisfied so that biological individuals relate to each other as parts and wholes. One of my central claims will be that the individuation and characterization of a biological individual as a whole constrains the individuation of its parts in several ways. This paper uncovers the various kinds of constraints by formulating different criteria for biological parthood.

Methodologically, my account of biological parthood arises from and is sustained by an analysis of a wide variety of paradigmatic examples of part-whole relations from the biological sciences. My analysis takes into account actual cases of biological part-whole relations as well as the explanatory and investigative strategies that biologists employ when studying part-whole relations. The account of biological parthood that I develop in this paper is thus an exercise in what I call a metaphysics of biological practice. First, it is a metaphysical account because it aims at describing a feature of reality, namely part-whole relations that exist out there in the biological world. It provides an understanding of the characteristics of biological part-whole relations and of the conditions under which they hold. Second, I agree with naturalistic metaphysics (e.g., Ladymann and Ross 2007; Chakravartty 2013) in that we should consult the sciences to develop metaphysical views about which kinds of entities exist and how they are like. But instead of considering physical theories only, a metaphysics of biological practice draws our attention to the metaphysical underpinnings of the non-physical sciences, and it develops metaphysical claims that take into account also the non-theoretical aspects of biological practice (e.g., scientific activities, epistemic values, reasoning strategies; Chang 2011, Waters 2014).⁴ Because of the relatively broad scope of my account (i.e., parts and wholes in the biological world, in general) I focus on analyzing examples of part-whole relations that are paradigmatic and figure in successful biological explanations. In addition, my analysis is backed up by philosophical case studies that are concerned with more specific kinds of part-whole relations (e.g., DNA sequences being parts of the human genome) and that investigate the concrete investigative practices and reasoning strategies that biologists employ (see, e.g., Kaiser forthc.).

A pluralistically inclined philosopher might object that my goal of paying attention to actual biological practice conflicts with my other goal of developing a general, systematic

⁴ I am aware of the fact that a metaphysics of biological practice understood in that way, presupposes scientific realism and requires an account of which elements of biological practice allow for drawing metaphysical conclusions (and which do not). A promising approach is to focus on successful and stable practices. However, it is a controversial question whether scientific success provides us with access to the world, as it really is. Those skeptical about this might prefer to adopt a weaker view of metaphysics, according to which metaphysics makes general claims about our conceptual apparatus, rather than about the world (e.g., Strawson 1959). I agree that these are urgent and very interesting questions but they lie beyond the scope of this paper. Fortunately, my analysis of biological parthood is compatible with both views of metaphysics.

account of biological parthood. According to the pluralist, a monistic account that specifies a single set of criteria supposed to apply to all part-whole relations in the biological world will fail to capture the diversity of biological part-whole relations and of individuation practices in the biological sciences (cf. Kellert, Longino, and Waters 2006). I agree with the pluralist that it might turn out that only a pluralistic notion of biological parthood that recognizes different, perhaps conflicting parthood criteria (such as Wimsatt 1972, 2007) accounts for the diversity of biological practice. However, diversity and difference is only one aspect of biological practice that philosophers can and should account for (Kaiser 2015, Chapter 2). From a philosophical perspective, it is also interesting to zoom out and look for generalities and for similarities between different practices of individuating parts and wholes. When traditional metaphysicians argue about the general structure of reality, they adopt such a general perspective and develop philosophical views that are supposed to apply universally. I think we should not reject the monistic aspirations of traditional metaphysics too hastily because we can learn a lot from striving for monism and from analyzing the obstacles we meet. Hence, the aim of my paper is twofold. First, I develop a monistic account of biological parthood that proposes two general, necessary conditions for the existence of biological part-whole relations, and I show why these criteria are preferable to alternative criteria. Second, my analysis enables me to explain why the search for a monistic account that specifies individually necessary and jointly sufficient criteria for biological parthood is so difficult. Understanding the reasons for these difficulties delivers valuable insights into the nature of biological part-whole relations.

This paper is organized as follows. In Section 2, I distinguish different kinds of questions that one can ask concerning biological parthood, and I specify the relation of biological part-whole relations. Section 3 develops spatial inclusion as the first criterion for biological parthood and introduces the notion of a natural boundary, which is central to the spatial inclusion criterion. In Section 4, I develop the second criterion for biological parthood, compositional relevance, which refers to the characteristic behaviors of the whole and specifies the relevance condition in terms of an insufficient but necessary part of a condition that is unnecessary but sufficient (INUS-condition). In Section 5, I discuss in how far my account of biological parthood can deal with hard cases, such as redundant parts or collective parts. I conclude in Section 6 by revealing the merits and limits of a monistic account of biological parthood.

2 Preliminaries

2.1 Relating Different Part-Whole Questions

I shall call the question of whether a particular biological object x (e.g., a vesicle) is a part of another biological object y (e.g., the Golgi apparatus) the *parthood question*. It is closely related to but less demanding than the *decomposition question*, which asks for not only one but for all parts into which a whole is partitioned. My account of biological parthood focuses

on the relation between *one* biological part and its whole (i.e., on the parthood question) and specifies the conditions under which this one-to-one relation holds. From this focus, it does not follow that the other parts of the whole are irrelevant to the existence of a part-whole relation. On the contrary, several authors have drawn attention to the fact that a biological part always is a member of a team of parts that interact with each other in very “intense” (Simon 1962, Haugeland 1998, McShea 2000) or “productive” ways (Machamer, Darden, and Craver 2000, Gillett 2013) and that exhibit a special “jointness” (Fagan 2012). How, exactly, the existence of a particular part-whole relation depends on other parts of the same whole will be examined in Section 4. This dependency does not imply that answering the parthood question presupposes answering the decomposition question. We can individuate one particular biological object as a part of a whole without having decomposed the whole into all of its parts (but not without knowing some of the other parts).

Whether a particular object is a biological part of another object, the whole, does not only depend on the other parts but also, and in particular, on how the whole is individuated and by which properties and behaviors it is characterized. I shall call the question ‘What is the whole, how can it be individuated and characterized?’ the *individuation-of-the-whole question*. A central idea that I will elaborate in the following sections is that answering the individuation-of-the-whole question constrains answering the parthood question. In other words, which object I pick out as the whole and how I characterize its properties, typical behaviors, and spatial boundaries constrains what counts as a biological part of this whole. For instance, biologists do not treat a green alga that is spatially included in a fungus as a part of the fungus. However, if the whole is referred to as a lichen, the green alga will be a part of the lichen. Likewise, if biologists conceive of a genome as having a specific chemical structure (i.e., as consisting of DNA only) transcription factors and histones fail to be biological parts of the genome because they are proteins. By contrast, if biologists characterize a genome in purely functional terms (e.g., as guiding development) transcription factors and histones turn out to be biological parts of the genome because they are central to gene regulation. The criteria for biological parthood that I develop in this paper specify the different ways in which the individuation of the whole constrains the individuation of its parts.

The individuation-of-the-whole question must be distinguished from the *demarcation question*, which concerns the outer boundary of the whole and asks how the whole can be demarcated from its context. One might claim that answering the demarcation question boils down to answering the decomposition question because to demarcate an object from its context is nothing but identifying all of its parts and classifying all non-parts as context. In Section 3.1, I shall argue that this view invites a circularity objection, which can only be avoided by a substantial notion of a spatial boundary that allows us to demarcate an object from its environment independently of individuating all of its parts. In other words, I will argue that answering the demarcation question is independent of answering the decomposition question. Identifying what I will refer to as the ‘natural boundary’ of a

biological object may be one aspect of individuating the object as a whole.⁵ Hence, answering the demarcation question may be part of answering the individuation-of-the-whole question.

In sum, we must distinguish four questions concerning part-whole relations:

Part-Whole Questions

- (1) *Individuation-of-the-whole question*: What is the whole, how can it be identified?
- (2) *Demarcation question*: Where does the outer boundary of the whole run? How can the whole be demarcated from its context?
- (3) *Decomposition question*: Into which collection of parts can the whole be decomposed?
- (4) *Parthood question*: Is a given biological object a part of another biological object, the whole?

2.2 The Relata of Biological Part-Whole Relations

Claims about part-whole relations in the biological sciences typically concern types or kinds of objects, not tokens. For instance, all individuals of the kind lichen are composed of green algae and fungi, not only a particular lichen. The fact that science is often concerned with kinds of part-whole relations, however, does not imply that the part-whole relation itself holds between types or kinds.⁶ Depending on one's ontology, kinds might be viewed as abstract entities (e.g., universals) that do not exist in space and time, or they might not be said to exist at all – at least not independently of our classification practices. It seems to me that the more parsimonious and less controversial assumption to start with is that part-whole relations in the biological realm relate token objects that exist in space and time. The account of biological parthood that I develop in this paper is thus a singularist account.⁷ According to a singularist account of biological parthood, part-whole relations exist between individual biological objects and claims about kinds of biological part-whole relations are generalizations that arise from investigating particular part-whole relations.

Even if kinds are not the relata of biological part-whole relations, they are still relevant to the conditions under which biological part-whole relations exist. Whether two particular biological objects are related as part and whole depends also on the kinds to which they belong. To see this, consider the question of whether a virus that has infected a host cell is a part of it. Answering this question depends not only on how biologists individuate the whole but also on how they classify it. Viruses are surely not among the parts that cells have, in general. But they may be parts of a subtype of cells, namely infected host cells. A virus normally does not contribute to but often hinders the behaviors that are typical for objects of

⁵ For instance, biologists spatially characterize a cell as being surrounded by a cell membrane and insects as being surrounded by an exoskeleton with a particular shape and structure.

⁶ This is not a trivial point because some authors claim that part-whole or constitutive relations exist between properties or types of events (e.g., Harbecke 2010).

⁷ My singularist account is in accordance with the fact that the part-whole relation in the classical, mereological sense is conceived of as a first-order relation between individuals.

the kind “cell”, such as growth, DNA replication, protein synthesis, and cell division. A token object that belongs to the kind “host cell”, by contrast, is characterized by different typical behaviors, such as reduced cell defenses, viral replication, and release of viruses. The virus is a biological part of a cell of the kind host cell because the virus is essential to the characteristic behaviors of host cells.⁸ I will pick up this point in Section 4.1 when I explain the notion of a characteristic behavior in more detail and incorporate it into my second criterion for biological parthood. To be clear, my claim that kinds are relevant to the conditions under which biological part-whole relations exist does not imply that the existence of biological part-whole relations depends on classification preferences of individual biologists. Not any biological kind that one might think of is scientifically legitimate and thus can be said to be real (in a promiscuous way; Dupré 1993, 36). Hence, from the fact that biological part-whole relations exist only relative to specific kinds it does neither follow that biological parthood is subjective, nor does it follow that my account of biological parthood is epistemological rather than metaphysical in character.

Some philosophers might agree that part-whole relations exist between tokens but reject the view that material objects – understood in accordance with endurantism⁹ – are the appropriate relata of part-whole relations. Process ontologists argue that an object-bias or “substance paradigm” (Seibt 2016) fails to acknowledge the processual nature of the living world (e.g., Whitehead 1929; Rescher 1996, 2000; Seibt 2003; Dupré 2012; O’Malley 2014). I agree that the ontological category of processes (or occurrents, which include processes, events, and states) is important to capture the constantly changing, complex biological world (see Kaiser and Krickel 2016). However, this does not commit one to the radical claim that “everything is process” (Bickhard 2011, 95)¹⁰ and that part-whole relations must exist between processes only. It is possible to identify material objects as the relata of part-whole relations and yet to acknowledge the importance of processes. As my analysis will show, the processes in which biological objects are involved co-determine whether these objects are related as parts and wholes. A static view of biological parthood that considers only the properties of and relations between material objects at a certain time is thus highly implausible. Biological part-whole relations essentially involve processes, even though processes are not the relata of part-whole relations.¹¹

⁸ There are several other examples that support this claim. For instance, the F_1 subunit seems not to be a biological part of a protein of the kind “transmembrane protein”, but rather a biological part of a protein of the kind “ATP synthase”.

⁹ Endurantists believe that material objects have spatial parts but no temporal parts and that material objects are wholly present whenever they exist. By contrast, perdurantists claim that material objects are four-dimensional space-time worms that are extended over time and that have also temporal parts.

¹⁰ It is unclear whether there is any philosopher of biology who subscribes to the radical view that only processes exist. Dupré claims that biological entities, such as organisms and genomes, are dynamical, constantly changing entities, which cannot be understood in terms of “properties of and relations between their structural constituents” (Dupré 2012, 8).

¹¹ Along these lines one might add that a part-whole relation between biological objects does not only depend on the processes they implement but also on the properties and powers they possess (Gillett 2013).

To conclude, I assume that part-whole relations in the biological world each exist between particular biological objects. My heart, for example, is a biological part of my circulatory system. Despite this focus on particulars and on material objects, I argue that we can only understand the conditions under which a certain part-whole relation exists if we broaden our perspective and take into account also other parts of the same whole, the processes in which the objects are involved, and the kinds to which they belong. The criteria for biological parthood that I develop in the following sections explicate how other parts, processes and kinds determine the existence of biological part-whole relations.

3 Spatial Inclusion

3.1 Why a Primitive Notion of Spatial Inclusion Fails

A widespread and intuitively plausible view is that the parts of material objects are spatial parts. There is a dispute in metaphysics about whether material objects have temporal parts as well, as the perdurantist believes, but everybody agrees that material objects have at least spatial parts. To be a spatial part of a whole means to be spatially included or contained in the whole, that is, to be located inside the spatial boundary that continuously surrounds the whole. The view that something is a part if it is spatially included in the whole seems to apply to the biological world as well (see Craver 2007, Clarke 2011, Gillett 2013). Chloroplasts are parts of cells because they are located inside cells. My liver is a part of me because it is spatially included in me. An individual black-headed gull is a part of a certain population because it is located in the spatial distribution of that population. A green alga is a part of a lichen because it is contained in the lichen. Bases on these intuitions, you might suggest to specify biological parthood as primitive spatial inclusion:

Primitive Spatial Inclusion (PSI)

An object x is a biological part of an object y if and only if x is spatially included in y , that is, x is located inside the continuous spatial boundary of y .¹²

Despite its initial plausibility, paradigmatic examples of part-whole relations from biological practice show that spatial inclusion is neither sufficient nor necessary for biological parthood. Consider first why it is not sufficient. In the case of lichens green algae are spatially included in the fungus but they are not conceived of as parts of the fungus (rather, they are parts of the composite organism, the lichen). Similarly, if a doctor leaves a cotton ball inside of my stomach during surgery we would not say that the cotton ball became a part of me just because it is spatially located inside of me. Another example is the individuation of the parts of the human genome. According to ENCODE (2012), not any arbitrary DNA sequence contained in the human genome is a biological part of it (Kaiser forthc.). Examples like these

¹² Note that spatial inclusion does not require spatial contact or proximity among the objects that are spatially included in Y . Spatial contact or proximity may have an influence on part-whole relations (e.g., by allowing for causal interactions) but it is not presupposed by spatial inclusion.

are widespread in the biological sciences. They show that there is more to biological parthood than spatial inclusion and that PSI specifies a criterion for biological parthood that is not sufficient.

Other cases show that spatial inclusion is not even necessary for biological parthood. Take the example of a population of black-headed gulls. As an individual, it might have a specific spatial distribution (e.g., at the North Sea coast around BÜsum) but this does not preclude that some members of that population are located outside of this region (if they potentially interbreed with members located in that region). In general, populations seem not to be the kind of objects whose identity depends on having a specific spatial boundary, contrary to, for instance, cells or mitochondria that are necessarily surrounded by a membrane. Gene regulatory networks and ecosystems are further examples of biological objects whose parts seem not to be held together by what I will call a natural boundary (see next section). PSI thus fails to provide even a necessary criterion for the existence of part-whole relations in the biological world.

Finally, PSI is problematic because it runs the risk of being circular (or trivial). PSI says that biological parts of a whole must be spatially included in the whole, which means that they must be located inside the spatial boundary of the whole. This raises the question of what is the spatial boundary of the whole and how can it be identified (the demarcation question, recall Section 2.1). The simplest answer is that we demarcate an object from its context by identifying all of its parts and drawing a three-dimensional boundary that encompasses all parts and a minimal set of other objects (this is similar to what Kaplan 2012 proposes). This suggestion, however, renders PSI circular because whether x is a biological part of y would depend on whether x is spatially included inside the boundary around y and y 's other parts. In other words, the individuation of one part of a whole would presuppose having individuated all of its parts. For example, whether the case of a Caddisfly larva is a biological part of the larva would depend on whether it is located inside the spatial boundary that surrounds all parts of the larva. To avoid the circularity of the spatial inclusion criterion we must find a way to individuate the spatial boundary of the whole *independently* of individuating its parts. The next section introduces the notion of a natural boundary, which provides us with such an independent demarcation of biological objects.

3.2 Natural Boundaries

The main idea behind the notion of a natural boundary is that there exist boundaries in the biological world that are of particular importance to the identity of many biological objects and to individuating their parts. Paradigmatic cases of natural boundaries include the skin of mammals, the exoskeleton of insects, the cell wall of plant cells, other membranes such as the blood-brain barrier or the alveolar-capillary membrane, and also things such as rivers or thick lines of scrub. I refer to these boundaries as “natural” to emphasize that they exist in reality, rather than being introduced solely through human demarcation. In short, they are

“bona fide boundaries”, not “fiat boundaries” (Smith and Varzi 2000, 401).¹³ Not all boundaries that biologists draw – for instance, when identifying the target of their investigation – correspond to natural boundaries. Sometimes biologists are interested in questions that require studying an object together with parts of its environment. On other times they ignore parts of an object because they are irrelevant to the behavior they investigate.

Demarcating a biological object, the whole, from its context by identifying its natural boundary is independent in two respects. First, it does not require identifying all of the biological parts of the whole (i.e., answering the demarcation question does not require answering the decomposition question). Second, demarcating a biological object by identifying its natural boundary is independent from characterizing the natural boundary, itself, as a biological part (i.e., answering the demarcation question does not require answering the parthood question about the natural boundary). These independencies arise from the fact that natural boundaries typically are identified by their function as selective barriers and by the material discontinuities or structural differences that they involve. Let me explain this in more detail.

First, natural boundaries that demarcate individuals function as selective barriers. They bind together the objects that are located inside of it and separate them from what is outside. In most cases, this separation will not be complete but rather selective. For instance, the nuclear membrane ensures that ribosomes stay outside the nucleus but its nuclear pore complexes allow some molecules to pass (e.g., mRNAs with specific signal sequences). As a result, natural boundaries reduce the causal interactions between objects inside and objects outside of them (e.g., between ribosomes and intranuclear mRNAs) and allow specific kinds of causal interactions among the objects they encompass (e.g., between mRNAs and enzymes during mRNA processing). The fact that interactions between the parts of a whole and parts of its environment are generally fewer and weaker than the interactions among the parts of the whole is the guiding idea of so-called intensity-of-interactions approaches to parthood (e.g., Simon 1962; Wimsatt 1972, 2007; Haugeland 1998; McShea 2000; McShea and Venit 2001).

Second, natural boundaries usually involve material discontinuities or structural differences (e.g., differences in the chemical structure, texture, or material constitution). The cell membrane, for instance, is composed of a lipid bilayer and transmembrane proteins and, as such, forms a unit that has a different material constitution and chemical structure than what is located outside and inside of it. In the case of the membrane of blood cells, for instance, the cytoplasm (inside) consists of a complex mixture of cell organelles, cytoskeleton

¹³ Artificially produced biological objects (e.g., in synthetic biology) can have natural boundaries as well because the term ‘natural’ denotes the independent existence of these boundaries in the natural world, not their natural origin.

filaments, dissolved molecules, and water, and the blood plasma (outside) consists mainly of water.¹⁴

In sum, natural boundaries exist in the natural world (independent from human demarcation), and they are individuated by their functions as selective barriers and by the structural differences and material discontinuities they involve. Natural boundaries play a crucial role in determining what is a part of a biological individual and what is not. In the next section I use the notion of a natural boundary to substantiate the condition of spatial inclusion and to turn it into a plausible criterion for biological parthood, which avoids the three objections that a primitive notion of spatial inclusion faces (recall Section 3.1). The substantial criterion of spatial inclusion that I develop in the next section relies on the idea that natural boundaries constrain relations between biological parts and biological wholes. However, it does not imply that *any* natural boundary demarcates biological individuals (because other necessary conditions might not be satisfied), nor does it imply that *any* biological individual must be demarcated by a natural boundary (because there can be individuals without natural boundaries).

3.3 A Substantial Criterion of Spatial Inclusion

The leading idea of developing a substantial spatial inclusion criterion is that natural boundaries of biological objects constrain the individuation of their parts insofar as their biological parts must be spatially included in or inside the natural boundary of the object. The dung ball that a dorbeetle rolls is not a biological part of the beetle because it is located outside its exoskeleton; the neurotransmitter molecule is not a part of the neuron because it is located in the synaptic cleft outside the cell membrane of the neuron; and a green alga is discussed to be a biological part of the lichen because it is located inside the fungal membrane. Paradigmatic cases like these give rise to the following substantive notion of spatial inclusion as a criterion for biological parthood.

Substantial Spatial Inclusion (SSI)

An object *x* is a biological part of an object *y* only if

- (1) if *y* has a natural boundary, *x* must be spatially located inside or in the region that the natural boundary occupies.

This criterion explicates one way that the nature of the whole – in this case, its spatial nature, that is, its feature of possessing a specific natural boundary – constrains the individuation of its biological parts. The disjunction ‘inside or in the region of’ is important because it captures also cases where a biological part is located in the natural boundary itself, such as a receptor molecule or an ion channel that are located in the region that the cell membrane occupies.

¹⁴ This is compatible with the fact that some natural boundaries are scattered (e.g., of the Golgi apparatus).

SSI avoids all the three problems that a primitive notion of spatial inclusion faces (recall Section 3.1). First, SSI is not formulated as a sufficient condition for biological parthood. In the next sections, I will supplement SSI by an additional criterion that allows distinguishing cases of mere spatial containment from cases of genuine biological parthood (cf. Jansen and Schulz 2014). Second, even though natural boundaries are of great importance to the identity of biological objects and co-determine their parts, this is not true for all cases. Some biological objects, such as gene regulatory networks, immune systems, certain populations and certain ecosystems, do not possess natural boundaries. Nevertheless, we can retain SSI as a necessary condition if we formulate it conditionally, that is, if we require biological parts to be spatially included in their wholes only if the wholes possess natural boundaries. The conditional form of SSI accounts for cases in which spatial inclusion is irrelevant to biological part-whole relations. Third, in the previous section, I have characterized natural boundaries as involving material discontinuities or structural differences and as functioning as selective barriers. These structural and functional features ensure that natural boundaries of biological objects can be individuated independently from identifying their parts. Hence, by referring to the spatial boundary of a biological object as a natural boundary SSI avoids the circularity objection because where the natural boundary of the whole runs is independent from what its parts are.

4. Compositional Relevance

Paradigmatic examples of biological part-whole relations show that biological parts are bound together to a whole not only spatially but also causally-functionally. To get an idea of what this means consider the following reasoning strategies for why something is a part of a biological object that can be found in biological practice. A vesicle in the cytoplasm of a cell is a part of the Golgi apparatus (rather than, e.g., of the endoplasmic reticulum) because it contributes to the processing and transport of proteins. A particular DNA sequence out of the billions of possible sequences is a part of the human genome because it plays a causal role in the human genome as a whole, that is, because it contributes to gene expression or regulation (Kaiser forthc.). Glia cells are not parts of the central nervous system because they do not directly participate in synaptic interactions and electrical signaling; rather, glia cells are parts of the brain because they provide physical support for neurons and regulate the internal environment of the brain. An amino acid sequence or protein region is a part of ATP synthase because it is necessary to the protein's function of synthesizing ATP through transporting protons. A leukocyte or antibody is a part of an immune system because it is crucial to the protection of an organism against diseases. A cotton ball left inside the stomach during surgery is not a part of the human because it does not contribute to the survival of the human, but rather impedes it if an infection occurs. Harmless strains of *E. coli* bacteria are parts of the human gut because they facilitate the survival of humans by producing vitamin K2 and preventing colonization of the intestine with pathogenic bacteria.

These paradigmatic examples reveal that we cannot understand the conditions under which biological part-whole relations hold if we consider biological objects and their properties only. We must also take into account the processes in which parts and wholes are involved and how these processes relate to each other, such as how the binding of a particular DNA sequence to a transcription factor contributes to the regulation of genes of the human genome.¹⁵ My account of biological parthood thus stands in the tradition of philosophies that emphasize the importance of processes and of activities (which I take to be subtypes of processes; Kaiser 2017) to the biological world (Dupré 2012; O'Malley 2014; Machamer, Darden, and Craver 2000).¹⁶

The above examples suggest that biological parts must be involved in processes (which I will refer to as 'parts-processes') that are in a certain sense relevant to – i.e., contribute to, are necessary to, play a causal role in, are crucial to – one or more processes that the whole engages in (which I will refer to as 'whole-processes'). In the following sections, I turn this rough idea into a specific, clear criterion for biological parthood. I argue that we should think of the whole-processes to which parts-processes must be relevant as the characteristic behaviors of biological objects, such as the characteristic behaviors of a Golgi apparatus to process and transport proteins (Section 4.1). I then draw attention to the parts-processes and explain why we cannot understand biological parthood by considering parts-processes alone (Section 4.2). Finally, I use Mackie's (1965) idea of INUS-conditions to specify the relevance relation that must hold between parts- and whole-processes (Section 4.3).

4.1 Characteristic Behaviors of Biological Wholes

Plausibly, not any arbitrary process of the whole should determine what its parts are because the whole might be involved in some processes only accidentally or exceptionally. For example, a lichen growing on the wall of a playground might be painted blue by school kids but this is not a process in which a lichen is typically involved. HIV might damage the immune system of a person suffering from AIDS but this process is not characteristic of human immune systems, in general.

Processes of this kind can be excluded by introducing the notion of a characteristic behavior of a biological object. Characteristic behaviors are processes in which a biological object engages very generally, that is, under a wide range of contexts in which the object is naturally found. For instance, a sunflower grows and attracts bees and other insects to promote its reproduction whether it stands in my garden, on a sunflower farm or at the edge of a grain field. Characteristic behaviors determine, at least in part, the character or nature of a biological object. For example, the functional nature of an ATP synthase is to use a proton

¹⁵ Note that my focus is still on objects as the relata of part-whole relations. There might also be part-whole relations between processes but this is not the focus of this paper. My claim is that if we accept objects as the relata we have to take into account processes as well.

¹⁶ With respect to part-whole relations, Gillett (2013) argues that we must adopt a dimensioned account that considers not only individual objects but also their properties, powers and the processes they engage in.

gradient to synthesize ATP, which is why molecules of this kind have been named ‘ATP synthase’. Contrary to mechanisms, which are always for a single behavior (Glennan 2002), most biological objects are characterized by more than one typical behavior. Cells, for example, divide, synthesize proteins, and grow. Which behaviors are characteristic of a particular biological object depends also on the kind to which it belongs (recall Section 2.2). Blood cells, for instance, exhibit other characteristic behaviors than muscle cells or than infected host cells.

Characteristic behaviors of biological objects will often be realizations of biological functions. The realization of the function of the heart to pump blood, for instance, is also a characteristic behavior of the heart. Likewise, the characteristic behaviors of a stem cell to differentiate into specific kinds of cells, to synthesize proteins, and to grow might be seen as realizations of functions of a stem cell. However, I prefer to speak about characteristic behaviors rather than about functions. Many etiological theories of biological function prioritize organisms and their characteristic behaviors to survive and to reproduce (e.g., Neander 1991). Such a restricted focus impedes our understanding of biological part-whole relations because biological wholes are not confined to the level of organisms and because even organisms display other characteristic behaviors than survival and reproduction (e.g., growth). Cummins’ causal role theory of function (1975) seems to provide an understanding of the concept of a biological function that is much more adequate to the present purposes. However, also Cummins’ account must be applied to biological part-whole relations with caution since it is misleading in some ways. Most importantly, Cummins argues that functions are dispositions or capacities, not processes (1975, 757). But the mere disposition to engage in a process seems not to be sufficient to an object being a biological part (more on this in Section 5). A mitochondrion, for instance, is a biological part of a cell because it produces ATP not because it has the disposition to produce ATP, which may never be manifested.¹⁷

4.2 Working Parts

Understanding the conditions under which part-whole relations in the biological realm hold requires taking into account not only the processes in which wholes engages but also the processes in which parts are involved. For instance, it is the process of a specific DNA sequence binding certain transcription factors that is relevant to the regulation of genes of the human genome and it is the process of antibodies recognizing and neutralizing pathogens that is relevant to the protection of an organism against diseases. This is the point where causation enters the scene. Many of the parts-processes will be causal processes that involve

¹⁷ Furthermore, Cummins (1975) states that functions are individuated with respect to the capacity of a containing system. Accordingly, Cummins’ functions are features of parts which they possess in virtue of being parts of a whole (the containing system). Cummins’ account thus applies very naturally to characterizing parts-processes as functions (if we ignore the capacity-process difference). By contrast, characterizing whole-processes (i.e., characteristic behaviors of wholes) as Cummins’ functions would require positing an additional whole, which contains the original whole as a part.

not a single biological part but causal interactions between two or more biological parts of the same whole (e.g., the DNA sequence interacting with transcription factors, or the antibodies interacting with pathogens). In a similar vein, van Inwagen has argued that “parthood essentially involves causation” (1990, 81).¹⁸

The observation that causal interactions are central to biological parts and wholes has led several authors to defend what can be called the intensity-of-interactions approach to biological parthood (Simon 1962; Wimsatt 1972, 2007; Haugeland 1998; McShea 2000; McShea and Venit 2001). The basic idea of this approach is that we can decompose a system into parts according to the principle that interactions among parts are generally weaker and less frequent than interactions within parts. For instance, different molecules in a cell can be distinguished from another because the atoms inside of each molecule interact more frequently and stronger with themselves (e.g., they form certain kinds of chemical bindings), rather than for instance with atoms that belong to different molecules. The intensity-of-interactions approach has initial plausibility but it encounters some serious objections. Most importantly, the approach overlooks that biological parts are not only determined by the intensity of causal interactions in and among parts but also by specific features of the whole.¹⁹ In Section 3, I argued that biological wholes spatially constrain the individuation of their biological parts through the natural boundaries they possess. In the next section, I will argue that biological parts must be involved in causal interactions that are relevant at least to one of the characteristic behaviors of the whole. If we consider the strength of causal interactions only, we overlook this directedness of causal interactions to the behaviors of the whole.

To conclude, considering only the processes in which parts engage is not sufficient to understanding biological part-whole relations. Instead, we must analyze how parts-processes relate to whole-processes and what makes biological parts to “working parts” (Mellor 2008, 68) that work to bring about one of the characteristic behaviors of the whole.

4.3 Specifying the Relevance Condition

Biologists conceive of a vesicle as a biological part of the Golgi apparatus if it contributes to the processing and transport of proteins. *E. coli* bacteria are regarded as biological parts of the human gut if they facilitate the survival of humans, for instance, by producing vitamin K2 and preventing colonization of the intestine with pathogenic bacteria. Neurobiologists treat glia cells as biological parts of the brain rather than of the central nervous system because they play no direct role in electrical signaling but provide physical support for neurons and

¹⁸ Van Inwagen thinks about causal interactions between simples, rather than between biological objects of various kinds.

¹⁹ Other major objections are that the intensity-of-interactions approach requires specifying a threshold of number and intensity of interactions above which they are included and under which they are excluded. Such a threshold seems arbitrary or highly context-dependent (Wimsatt 1972). Furthermore, the intensity-of-interactions approach fails to exclude non-parts or background conditions that possess relatively many and strong interactions to other parts (e.g., Craver 2007, 143f).

regulate the internal environment of the brain. What unifies all these paradigmatic cases of part-whole relations is that biological parts engage in processes (e.g., a vesicle budding off the Golgi apparatus and moving towards the cell membrane) that are relevant to at least one of the characteristic behaviors of the whole (e.g., the Golgi apparatus transporting proteins). Under which conditions, exactly, is the relation of relevance satisfied? What does it mean that a part-process must contribute to, play a role in, or be crucial to one of the characteristic behaviors of the whole (a whole-process)? The philosophical literature yields different ideas that one could pursue further. In this section, I briefly introduce the major ideas and point out their shortcomings, before I then present my own relevance condition, which I refer to as compositional relevance.

One idea is that biological parts must have significant causal effects on the properties of the whole such that they give the whole a “causal unity” (Mellor 2008, 67). This is not an implausible idea but it does not help to specify the relevance condition because it remains unclear what makes a causal effect significant and under which conditions causal unity is reached. Gillett argues that a part-whole relation between individual objects exists only if the part is a “member of a spatiotemporally related team of individuals many of whose members bear powerful and/or productive relations to each other” (2013, 321). Gillett nicely draws attention to the fact that biological parts are not isolated but *jointly* working parts (see also Fagan 2012). However, the parthood criterion he specifies – namely that a biological part must bear powerful and/or productive relations to other parts of the same whole – runs the risk of becoming circular (at least it requires that other parts of the whole are already fixed). It also seems too weak because it does not restrict the kinds of dispositions that a biological part must have and the kinds of processes it must engage in (also the cotton ball left inside my stomach during surgery, e.g., has some dispositions and engages in some processes). Moreover, to capture cases, such as inactive parts, Gillett backs away from formulating the parthood criterion as a necessary condition. His account thus fails to provide a satisfying answer to the central question under which conditions a biological object is a member of a jointly working team.

Craver’s account of “constitutive relevance” (2007, 139) applies to the components of mechanisms but one might suggest that its mutual manipulability condition can be used to specify also the sense in which biological parts must be relevant to their wholes. The mutual manipulability condition requires that the components of a mechanism (which are acting entities, i.e., material objects engaging in processes of a specific kind; Kaiser 2017) and the phenomenon that a mechanism is responsible for (e.g., an object-involving process; Kaiser and Krickel 2016) must be mutually manipulable. That is, some change in the component must change the phenomenon and vice versa. Craver’s mutual manipulability condition is criticized, for instance, for being epistemic rather than metaphysical because it specifies how researcher get evidence about the components of mechanisms, rather than specifying which

features in the world determine component-mechanism relations (Couch 2011).²⁰ Even more importantly, Craver's account of constitutive relevance requires components and mechanistic phenomena not only to be mutually manipulable but also to be related as parts and wholes.²¹ Using the mutual manipulability criterion to specify biological parthood thus introduces a vicious circularity into Craver's account of constitutive relevance.

In the early literature on functional explanation and functional analysis, Hempel (1965) and Nagel (1961) put forward the idea that a biological part must be a bearer of a function in the sense that it must have certain effects that contribute to some activity of the containing system, the whole (cf. Cummins 1975, 741). Much of the discussion focuses on the question of whether the effects that biological parts have on their wholes can be understood as necessary conditions, such as the heart circulating blood might be a necessary condition for the proper working of the organism. However, counterexamples such as artificial pumps show that a heart pumping blood is not necessary for an organism's survival, and even if one excludes things such as artificial pumps by adding the phrase 'under normal conditions' one still has to face counterexamples such as redundant parts (e.g., the second kidney which is not necessary for the organisms survival but is a biological part of it) and relevant non-parts (e.g., the case of the caddisfly larva which seem to be necessary for the larva's survival but is not a biological part of it). Still, the idea that biological parts must in a certain sense be necessary to their wholes is appealing because it may give rise to a criterion of compositional relevance that is specific and strong enough.

Mackie (1965) claims that we should understand causes as INUS-conditions, that is, as being insufficient but necessary elements of overall conditions that are themselves unnecessary but sufficient for their effects. Mackie's idea provides us with a promising tool to maintain the idea that biological parts must be necessary to their wholes, while it allows us to weaken the relevance criterion in a way that it accounts for cases, such as redundant parts (e.g., the second kidney) and collective parts (e.g., the calcium ions in a muscle fiber that only collectively have a significant effect on muscle contraction).²² I have argued in the previous section that we cannot individuate biological parts by considering their causal interactions only, as the intensity-of-interactions approach proposes. Instead, the processes in which parts engage (which comprise causal interactions) must be examined with regard to how they affect the characteristic behaviors of the whole. The contribution that a part-process makes to one of the characteristic behaviors of the whole need not be necessary because it can be redundant (e.g., the second kidney filtering blood is not necessary for the human's survival) or only collectively significant (e.g., the transport of a single calcium ion into the sarcoplasmic reticulum does not raise the electrostatic potential). Instead, a part-process must be an INUS-

²⁰ Other objections can be found, for instance, in Harbecke 2010; Couch 2011; Leuridan 2012; Harinen 2014; Baumgartner and Gebharder 2016.

²¹ More specifically, the component-objects *X* must be parts of the system *S* that is involved in the phenomenon that the mechanism is responsible for (Craver 2007, 153; Kaiser and Krickel 2016).

²² In a similar vein, Harbecke (2010) and Couch (2011) use Mackie's account to specify the conditions under which an acting entity is a component of a mechanism.

condition for at least one of the behaviors that the whole characteristically displays. That is, biological parts must engage in processes that are necessary members of a minimal subset of parts-processes, which are jointly sufficient to a characteristic behavior of the whole.²³ Applying Mackie's idea of INUS-conditions to the question of biological parthood gives rise to the following second criterion for biological parthood.

Compositional Relevance (CR)

An object x , which engages in biological process p , is a biological part of an object y , which shows characteristic behaviors b_1, \dots, b_n , only if

- (2) p is relevant to at least one of b_1, \dots, b_n , that is, p makes a necessary contribution to a condition that is minimally sufficient to one or more of b_1, \dots, b_n .

CR is a clearly ontological criterion (contrary to, e.g., Craver's mutually manipulability condition) because it specifies how the processes in which putative biological parts engage must relate to the characteristic behaviors of the whole. CR is also more specific than other approaches because it specifies precise conditions under which a (causal) process of a putative part is relevant to a whole. In other words, CR specifies the conditions under which causal effects of putative parts are significant (Mellor 2008) and the conditions under which putative parts bear powerful and/or productive relations to each other (Gillett 2013).

5 The Hard-Cases Challenge to Monism

The goal of this paper is to specify the general conditions under which particular biological objects stand in a part-whole relation to each other. To sum up, my analysis of paradigmatic examples from biological practice reveals two criteria for biological parthood.

An Account of Biological Parthood

An object x , which engages in biological process p , is a biological part of an object y , which shows characteristic behaviors b_1, \dots, b_n , if and only if

- (1) **Substantial Spatial Inclusion (SSI)**: if y has a natural boundary, x must be spatially located inside or in the region that the natural boundary occupies and
- (2) **Compositional Relevance (CR)**: p is relevant to at least one of b_1, \dots, b_n , that is, p makes a necessary contribution to a condition that is minimally sufficient to one or more of b_1, \dots, b_n .

²³ Compositional relevance thus turns out to be a subtype of causal relevance (if one accepts Mackie's claim that causes are INUS-conditions for their effects). Note, however, that this does not imply that biological part-whole relations are special kinds of causal relations. Biological parts must satisfy further criteria (e.g., they must be spatially included in the whole in a substantial way) and, thereby, violate conditions that many authors regard as characteristic of causal relations (e.g., that cause and effect are distinct).

This is a monistic account of biological parthood because it specifies two criteria that are individually necessary and jointly sufficient for a biological part-whole relation to exist.²⁴ That is, my account identifies a single set of criteria that is supposed to hold for any object in the biological world.

My analysis also shows that there exist certain kinds of part-whole relations that can be referred to as ‘hard cases’ because they place requirements on a monistic account of biological parthood that pull in different directions. Understanding what these hard cases are and why it is so difficult to account for them at once sheds light on the merits and limits of monism.

Hard Cases for an Account of Biological Parthood

- (1) **Redundant parts** (e.g., kidney of humans removing waste products from the body): Some biological parts are redundant because there are other token objects that engage in the same kind of process, only one of which is necessary to a behavior of the whole.
- (2) **Irrelevant parts** (e.g., appendix of humans): Some biological parts engage in processes that are irrelevant to any characteristic behavior of the whole (e.g., because they have become non-functional during evolutionary history).
- (3) **Inactive parts** (e.g., members of a population not interbreeding): Some biological parts do not actually engage in relevant processes; they merely have the disposition to do so, which is not manifest.
- (4) **Collective parts** (e.g., calcium ion in a muscle fiber being released into the cytosol): Some biological parts only collectively have a significant effect on the behavior of the whole.
- (5) **Relevant non-parts** (e.g., case of a caddisfly larva that protects it from predators): Some biological objects engage in processes that are relevant to the behavior of the whole but are treated as background conditions or as parts of the context.

How does my account of biological parthood cope with these hard cases? The Compositional Relevance (CR) criterion accounts for redundant parts because the processes in which parts engage need not be necessary to one of the characteristic behaviors of the whole, they must only be necessary members of a set of biological parts, which are sufficient to one of the characteristic behaviors of the whole. Each kidney of a human, for example, is an INUS-condition for the human’s survival – even though they are not necessary parts of the same condition. Cases of collective parts do not present a problem for CR because even if a biological part, such as a calcium ion, on its own, lacks a significant effect on the contraction of a muscle fiber it still belongs to an INUS-condition for muscle contraction. CR is only a necessary but not a sufficient condition for biological parthood. Cases of relevant non-parts,

²⁴ In what follows I provide support for the claim that these criteria are jointly sufficient. I consider and dismiss additional criteria (e.g., common origin/history or genetic identity) for biological parthood because they are not necessary.

such as the blood that is transported to the heart and thus is an INUS-condition for the blood pumping of a heart, pass CR but are excluded by the Substantial Spatial Inclusion (SSI) criterion because only the blood inside the ventricles and atria is located inside the natural boundary of the heart. This is a major reason for why SSI is a separate criterion for biological parthood that cannot be reduced to CR.

Inactive parts present a much stronger challenge to CR because they only potentially engage in processes that are INUS-conditions for one of the characteristic behaviors of the whole and thus call into question that CR is a necessary condition. For example, not all organisms that belong to a particular population actually interbreed with other members of the population. The mere capacity to interbreed suffices to be a biological part of the population. One might argue that examples like this require that CR must be weakened, for instance, by replacing 'x engages in biological process p' by 'x has the disposition to engage in biological process p'. A weakened CR criterion, however, invites more counterexamples than it copes with because several non-parts would turn out to be relevant. T-helper cells, for example, have the disposition to recognize antigens and thus would count as biological parts of our immune system. In addition, a dispositionally formulated relevance criterion neglects the fact that processes are central to biological parthood (recall Section 4).

Cases of irrelevant parts also challenge the status of CR as a necessary condition. For example, our appendix does not engage in processes that are INUS-conditions for one of our characteristic behaviors, such as our survival, reproduction, reasoning or cooperation with others but we typically consider our appendix to be a biological part of us. Again, one might argue that examples like this show that we must replace CR by a weaker relevance criterion. But if we weaken the relevance criterion we will face many new counterexamples of biological objects which pass the weaker relevance criterion but which we do not regard as biological parts (i.e., relevant non-parts), such as the cotton ball that is left inside our stomach during surgery.

Alternatively, one might argue that the two criteria that I present in this paper are not sufficient to biological parthood and must be supplemented by additional necessary criteria. In the case of our appendix, for example, referring to the common history or origin of the appendix and the human body as a whole or to the genetic identity of most of their cells might provide us with a criterion that individuates the appendix as a biological part, but not the cotton ball inside my stomach (cf. Jansen and Schulz 2014). The impression that spatial and causal-functional relations are only part of the story about biological part-whole relations is confirmed by examples that show how some biological wholes also structurally constrain their parts. For example, it follows from the chemical-structural nature of the human genome (i.e., from the fact that it is a nucleic acid) that its biological parts must be sequences of nucleotides rather than, for instance, proteins.²⁵ Each of these putative additional criteria,

²⁵ Likewise, the structure of the Golgi apparatus implies that its parts must be membrane-enclosed compartments or vesicles, and a population of black-headed gulls consists only of organisms of the species *Chroicocephalus ridibundus* (not of the beach or of other kinds of birds).

however, captures only a small subset of biological part-whole relations and thus does not constitute a necessary criterion that is universally applicable to the biological world. For instance, only some biological wholes have a structural nature that constrains their parts in a non-trivial manner.²⁶ The criterion of genetic identity is violated in many cases (e.g., genetic chimera, symbionts, ecosystems, etc.), and also the requirement that biological parts must originate together with or inside the whole does not hold for the majority of part-whole relations because most biological objects continuously lose and acquire particular parts.

6. Conclusions: On the Merits and Limits of Monism

My analysis of hard cases reveals at which point monism reaches its limit. For a monistic account of biological parthood, it is impossible to cope with all hard cases at once. If you weaken the Compositional Relevance (CR) criterion to account for irrelevant parts and inactive parts, you will not be able to exclude several cases of relevant non-parts (and the other way round). You might solve the problem by introducing additional criteria that capture other kinds of constraints on biological part-whole relations (e.g., historical, genetic, or structural constraints). These additional criteria, however, will apply only to certain kinds of biological objects and not hold universally. The goal of universality thus runs contrary to the goal of descriptive adequacy (Kaiser 2015, Chapter 2) and it seems as if we need to make a principled decision at this point – in favor of more descriptive adequacy and pluralism or in favor of more universality and monism.

Among the virtues of my monistic account is that it gives a clear and precise answer to the general question under which conditions one biological object is a part of another biological object. Monism highlights the commonalities of part-whole relations from different levels of organization (e.g., a vesicle being a part of a Golgi apparatus and an organism being a part of a population) and it reveals how biological wholes in general constrain their parts. A monistic account of biological parthood thus provides unification. On the other hand, monism runs the risk of yielding an overly simple and descriptively inadequate view of biological parthood, which fails to account for the diversity of biological part-whole relations, reflected in the various approaches that biologists adopt to individuate part-whole relations (cf. Kellert, Longino, and Waters 2006).

The goal of this paper is not to defend my monistic account against pluralistic alternatives. Rather, I presuppose the goal of monism, defend my account against monistic alternatives, and use my analysis to point out the limits that monism faces. Recognizing these limits allows us to distinguish general constraints on biological parthood from constraints that arise more locally and it helps us to specify in how far the individuation of part-whole

²⁶ One might argue, for example, that the heart might be structurally characterized as having two ventricles, two atria, connected by valves, etc. This structural description, however, is nothing but a description of the biological parts of the heart.

relations in the biological world is diverse. Understanding the limits of monism thus allows us to draw general conclusions about the nature of biological parthood.

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