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Essay Review

The new puzzle of biological groups and individuals

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From groups to individuals: Evolution and emerging individuality. Frédéric Bouchard and Philippe Huneman (Eds.); MIT Press, Cambridge (Massachusetts), 2013, pp. viii+278, Price £37.95 hardcover, ISBN 978-0-262-01872-2.

1. Introduction

The world is in constant change. Much that once individually struggled for survival is now coevolving, cooperating, and entering symbiosis—and the day will come where higher-level individuality emerges out of it, where formerly loose collections become individuals in their own right. For human beings, this day, this evolutionary transition, already lies in the past, and has happened more than once as the integration of mitochondria, the emergence of multicellularity and the functional role of symbiotic gut bacteria for our survival show. We now stand before another possible transition, and only the future will reveal what is awaiting our species. This is our not-yet-written book, open for fascinating speculation.

From groups to individuals—Evolution and emerging individuality offers conceptually precise reconsideration of empirical data on the emergence and maintenance of biological individuality in evolutionary transitions and of the implications for closely connected issues such as fitness, selection and adaptation at different levels. Careful editing prevents the differences among the eleven thought-provoking individual contributions from hindering the emergence of a coherent whole, aiming at a theoretical framework for the notion of biological individuality. The book is structured around three complementary foci: on organisms and individuality; on adaptation and complex individuals; and on groups and collectives as individuals. Whilst advanced knowledge of key issues in the philosophy of biology may sometimes be required, there are many well-developed considerations and new arguments that invite us to see familiar issues from different angles, so that, taken as an individual whole, the book merits positive selection.

Unavoidably for any review about something so rich in content, my focus here neglects many valuable pages. I will follow the structure of the book and retrace the central threads of chapters one to four (the first of the three parts of the book) to introduce and connect some central issues and views. Against this background, I then provide a more general reflection linked only with specific parts of the other, no-less-interesting contributions. The result is a fusion of possible lessons drawn from the individual chapters that, like pieces of a puzzle, fit together such that a particular higher-level whole emerges. The reader is invited to construct his or her own puzzle from the arguments made in this challenging book and debate.

2. Four visions of the individual

Chapter one, "Darwinian individuals", by Peter Godfrey-Smith, begins with a historical sketch of the notion of biological individuality and its changes due to evolutionary theory on the one hand, and the study of problem cases on the other. For instance, if "reproduction is making a *new* individual, while growth is making more of the same" (p. 18), then examples such as aspen groves, where apparently distinct "trees" can be united by a common root system from which they all grow, put into question an easy distinction between reproduction and growth, making it unclear what *the* individual exactly is. Matters get worse when it comes to collective entities that seem to be individuals in their own right, like bee colonies or symbiotic associations. Still, even if there might not be *the* individual in biology, Godfrey-Smith highlights two related special kinds of individuals: Darwinian individuals and organisms. In identifying a Darwinian individual, an entity that takes part in evolution by natural selection, "things that matter…are things that can *reproduce*" (p. 20), where reproduction can be simple, scaffolded or collective. By having a closer look at collective reproduction, Godfrey-Smith argues for a quantitative analysis in terms of different degrees to which entities possess three essential features: a bottleneck (a narrowing that divides generations); a germ line (reproductive specialization); and functional integration (mutual dependence of parts). This enables comparison of, for instance, slime moulds, different species of bees and us, where a human-

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being collection of cells is a reproducer in its own right to a higher degree than the other examples.

By contrast, the notion of organism follows traditionally from a *non-evolutionary* perspective, one that takes a physiological or "*metabolic* view: organisms are systems comprised of diverse parts which work together to maintain the system's structure, despite turnover of material. [...] Organisms are essentially persisters, systems that...only contingently...reproduce" (p. 25). Despite this contrast, organismality also comes in degrees, disqualifying any dichotomy of *whether or not* something is an organism. Additionally, just as Darwinian individuals may make up collectives of higher-level Darwinian individuals that "tend to partly de-Darwinize their constituent parts" (p. 26), collectives of organisms may make up higher-level organisms where "a high degree of organismality at one level in a hierarchy implies lower degrees at others" (p. 26).

Keeping both special kinds of individuals in mind, Godfrey-Smith identifies the degree to which certain entities are both Darwinian individuals and organisms or rather one than the other. Viruses are Darwinian individuals to a very high degree while their organismality appears to be absent, whereas it is the other way round in the case of sterile social insects or sterile animals like mules. Symbiotic associations (mostly plants or animals in association with bacteria) can have a high degree of (multispecies) organismality without forming the sort of parent–offspring lineages that are necessary to being a Darwinian individual, such as in the case of squid–*Vibrio* symbioses. However, there are also cases of stronger metabolic connections among the symbiotic partners, like in the case of aphids and *Buchnera*, which do form parent–offspring lineages. The upshot of chapter one is not only that Darwinian individuality and organismality come in degrees (and should be so understood) but to study further the dynamic linking among both kinds.

Chapter two, "Defining the individual", by Charles J. Goodnight, uses an "intuitive concept of shared evolutionary fate" (p. 37) to guide a formal approach to entities and groups in terms of contextual analysis and multilevel selection. Goodnight offers a detailed discussion of three competing definitions. To the extent that the level at which fitness is assigned follows practical constraints, the "individual" is an "arbitrary construct of the observer" (p. 42), which affects the interpretation of how selection is working. One problem is "that the species selection we see when we assign fitness at the level of the species may be revealed as organismal selection when we assign fitnesses at the level of organism" (p. 44) such that qualitatively different interpretations of how selection is acting emerge if fitness is assigned above the level at which selection is actually acting. Against this background, Goodnight generates a second definition via the logical move of putting individuality at the *lowest* measurable level. However, as well as practical constraints, difficulties arise for this definition in the context of cells within metazoa, where not only germ line cells but also somatic cells, owing to mutation in mitotic cell division, satisfy classical criteria for evolution by natural selection. Employing the second definition would imply that these "cells within a metazoan are not qualitatively different than, for example individual bees or ants within a colony" (p. 46). To distinguish them, Goodnight introduces quantitative considerations that take into account mechanisms suppressing the potential for evolution of certain entities. For example, germ and somatic cell lines are segregated early in the development of higher animals, which reduces evolution by natural selection among these cells. The consideration of such mechanisms thus leads to a third definition of individuality that is about the lowest level at which a *response* to selection can occur, taking into account the potential for selection to *actually lead* to evolutionary change. This third definition faces even more experimental constraints than the second, since the possibility of seeing a response to selection depends on many parameters that may be very complex and may vary in time.

Chapter three, "Species and organisms: What are the problems?", by Ellen Clarke and Samir Okasha, provides another viewpoint in the debate by considering not only the *sources* of but also revealing *parallels* between the species problem and the problem of individual organisms. A central question in the former problem is whether species are natural kinds that "partition the set of all living things into non-overlapping groups in an objective way" (p. 56), whereas the latter problem is about how to parcel up certain portions of living things into *individual* organisms that play a "pivotal role in evolutionary biology as the bearer of fitness and as the demographic unit" (p. 58). As a key problem case the authors discuss slime mould, a single-cell amoeba which reproduces clonally but which, in the case of famine, aggregates with thousands of other amoebae into a morphologically differentiated and thus organism-like higher-level structure with quasi-germ line parts.

One parallel between the species problem and the problem of individual organisms is that both suffer from the issue of 'vagueness', in that unavoidably there are intermediate and thus vague borderline cases of species and, similarly, organismality comes in degrees and may change in time, as the example of slime mould illustrates. Another parallel issue is that of 'multiple criteria'. Because biologists use multiple criteria for defining species (e.g., reproductive isolation, genetic relatedness and phenetic similarity), different and partly overlapping sets of entities are identified—which is also true in the case of organisms where, for example, bottlenecks, germ soma separation and functional integration are debated criteria.

The relatedness of 'vagueness' and 'multiple criteria' in both the species and the organism problem is further analysed in two crucial contexts of inquiry: diachronic and synchronic contexts. Species seen from a diachronic perspective always face vagueness, which often disappears from a synchronic perspective, where it is rather a question of choosing from multiple defining criteria. Similarly, vagueness of organismality is more a problem from a diachronic perspective, notably in cases "where individuals at one level of hierarchy emerge over time from ancestors at a lower level of hierarchy" (p. 68). Still, to the extent that evolution is gradual, vagueness also affects synchronic contexts of inquiry since each definition criterion for species and organisms comes, at least for some species and some organisms at some point in time, in degrees.

After discussing possible solutions promoted by punctuated equilibrium theories, the authors consider a distinction between category and taxa questions to clarify where 'vagueness' and 'multiple criteria' are the predominant problems. Category questions, such as "Is *x* a species/organism?" (p. 69), concern the *generality* of the category across all cases; i.e. what it generally means to be a species and not a variety or to be an organism and not only part of it. While for such questions the problem of multiple criteria becomes predominant, taxa questions, such as whether *y* is a member of the considered species *x* or whether *y* is part of the specific organism *x*, are more concerned with the *gradualness* of evolution and organismal transitions, where vagueness is what is more troublesome.

Chapter four, "Immunity and the emergence of individuality", by Thomas Pradeu, analyses further the relation between evolutionary and physiological/metabolic views, where he promotes an immune-system-based *physiological* view of biological individuality and its *complementarity* with evolutionary approaches. Physiologically speaking, the immune system establishes organismal boundaries by including some entities while rejecting others, thereby enabling a distinction between what is part or is not part of an organism. Furthermore, from an evolutionary perspective, the immune system is "one of the main "policing" mechanisms

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