Woese on the received view of evolution

Sahotra Sarkar

Departments of Philosophy and Integrative Biology; University of Texas at Austin; Austin, TX USA

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As part of his attempt to reconstruct the earliest phase of the evolution of life on Earth, Woese produced a compelling critique of the received view of evolution from the 20th century. This paper explicitly articulates two related features of that critique that are fundamental but the first of which has not been sufficiently clearly recognized in the context of evolutionary theorizing: (1) according to Woese’s scenario of communal evolution during life’s earliest phase (roughly, the first billion years of life on Earth), well-defined biological individuals (and, thus, individual lineages) did not exist; and (2) during that phase, evolutionary change took place through ubiquitous horizontal gene transfer (HGT) rather than through vertical transmission of features (including genes) and the combinatorics of HGT was the dominant mechanism of evolutionary change. Both factors present serious challenges to the received view of evolution and that framework would have to be radically altered to incorporate these factors. The extent to which this will be necessary will depend on whether Woese’s scenario of collective early evolution is correct.

Introduction

“It was a pleasure to meet you at Royamaunt and to compare our ideas on coding. I still feel in contrast to yourself, that there is (or was at one time) a rational basis behind the coding assignments,” so wrote Woese, then at the General Electric Company, Schenectady, NY, to Crick at the Cavendish Laboratory, Cambridge (UK), on 29 August 1962. “I look forward to hearing your ‘rational basis,’” responded Crick on 21 September 1962. By this point Crick was convinced that codon assignments (of individual codons to specific amino acid residues) were arbitrary—an assumption later incorporated into his “frozen accident” model for the origin of the genetic code, and constituting perhaps the most important molecular exemplar of the evolutionary contingency thesis. Regular correspondence between Woese and Crick, mainly about the origin and evolution of the genetic code, lasted for over a decade, until the mid-1970s, when Crick turned away from molecular biology to focus on the neurosciences. (There were a few exchanges later—for example, on directed panspermia.)

Woese never accepted the arbitrariness of the genetic code or the evolutionary contingency thesis. For him, the origin of the genetic code and other features of the genetic apparatus, including (especially) the mechanism of translation, reflected an evolutionary order manifest in the early history of life on Earth though the problem of adequately identifying this order was unsolved at the time and remains unresolved even today. That this position put Woese at odds with the most popular tenets of much of molecular biology and evolution during the 1980s and 1990s is not puzzling: the evolutionary contingency thesis was central to the neutral and nearly neutral theories of evolution. But Woese also rejected the alternative received view of evolution, what he called the Charybdis of the Modern Synthesis, claiming that: “biology in the 20th century neglected and otherwise mishandled the study of what is arguably the most important problem of all of science: the nature of the evolutionary process.”

The purpose of this paper is to articulate Woese’s rejection of the received view. Pace et al. have recently noted: “Woese’s overarching interests in fundamental evolutionary questions have been relatively neglected.” Like Pace et al., but with an emphasis on different issues, this paper is an effort to remove this lacuna. It makes no attempt to decide whether Woese’s rejection of the received view is ultimately justified: that depends to a large extent on whether Woese’s progenote hypothesis (or at least that of a collective phase) of early evolution is correct, a question that appears unlikely to be resolved in the immediate future. Rather, given the typically cryptic and occasionally polemical nature of Woese’s critiques of the received view, this paper is an attempt to clarify how his claims about early evolution challenge the received view which they do so perhaps to an even greater extent than what he stated.

The characterization given here partly goes beyond what Woese explicitly says in his comments on evolution (see Section 3). However, this elaboration facilitates placing Woese’s views in the context of ongoing discussions of the received view of evolution (and a recognition of problems with its framework is more prevalent among evolutionary biologists than Woese’s polemics sometimes suggest). Nevertheless, the elaboration here remains open to the objection that it misinterprets Woese’s intentions.

This paper also ignores four themes that Woese explicitly develops: (1) The significance of Woese’s identification of archaea is beyond reasonable dispute. However, the discussion below ignores the question of whether taxonomy should recognize two or three domains—from a historical perspective, Sapp has treated this issue in detail. (2) What follows takes for granted the importance of Woese’s search for a universal tree of
life (reviewed by Woese et al.\textsuperscript{4}) but does not discuss it explicitly. (3) This account ignores Woese’s rejection of reductionism\textsuperscript{4} only because it is largely irrelevant to the evolutionary issues discussed here—his characterization of that doctrine is insightful and pertinent to recent explications of reductionism in the philosophy of biology.\textsuperscript{3} (4) Woese emphasizes a focus on processes (rather than outcomes) in discussions of evolution. However, what this amounts to in practice remains nebulous in his writings,\textsuperscript{6} and it is also incorrect to suggest that the received view of evolution paid no attention to process.\textsuperscript{10-12} That there should be a focus on evolutionary processes will be taken to be uncontroversial in what follows. (Some of the evolutionary themes ignored in this paper are insightfully treated by Pace et al.\textsuperscript{7})

Section 2 briefly characterizes those aspects of the received view of evolution that are necessary to ground the subsequent discussions of evolution in this paper. From this perspective, two related assumptions are central to the received view: (1) that evolution always occurs in populations of well-defined biological individuals; and (2) that the transfer of individual features between organisms is almost entirely through vertical inheritance. The importance of Woese’s challenge to the received view is that he rejects both these assumptions for the earliest phase of evolution, before the emergence of a categorical translation apparatus crystallized a clear genotype–phenotype distinction.\textsuperscript{13}

The first of these assumptions is taken up in Section 3; the second in Section 4. Section 5 consists of a few concluding remarks.

**The Received View of Evolution**

What Woese finds problematic is the framework for evolutionary theory that had become established by around 1932, largely due to the work of Haldane,\textsuperscript{14} Fisher,\textsuperscript{15} and Wright,\textsuperscript{16} and extended thereafter by many others (e.g., Dobzhansky\textsuperscript{17} and Mayr;\textsuperscript{18} for historical discussion, see Provine;\textsuperscript{19} Mayr and Provine;\textsuperscript{19} Sarkar;\textsuperscript{12,20,21} and Smocovitis\textsuperscript{22}). According to this received view, evolution occurs in populations of individuals that reproduce in accordance with established laws of heredity (e.g., Mendelian genetics for diploids). Changes occur and accumulate during this process due to stochastic factors (e.g., mutations in the genetic material or sampling effects during reproduction in finite populations) as well as deterministic factors, most notably, natural selection but also including, for example, the transfer of individuals between populations (immigration and emigration). The changes mentioned above lead to changes in gene frequencies; yet other (generally deterministic) processes such as inbreeding and assortative mating change genotype frequencies (in non-haploid populations) but not gene frequencies.

This framework (and the received view) admit a range of possible evolutionary trajectories, from those exemplifying complete contingency (e.g., due to stochastic changes from sampling [what is usually referred to as drift] or founder effects) to those that are almost entirely a result of natural selection. The issue of which of these has been more important in the history of life on Earth famously divided Fisher’s and Wright’s reconstruction of evolutionary change.\textsuperscript{11,12,21} It also placed Kimura,\textsuperscript{23} who proposed a neutral model of molecular evolution, against those who persisted in defending the relevance of selection at the molecular level (e.g., Lewontin\textsuperscript{24}). The received view almost always emphasizes the importance of natural selection but the framework does not require such a commitment.

Further, evolution by natural selection minimally assumes that:\textsuperscript{25} (1) there is variation between individuals in the population (phenotypic variation); (2) that this variation tends to be transmitted to offspring during reproduction (inheritability of phenotypes); and (3) some variants systematically produce more descendants than others (differential fitness). When these three criteria are satisfied those variants that are the most successful in the production of descendants (that is, the fittest ones) eventually come to dominate a population. As noted earlier, the received view often assumes that this process is central to evolution though its relative importance for the history of life on Earth is debated. Recent work in the evolution of genome architecture strongly suggests that selection may be largely irrelevant compared with other mechanisms of evolution.\textsuperscript{26-28}

The relevant point here is that the received view makes two related assumptions that have been so pervasive in 20th century evolutionary biology that they almost never warrant explicit mention: (1) that there are well-defined biological individuals (and, thus, individual lineages); and (2) that the transfer of individual features between one organism and another is vertically vertical, that is, through inheritance from parent to offspring. Woese’s critique of the received view rejects both of these assumptions for the earliest phase of the evolution of life on Earth.

**The Evolution of Individuality**

In Woese’s work the challenge to individuality, though not articulated as explicitly as it will be done below (see Goldenfeld and Woese\textsuperscript{29} for the clearest statement), historically came earlier, beginning with a well-known paper with Fox, ostensibly on cellular evolution, but more important for postulating the existence of “progenotes” that were on the verge of evolving the translation machinery of “modern” cells.\textsuperscript{13} This paper was one of the original series from 1977 that announced the identification of what were then called archaebacteria and were claimed to form a fundamental taxonomic group distinct from and on par with both “ordinary” bacteria (eubacteria) and eukaryotes.

In progenotes the translation machinery was supposed to be still evolving. Endosymbiosis was supposed to be an “aboriginal” property of progenotes and dominate their evolution. In correspondence with Woese (15 April 1977), Zuckerandl (the Editor of the *Journal of Molecular Evolution*) characterized the progenote even more succinctly than Woese and Fox: “the progenote is a much more fluid cellular entity than either the prokaryote or the unicellular eukaryote, in the sense that exchanges of components between different evolutionary lineages of cells was much more generalized than ever after.”\textsuperscript{93} At this stage there were no species in anything like the customary sense of the word—as Woese, Fox, and Zuckerandl all explicitly recognized. (Pace et al.\textsuperscript{7} note that the definition of microbial species, if at all possible, remains unresolved today.)
Archaea, bacteria, and eukaryotes were postulated as emerging as distinct evolutionary lineages from the progenotes: critically, eukaryotes were not viewed as having evolved from a more primitive prokaryotic stage. What is more important in the present context is that rampant exchange of components between progenotes presents a problem, not only for there being species, but also for there being individuals in the sense required by the received view of evolution. The discovery of ubiquitous horizontal gene transfer (HGT) exacerbates this problem, as Woese\(^ {3} \) emphasized later, and as will be further discussed in Section 4. One consequence of HGT is that “the ancestor was a communal entity, a community that survived and evolved as a whole, as an aggregate, not as individual lineages.”\(^ {30} \)

The salient point is that the evolution of such a system cannot be understood within the received view of evolution for two reasons: (1) If the system evolves as a whole because of the interchange of parts, there are no distinct individuals within an evolving population, more specifically, individuals that show phenotypic variation and are, therefore, potentially subject to natural selection. Thus, the first criterion of evolution by natural selection (Section 2) is violated. (2) Satisfaction of the first criterion is a prerequisite for the other two criteria for natural selection to be applicable—ipso facto, these are also not satisfied.

The problem faced here goes beyond natural selection: communal (or system-wide) evolution, as envisaged by Woese for this phase of evolutionary history, cannot be formulated within the framework of the received view irrespective of the relative importance of the different mechanisms of evolution. Woese\(^ {31} \) is clearly aware of this issue though, surprisingly, it is not quite as explicitly formulated as it was done earlier. This may well be due to the fact that Woese’s views on the evolutionary process did not receive sufficient attention from traditional evolutionary biologists—perhaps because of the extent to which it challenges its basic framework. Consequently, Woese seems to have felt no reason to place his views within the conceptual framework of the received view as has been attempted here. (This lack of attention by traditional evolutionary biologists stands in sharp contrast with their heated reaction to Woese’s efforts to change taxonomic practice, which generated strong opposition—see Sapp\(^ {3} \) for a history.)

However, it should be noted that the problems posed by biological individuality for the framework of evolutionary theory have also been recognized within that framework independent of Woese’s critique. Most intuitions about biological individuality typically come from biologists’ familiarity with relatively large eukaryotes, particularly animals.\(^ {32} \) But individuality, so envisaged, which requires spatial containment and discreteness of the individuals, is problematic in many well-recognized cases: e.g., in large spatially extended fungal systems interconnected by a mycelium below the soil, in the case of individual cells of Dictyostelium discoideum (a cellular slime mold) aggregating to form mobile slugs, or the case of genetically identical fields of dandelions.

Buss\(^ {33} \) has hypothesized a relation between biological individuality and sexual reproduction (see, also, the reconstruction and critique of this argument by Falk and Sarkar\(^ {35} \)). The point is that every biological feature has an evolutionary history—as Fisher\(^ {34} \) was perhaps the first to emphasize when he speculated on the evolutionary origin of dominance in Mendelian systems. Nevertheless, problems presented by the progenote for the received view are more extreme than the other cases mentioned here, which can be reasonably modeled as systems undergoing evolution at multiple levels of a hierarchy but with well-defined individuals at each level of that hierarchy. For instance, multi-level selection theory attempts to model such systems.\(^ {39} \) The same does not appear to be the case for progenote evolution. However, the extent to which progenote evolution (or communal system-wide evolution in general) presents a problem for the received view of evolution can only be judged after systematic elaboration of formal models—but such efforts may only become apposite if there is more experimental support for Woese’s hypothesis than currently available (see, however, Goldenfeld and Woese\(^ {3} \)).

### The First Three Billion Years of Life

In the early 2000s Woese\(^ {3,36} \) realized that the ubiquity of horizontal gene transfer (HGT) in the microbial world revealed by whole genome sequence analyses also provided strongly suggestive evidence for an early phase of evolution that cannot adequately be modeled within the received view. One important consequence of HGT in early evolution is that it provides an alternative explanation of universal biochemistry than common descent (as postulated by the received view). This, in turn, supports a basically reticulate model of microbial evolution rather than one that postulates a universal tree structure. Sapp discusses Woese’s initial reaction to HGT insofar as it provided a problem for reconstructing a universal tree of life.\(^ {3} \)

However, as Woese put it later: “the primitive cell is a loose confederation of a relatively small number of rather simple modules. For cells of this type, most if not all cellular componentry would be open to HGT, making the combinatorics of gene transfer far and away the major factor in early cellular evolution.”\(^ {44} \) Returning to the theme of the last section, Woese went on to argue: “Because of the high levels of HGT, evolution at this stage would in essence be communal, not individual.”\(^ {44} \) Conventional cellular evolution began as a later stage, after a “Darwinian threshold or Darwinian transition”\(^ {44} \) produced relatively distinct lineages of eubacteria, archaea, and eucarya (the order is not relevant here though Woese,\(^ {44} \) following Kandler,\(^ {37} \) came to prefer this order). HGT does not entirely disappear—it becomes far less prevalent. The framework of the received view of evolution becomes applicable.

Note that even symbiosis, because it involves non-vertical transfer of features (including genes) between organisms (and lineages), presents problems for the received view of evolution and has never been fully incorporated into its framework.\(^ {38,39} \) Profligate HGT is obviously far worse from this perspective. By and large, evolutionary biology of the 20th century ignored symbiosis—as it ignored many other recalcitrant phenomena such as non-Mendelian inheritance or the occasional inheritance of acquired characters—by acknowledging it but treating it as an exception not sufficiently important to induce an alteration of the basic framework of evolutionary theory.
For the received view of evolution, the problem posed by Woese’s scenario for the earliest phase of evolution is that it cannot be dismissed so easily: not only does it encompass a significant part of evolutionary history (in terms of elapsed time), it involves the critical foundational stages that provided the basis for life as it is seen today (after subsequent “Darwinian” evolution). It is what made evolution by natural selection possible. The question of the nature of evolution in “deep time” came to the forefront during Woese’s debate with Mayr about whether archaea and eubacteria should be clumped together as prokaryotes (in spite of violating monophyly) and then be contrasted with eukaryotes. For Mayr, the eukaryote–prokaryote dichotomy made sense because eukaryotes show much more diversity—at least in the eyes of classical biologists. Woese responded tellingly: “Dr. Mayr’s biology reflects the last billion years of evolution; mine, the first three billion.” Not all of these three billion years occurred before the “Darwinian transition,” which (assuming it occurred) cannot yet be dated precisely: one billion years is a reasonable estimate. This temporal extent makes it impossible to dismiss communal evolution through the combinatorics of HGT as a mere exception to the processes incorporated within the received view (Section 2): it would have encompassed a quarter of evolutionary history. In the subsequent two billion years—that is, before the “modern” era—HGT continued to be important even though individual lineages could now be distinguished.

As noted earlier, the significance of Woese’s critique of the received view of evolution, in particular, the rejection of evolving individual lineages, depends on the status of the hypothesis of a progenote (or, at least, communal) stage of evolution before individuated lineages emerged to evolve into the eubacterial, archaeal, and eukaryotic lineages seen today. However, the details of the progenote stage as formulated by Woese need not all hold for the viability of his critique of the received view of evolution articulated in the Sections 3 and 4. All that matters are that there is a communal phase in which the living system evolves as a whole and that HGT or some other non-vertical mode of transfer of features is common.

**Final Remarks**

The main conclusion to draw is that, once Woese’s views on evolution are properly contextualized within the framework of the received view, it becomes clear that the challenges he posed will require changes in the basic structure of that framework—for instance, by enabling evolution to occur without distinct individuals and lineages. As such, this challenge is much more serious than those posed by the many exceptions already noted during the 20th century including, but not limited to, directional mutation, occasional inheritance of acquired characters, cytoplasmic, and other non-Mendelian inheritance, or even symbiosis. Woese’s significance for evolutionary biology may go well beyond the recognition of archaea and his many seminal contributions to microbial phylogeny.

Toward the end of his life, many of Woese’s remarks on the received view of evolution became polemical. The discussion earlier has intentionally avoided that polemic. It has also not addressed some of Woese’s more speculative claims, for example, that the major transitions in pre-cellular and other earliest phases of evolution will turn out to be similar to (physical) phase transitions in complexity.

What deserves emphasis is that, beyond the rhetoric and the speculation, the evolutionary biology of the future must address the compelling fact that a significant part of evolutionary history (in terms of elapsed time) apparently cannot be incorporated into the framework of the received view with its reliance on well-defined biological individuality and veridical vertical transmission. Woese was well aware that his critique and speculations were no substitute for full-fledged theory: many of his last writings were taken up with encouraging 21st century biology to take up the challenge of formulating such a theory. In these pieces, the point that he emphasized most strongly is that the biology of the future must move beyond the strictures of the received view. That point is well-taken.

Returning to the question with which this paper began, does communal evolution based on the combinatorics of HGT provide the rational basis for codon assignments that Woese sought when he wrote to Crick in 1962? This question still has no answer. Woese continued to worry about the origin of the genetic code into the 2000s. While the problem remains unsolved, some recent results suggest that stereochemical complementarity, which Woese explored in the 1960s but ultimately abandoned, may hold part of the answer to the question of codon assignments. If this turns out to be true, there is order in the code; it is not a frozen accident and, perhaps most importantly, it has no selectionist explanation. The greatest tribute one can pay to Woese is to continue with these enquiries.

**Disclosure of Potential Conflicts of Interest**

No potential conflicts of interest were disclosed.

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