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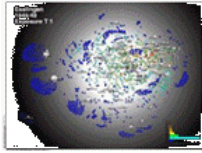
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Discoveries of modern biology are forcing a re-evaluation of even the central pillars of neo-Darwinian evolution. Anthropologists study the processes and results of biological and biocultural evolution, so they must be aware of the scope and nature of these changes in biology. We introduce these changes, comment briefly on how will influence anthropology, and suggest numerous readings to introduce anthropologists to the significance and substance of the new evolutionary synthesis.

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What Anthropologists Should Know About the New Evolutionary Synthesis

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Abstract: Discoveries of modern biology are forcing a re-evaluation of even the central pillars of neo-Darwinian evolution. Anthropologists study the processes and results of biological and biocultural evolution, so they must be aware of the scope and nature of these changes in biology. We introduce these changes, comment briefly on how they relate to anthropology, and suggest numerous readings to introduce anthropologists to the significance and substance of the new evolutionary synthesis.

1. A New Evolutionary Synthesis

Three decades of intense microbiological, biochemical, and genome research have resulted in significant new understanding of the evolutionary process. Central to this understanding has been the sequencing and functional decoding of the genomes of many species, including *Homo sapiens sapiens*. In short, biology is currently negotiating a synthesis of the same gravity as the ‘modern’ synthesis of mid-20th century (see Goldenfeld and Woese 2007, Rose and Oakley 2007, Koonin 2009a and Koonin 2009b; for an historical review of the ‘modern’ synthesis see Mayr and Provine 1998). In 2009 E.V. Koonin wrote that “In the post-genomic era, all the major tenets of the modern synthesis have been, if not outright overturned, replaced by a new and incomparably more complex vision of the key aspects of evolution. So, not to mince words, the modern synthesis is gone.” (Koonin 2009a:474). Of course, not all biologists are convinced that biology is undergoing such a structural resynthesis, but universal consensus is rare in science and there is indeed a general atmosphere of significant new genomics-driven understanding throughout the field of evolutionary studies (e.g. Pigliucci and Müller (2010)). Anthropologists—who, by definition, study biocultural evolution—must have at least a working understanding of the issues under review in the new synthesis. Physical anthropologists study the biological and biocultural evolution of *Homo* and other members of the primate order, so their understanding of these issues must be complete. Archaeologists documenting and attempting to explain the change of human culture through time often invoke evolutionary principles or explicitly consider human culture to be an evolving information system with nontrivial parallels with biological evolution (e.g. Eerkens and Lipo 2005, Shennan 2009), so they must understand it as well. Some cultural anthropologists (e.g. Durham 1993, Hewlett 2001, Hewlett and Lamb 2005, Rappaport 1999) characterize culture as genuinely evolving—though without the archaic, progressivist, unilineal and sociobiological concepts that informed early cultural-evolution approaches (e.g. see Durham 1993:1-41)—and they should also be aware of the new evolutionary biology.

Below we introduce some of the most important fields of investigation in the currently emerging synthesis. While the field is in flux, anthropologists should be aware of these dynamics at least in as much as they condition the basic concepts of neodarwinian (perhaps soon to be renamed postgenomic) evolution. Since anthropology studies humanity, and humanity is a continuously evolving product of the evolutionary process, these developments will eventually touch every facet of anthropology. Below we do not suggest how anthropologists should incorporate new evolutionary understanding to their own studies (though we do briefly comment

on implications for anthropology); rather we introduce important new perspectives and direct the reader to relevant summary reading material.

Horizontal Gene Transfer (HGT). It is now apparent that HGT—the acquisition of genetic material by one life form from another, unrelated life form, during the life course, and the passing of that novelty to the offspring—is not an occasional phenomenon but is prevalent in the world of asexually reproducing species (Choi and Kim 2007a, Gogarten, Doolittle and Lawrence 2002). Since many species reproduce asexually this means that much evolution proceeds in a somewhat Lamarckian fashion; not in the ‘use-disuse’ sense, but in the ‘inheritance of acquired characteristics’ sense. Horizontal gene transfer has also been documented among a few sexually reproducing species, and biologists warn that it is too early to relegate HGT to the asexual world (Keeling and Palmer 2008). An accessible overview of HGT, and its importance, can be found in Gogarten and Townsend (2005).

Specifically regarding anthropology, increased understanding of the phenomenon of horizontal gene transfer will better our understanding of culture change. As mentioned, HGT indicates a significant component of somewhat Lamarckian genetic inheritance, and it has long been understood in evolutionary approaches to culture change that the spread of ideas—the units of information in cultural evolution sometimes referred to as “memes”—can in significant ways also be characterized as Lamarckian, in that ideas are acquired not only by members of generation B from its parents (of generation A), but also from peers of generation B (e.g. Durham 1991: 180). Whether or not the term *meme* can be rescued after decades of debate is somewhat beside the point (see Shennan (2002)); whatever we want to call the unit of transmission in cultural evolution, it is central to understanding cultural evolution, and the concept has been used profitably in studies of cultural transmission among chimpanzees (e.g. Lycett, Collard and McGrew, 2007) and in humans, for example in the transmission of traditional modes of textile designs in Iran (Tehrani and Collard 2009).

Critics of evolutionary approaches to culture often point out that culture is not biology, but in our view that does not matter; biology is currently better understanding what it, itself, is, and it is finding that evolution occurs in more than one mode. As Daniel Dennett has pointed out, in regard to this critique: “Once we shift our focus away from our own multicellular, sexually reproducing lineages to the more numerous lineages on the planet, these standard objections lose much if not all their force. Memes are indeed not very much like elephant genomes, but so what?” (Dennet 1998). Thus the decades-old critique that ‘biology evolves in ways different from culture’ is hopelessly out of date; of course it does, but evolution proceeds in many ways, and they include the evolution of sets of horizontally-transmitted cultural as well as genetic information. Recently, Gabora (2011) has argued that darwinian natural selection is unable to account for the complexity of cultural evolution, advancing a cultural-evolution model that is significantly informed by the revelations of HGT.

Understanding HGT will also, of course, simply improve our understanding of physical anthropology and hominin evolution, even if HGT is not found to directly structure much vertebrate evolution (see Generoux and Logsdon 2003, Salzberg et al. 2001 and Brown et al. 2001, but note these studies are each over decade old and the issue is clearer today, as suggested in Alvarez et al. 2006 and discussed in Keeling 2009). This is because HGT may well be found to significantly structure the many species with which humanity coevolves, and that coevolution—as we discuss below—is not trivial or of only passing interest, but can, on multiple levels, be evolutionarily significant.

Epigenetics: In another examination of evolutionary mechanisms that are unexpected in the strict neodarwinian approach, the field of “epigenetics” explores environmentally induced, heritable variations in gene function. As with HGT, recent discoveries of epigenetic mechanisms have caused biologists to rethink the mechanisms, significance, and magnitude of inherited and heritable variation. Three processes—DNA methylation, RNA-associated silencing and histone modification—initiate and sustain epigenetic silencing (for reviews see Aguilera, 2010, Egger et al., 2004 and Choi and Kim, 2007b). What all of this means is that heritable gene expression may be caused by mechanisms other than changes in the underlying DNA; as with HGT, then, a life form’s environment does more than just select for or against certain traits. Accessible introductions can be found in Bird (2007) and Egger et al. (2004).

Specifically regarding anthropology, the greater understanding of epigenetics holds promise to enormously improve our understanding of the oft-mentioned, but poorly-defined, ‘functional complexes’ of anatomical traits. For example, since the 1970’s it has been appreciated in palaeoanthropology that anatomical characteristics or traits should not be understood as independent entities, but owe some of their given states to their relationship to other traits (examples of an appreciation of this approach include Howell, Washburn and Ciochon 1978 and especially Oxnard 1987). While this move away from studying ‘puzzle pieces’, and towards ‘the fit-together puzzle’ was certainly an advance, epigenetics takes us further. In a recent epigenetics-informed consideration of the hominin head, Lieberman recently shed light on just how epigenetic effects of one trait upon another can help clarify these ‘functional complexes’ in a more subtle way, noting, for example, that certain genetic signaling factors are expressed as growth of certain portions of the neurocranium create tensions in the overall structure, and that the overall modular structure of the head must be considered in light of such factors, not just the usual waving of the wand, so to speak, of selection and adaptation (Lieberman 2011). Essentially, such an approach not only clarifies the nature of ‘functional complexes’ but leads to a more realistic—although enormously more challenging—understanding of the variables influencing the phenotype. Now, even fossil anatomists must confront not just genetics but epigenetic effects.

Mutagenesis: Mutation, any difference between parent and offspring genomes, is now understood to be common rather than rare; it is also understood to be less the result of unusual, ‘one-off’ events, like cosmic ray bombardment of DNA, than a result of many DNA-degrading mechanisms. In short, mutagenesis has been re-cast with a new perspective emphasizing *the failure of DNA-repair mechanisms*. A good entrance to the topic is found in Friedberg (2006).

Naturally, this tidal shift in understanding mutagenesis will improve anthropological understanding of the origins and nature of biological variation, a fundamental element of the evolutionary process that has shaped all primates, including hominins. We will better understand, for example, different classes of both mutations and mutation-repair mechanisms. Extending from biological evolution, such insights could well inform a subtler understanding of the nature of innovation as a mechanism of cultural variation, tackled early on by Barnett (1963) and has more recently explored in studies as diverse as consideration of traditional basketry design transmission (Jordan and Shennan 2003), the role of cultural innovation in the evolution of behavioral modernity (Shennan 2001) and the neural bases of innovation and novel idea association itself (e.g. Gabora 2010, 2011). Recently, the parallels between varieties of biological and cultural innovation have been explored in a volume published as part of the M.I.T. Press’ *Vienna Series in Theoretical Biology*, indicating how thoroughly continental scholars (mostly) have adopted the cultural-evolutionary approach (O’Brien and Shennan 2010), and in that

volume fundamental issues such as rate of novelty production (read ‘mutation rate’) and appropriate definitions of cultural innovation are discussed in light of evolutionary biology—including mutagenesis—at large (e.g. Ariew 2010:34-35), indicating this early and exciting state of affairs.

Developmental Evolutionary Biology (evo-devo): Molecular data show that most animals, “...no matter how different in appearance, share several families of genes that regulate major aspects of body pattern.” (Carroll 2000:577), indicating that while phenotypes are of course a product of genetic instruction, the relationship of gene to trait is vastly complex because the timing of gene activation in the life-course is, among other factors, crucial to development of the phenotype. Thus the simplistic mapping of ‘gene → protein → phenotypic trait’ is liable to be a gross oversimplification because it does not include the dimension of time. To update the common conception of “one gene to one trait”, Miquel Porta has characterized the genome as a ‘jazz score’ (Porta 2003) rather than a blueprint. We are only beginning to understand how the environment influences gene expression (activating or repressing genes) at different stages of development (see Adams 2008, Lobo 2008, and Philips 2008). An excellent popular-science introduction to ‘evo-devo’ is found in Carroll (2005).

With the proliferation of ancient DNA (A-DNA) studies, our understanding of evolution can now include not just the comparison of past and present genes, but their specific functions and the history of gene regulation itself. This proliferation (A-DNA studies are common in palaeoanthropology and archaeology today, whereas they were a novelty just ten years ago) is a result of new methods that allow the recovery and analysis of DNA from specimens tens of thousands of years old. Recently, A-DNA expert Svante Pääbo suggested that A-DNA might be recovered from specimens as old as a million years (Pääbo 2004), and researchers will surely try to push further back in time.

Mutualisms and Coevolution: While a recent emphasis on cataloging gene functions has philosophically removed many organisms from their environments (see comments in section 3, below), molecular biology has also fortified ecological and systems biology perspectives by showing that most, if not all species have significant evolutionary relationships with other species (Douglas 2010:1-23). Coevolution, according to Thompson (1999:2116), “...may be the most important process organizing the diversity of life.” For example, in humans, entire ecologies of microscopic life forms live in the mouth, nose, throat, and intestines, and these have coevolved with their host species (see, for example, Bäckhed et al. ., 2005 and Les Dethlefsen et al. . 2007). In short, systemic, integrative, and ecological studies of mutualisms such as parasitism and symbiosis will flourish under this paradigm, forcing a reconsideration of basic units and hierarchies (e.g. see Michod 1999 and Vermeij 1994). Good reviews of these topics are available in Douglas (2010) and Herre et al. (1999).

Most anthropologists have long since made the transition from seeing humanity as the specific product of a somehow internally-guided evolutionary process to seeing humanity as one of many coevolving community members; in palaeoanthropology, for example, by placing early hominin evolution into a larger context of Plio-Pleistocene grassland evolution (e.g. see Brantingham 1998, Foley 1987). These approaches, however, will be updated with a greater appreciation for the significance and subtleties of coevolution. For example, humanity has coevolved with its domesticates, as seen in the case of the independent evolution of lactose tolerance among several different ancient pastoralist populations (Tishkoff et al. 2006). And the parasites that have attended human migration and evolution can help us understand and even assemble new lines of evidence to date such migrations, as in the case of human-infecting

schistosomes (blood worms), evolutionary ‘hitchhikers’ whose divergence from an African origin have been used to assist in understanding the Pleistocene colonization of the globe by the genus *Homo* (Morgan et al. 2005).

Phenotypic Plasticity and Phenotypic Integration: In a 2004 survey of the history of biology, Carl Woese suggested that “A heavy price was [in the past few decades] paid for molecular biology’s obsession with metaphysical reductionism. It stripped the organism from its environment; separated it from its history, from the evolutionary flow; and shredded it into parts to the extent that a sense of the whole—the whole cell, the whole multicellular organism, the biosphere—was effectively gone.” (Woese 2004:179). Recent interest in reintegrating species with environments, as mentioned above, has led to the re-examination of two concepts. The renewed study of *phenotypic plasticity*—summarized as “environmentally-induced phenotypic variation” (Stearns 1989:436)—recognizes both putting species back into environments and accounting for the complexities of developmental biology, with unexpected new results: for example, stress responses in a life form can include mutagenesis (Galhardo et al. 2007). The evolution of adaptive phenotypic plasticity has led to the success of organisms in novel habitats, and potentially contributes to genetic differentiation and speciation (Agrawal 2001, Chown et al. ., 2007). The renewed study of *phenotypic integration* (complex patterns of covariation among functionally related traits) operationally addresses the details revealed by the study of phenotypic plasticity. Both fields reveal greater coevolutionary complexity than is emphasized in the ‘modern evolutionary synthesis’. Phenotypic plasticity may be approached in Stearns (1989) and DeWitt and Schneider (2004); Pigliucci and Preston (2004) introduce phenotypic integration.

The study of phenotypic plasticity and integration both tackle, in large part, complexity in biological systems; again, nothing is as simple as we may have wished. Complex systems, we have learned in the past few decades, are composed of variables of all manner of states (at any given moment) that interact in complex ways—including feedback relationships glimpsed in studies of phenotypic plasticity—such that changes in the system might result in unpredictable and qualitatively new phenomena, including complex adaptive systems (e.g. Kauffman 1993). Exactly how studies of phenotypic plasticity and integration will condition anthropological understanding is unclear (beyond the obvious improvement of physical anthropological understanding), but inasmuch as they will improve understanding of biological evolution, surely they will improve understanding of cultural evolution (even if to point out differences between the two).

Niche Construction: Niche construction theory (NCT) addresses the fact that life forms—consciously or not—alter their selective environments and are not always simply passive precipitates of a given selective regime. Again, this address the actual complexity of evolving systems that lies behind the philosophical façade of evolution’s essential simplicity. For example, “Organisms do not just build environmental components, but [dampen] out variability in environmental conditions. Beavers, earthworms, ants, and countless other animals build complex artifacts, regulate temperatures and humidities inside them, control nutrient cycling and stoichiometric ratios around them, and in the process construct and defend benign and apposite nursery environments for their offspring.” (Laland and Brown 2006:95). While such interactions are not ignored in traditional evolutionary studies, niche construction theory is a coherent body of theory that can guide investigation, explanation and understanding of such interactions. A good introduction to niche construction theory is found in Odling-Smee, Laland and Feldman (2003); it is more concisely reiterated (with regard to humanity) in Laland, Kendal and Brown (2007). Finally, volume 366 (2011) of *Transactions of the Royal Society (B)* is dedicated to

niche construction theory. As ever, universal consensus is hard to find, and niche construction theory has been critiqued as unoriginal (e.g. Keller 2003) and obvious; Brodie (2005:249) has written that “Few ecologists or evolutionary biologists would be surprised to learn that organisms interact with their environment in ways that change both the environment and the organism's perception of it. What, then, is the importance of defining a new concept to encompass all such actions?”

Even if NCT is only new terminology for old knowledge, however, at the very least it provides a more considered terminology (we should always be careful of ‘common sense’), and we argue that the significance of niche construction theory to anthropology is profound, as humanity has survived and proliferated not because of its biological equipment, but, in fact, in spite of this frail equipment and because of behavioral complexity and the ability to rapidly adapt via cultural innovation; this ability includes, in the new terminology, niche construction, the invention, building and maintenance of ecological niches by humanity for humanity, rather than humanity's simply being shaped by selective pressures of certain environments. Laland and Brown (2006) suggest that this recognition negates the claim, by opponents of evolutionary approaches to culture, that humanity is characterized in evolutionary approaches as simply a passive product of selective pressures. Also, Smith has applied niche construction theory to human / domesticate interactions, pointing out its utility by writing that “...human efforts at shaping their natural landscapes have been classed under a number of terms [including] indigenous management...domesticated landscapes...indigenous resource management...all of these roughly synonymous terms...fall comfortably under the now far more general heading of niche construction.” (Smith 2007:191.) How else niche construction theory will play out as an element of anthropology is unknown, but it seems sure to be significant, considering that the capacity for active niche construction appears to be one of humanity's most potent adaptive tools.

2. What Now?

Considering these insights, what's left of neodarwinism? A parallel with the split between Newtonian and Einsteinian physics may, for some time, be useful—or at least ease the transition to a new synthesis. In many cases, neodarwinian principles are sufficient to sketch out macroevolutionary phenomena; there are different types of life, and—for example—fossil material of these different forms can be discerned, and those life forms did change through time by the core evolutionary processes of replication, variation, and selection (Gingerich 2009:658). But deep down, on the molecular level, we know today that things are happening that we are only just perceiving, and they do not always adhere to standard neodarwinian conceptions. This should caution us, as ever in science, about proclaiming absolutes, and in anthropology it should cause us to educate ourselves on the new conceptions of evolution deriving largely from genomic research.

Koonin (2009, Table 1) reviews the central tenets of neodarwinism in the pre- and post-genomic eras. We reiterate his review below in our own words.

Is random, heritable variation the principal material for natural selection? Yes; but we must remember that mutation has many sources, and that randomness may apply less than we have thought.

Does natural selection generate increasingly complex adaptations through time? Not necessarily; maladaptation and extinction are common, and genomes do not necessarily become more complex through time due to a number of constraints on variation.

Does evolution proceed by making small changes? Not necessarily; much evolution occurs on a radically short timetable (e.g. see Koonin 2007), as in the case of bottlenecks. Rapid speciation may occur after extinction or arrival on “islands” opens up niches previously unoccupied (Drossel, 2001, Latimer et al. 2005).

Has evolution always proceeded in the same way? To an extent, yes; the essential processes of replication, variation and selection are required (see Dawkins 1983, Nelson 2007); however early evolution of Earth life was substantially different from that today, and in the last four million years the phenomenon of the *decoupling of behavior from anatomy* in the genus *Homo* (Pilbeam 1998:526)—largely synonymous with *Homo*'s increasing reliance on extrasomatic means of adaptation to survive—has led to the “evolution of evolution”, in which culture appears as a second, parallel evolving information system of tremendous power (see Brosius 2003 regarding pros and cons of this power).

Can we draw a line around a species? Yes and No; there are clearly different kinds of life, as in the case of an elephant and a cactus; but these must be recognized as shades in a spectrum of life forms, and among the asexually-reproducing species the entire concept of species, considering the revelations of HGT, must be reconsidered. Because species never stop evolving, and evolution is thus characterized by change, we must recognize that the lines drawn around or between species can in some ways be considered arbitrary. Baptiste and Boucher (2008, Figure 3), and Baptiste et al. (2004, Figure 4) describe new methods for visualizing the relationships of species in the light of HGT.

Can we continue to use the 'Tree of Life' as a metaphor? To a degree; but it must be remembered that genome elements are increasingly found to be mobile, and, as in the case of the previous question, we must be cautious with this device (see Baptiste et al. 2009 for a review of the metaphor).

Do all life forms descend from a common ancestor? Yes, but the Last Universal Common Ancestor (LUCA) would not have been very similar to modern cells.

3. Comments

Whether studying nonhuman primates, early *Homo*, or recent and modern *Homo*, anthropologists are studying the processes and products of biological and biocultural evolution. Recent advances in biological understanding show that evolution has multiple modes. Some evolution is essentially Lamarckian, some evolution is essentially neodarwinian, and different modes might have prevailed at different times in the history of life. In sum, there is much more to evolution than the simple neodarwinian principles most of us have learned. This does not mean that Darwinism is dead, that neodarwinism is dead, or that ‘evolution is wrong.’ Rather than throwing out evolutionary principles we are better understanding the actual complexity of evolution.

How biology itself proceeds in the future will condition, to an extent, how and what anthropologists will learn about evolution; as ever, there are social, political, and economic factors involved in biological science. In a review of the last century of biology, Woese has recently called for a philosophical discussion of the purpose of biology today and in the future (Woese 2004). Concerned that too much emphasis has been placed on genome mapping (often funded by pharmaceutical companies and their interests) Woese asks whether, generally, biology will be used to better understand the world of living things or to modify it, becoming “an engineering discipline.” (Woese 2004:185). While much basic research addresses how the evolutionary process occurs, genome engineering is proceeding at a fast pace; in 2010

researchers at the J. Craig Venter Institute created the first self-replicating synthetic life, inserting chemically synthesized artificial genetic into natural living cells. So, both a new understandings of biology, and engineering it (for better or worse; see Brosius 2003 for a review), are well underway.

An evolutionarily-informed anthropology cannot ignore these developments. We invite anthropologists to familiarize themselves with the new evolutionary synthesis.

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