

We Hold These Truths to Be Self-Evident

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Evolutionary biology rests more deeply on axioms than we may wish to believe. What are they and how sound is their logical standing?

Evolution is a pervasive cultural as well as scientific metaphor of our age. An evolutionary worldview is as fervently held by biologists today as were the prevailing views that evolution displaced. Ultimately everything is credited to genes, and given a *genes-for* evolutionary explanation: genes for upright posture, dominance hierarchies, language, IQ, heart attacks. We've seen a century of spectacular progress in biology but this does not mean the foundations on which evolutionary explanations rest are unambiguously established. It is not entirely clear how well some of our venerable concepts jibe with new genetic and developmental data pouring out of laboratories today.

I thought it would be timely to try to identify aspects of traditional ideas that still hold up well and areas that don't do as well. *Crotchets & Quiddities* will attempt to do that. *Crotchets* are eccentric or idiosyncratic opinions, and this will certainly reflect mine. A *quiddity*, a term I first learned from W.V. Quine¹ (1987), is a philosophical essence or trifle, from the Latin *quid*, or 'what.' It can refer to the sometimes-intangible quirks, or niceties, of a thing or idea (which I hope readers will not equate dismissively with today's "Whatever!"). I hope not to be too crotchety, but "the intensity

of the conviction that a hypothesis is true has no bearing on whether it is true or not" (Medawar, 1979). In this column I want to examine some of our assumptions, to stimulate thought about them.²

The prevailing cosmology that greeted Darwin's *Origin of Species* in 1859 rested on the theologically based assumption that the universe was created at a single point in time by a purposive intelligence who selected a bestiary of species designed to be adapted to their environments. This was assumed to be given truth rather than something one had to infer from observation. By comparison, in biology we believe we are practicing a rigorous, objective, empirical method-of-knowing that does not rest on wishful thinking. Yet much of our work rests on axioms—conventional wisdom or laws of Nature, if you will—that we *assume* to be true, but cannot actually prove.

THE FORMAL BASIS OF MODERN BIOLOGY

We can quibble ("quiddit"?) over what should be included or excluded, but among the basic principles of darwinian biology are (1) all life ultimately came from a point source in the primeval molecular slime; (2) descent with heritable modification of biological traits; (3) the origin of biological form and of species by adaptation due to natural selection via differential reproduction; and (4) a uniformitarian extrapolation of these phenomena back to the origin of life.

Although descent with modification is directly observable today, evolu-

tionary biology insists on its universality, which is an assumption. The other three principles are clearly assumptions. Nobody taped the start of life. We do not really know from direct experience how speciation occurs (and have some difficulties even defining species). And "uniformitarian" is too big a word to be anything but made up (assumed).

The success of physics in the 19th century, with its formal theoretical basis (e.g., Newton's laws) had widespread impact; anything less is "soft," "descriptive," "natural history." In the 1930's and 40's the neodarwinian synthesis provided biology with its own universal, axiomatic theoretical foundation, in the form of population genetics. That formalized the basic principles of evolution into a theory that gives theoretical cover for evolutionary inference and is the pervasive framework for designing and interpreting biological (including anthropological) studies. The theory was subsequently augmented with its own atomic units—genes—and the additional axiom of the Central Dogma, that a gene is a discrete molecular structure that codes for one protein by a unidirectional information transfer from DNA through RNA to protein.

Population genetics begins by positing a Platonic kind of idealized infinite, freely mixing population, with no mutation, no migration, and no differential reproduction. This still-life would not generate evolution as we know it, so we relax each of the ideal conditions in an orderly way, to analyze the consequences. Relaxing the idealistic assumptions makes things realistic, but at the price of making evolutionary biology probabilistic in theory,³ because the modifications to the idealized population are all stochastic: random mutation, random change in

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frequency due to sampling across generations in finite populations, random effects of migration, random mendelian segregation and recombination, and the randomness of changing environments relative to existing genetic variation.

The assumption of a point source is important to the entire theory, so we insist upon spontaneous generation in the beginning, but must forbid it at any other time. Under the assumption that genes don't "blend" in the Darwinian sense each generation, the accumulation of mutation change leads to divergent evolution. Mutational changes have accumulated from Day One, so that genomes today reflect the surviving sequences of their entire past history. The extrapolation of these processes over long time periods provides theory for the directed change in frequencies of randomly occurring genetic variants in response to selection, and hence adaptive divergence and speciation. Under these conditions, the biosphere is connected, contingent, and hence unique.

HOW TRUE ARE THE AXIOMS?

It's nice to know that population geneticists are on guard (even if they're a bit too geeky for *our* department), but truisms can become vacuous or lead to uncritical thought. The core notions of evolution may be basically right, but they do have problems, not all of which are trivial. As we look at some of them we should keep in mind that modern evolutionary theory assigns biological meaning ultimately to genes. The theory provides no explicit help in understanding the evolution of phenotypes unless we separately specify the genotype-phenotype relationships that apply, and these (when known) usually have a probabilistic element of their own. The probabilistic aspects of the theory are somewhat strange: they don't refer to repeated scenarios, and we can't specify or confirm their actual values or distributional properties, because of the axiom that life has evolved but once from a single origin. Yet many biologists have an assured, deterministic worldview, and this certainly characterizes much of biological anthropology.

A Point Source For All Life

The grandeur of Darwin's view was "of life having been breathed by the Creator into a few forms or into one." But is there a Tree of Life all descended from a single beginning? Ignoring those who argue that life is seeded from space,⁴ earthly inheritance itself does not go strictly vertically from parent to offspring, but regularly occurs across species. Deep branches of gene phylogenies for the major classes of life are inconsistent, in part because of the transfer of entire bacterial operons (clusters of functionally related genes), plasmids, mitochondria, chloroplasts, viral DNA, and even perhaps the basic recombinational component of our immune system. We have no way to be sure that there was not a diffuse rather than single point source of life in the primal soup, because traces of any initial diversity may have been replaced by subsequent forms.

Most horizontal transfer may have occurred before the evolution of multicellularity, and hence be peripheral to the evolution of later species (such as primates). Nobody suggests we derive our genes for limb development by horizontal transfer from frogs, say, but a percent or more of our entire genome comprises exogenous (mainly viral) genes, and about 35% is comprised of repeated sequence elements shuffling around within the genome before being transferred to the next generation. These are not trivial fractions of our entire genome.

We routinely seek homologies by constructing trees of gene sequences, or gene families, but the origin of genes by duplication or recombinational mechanisms sometimes plays havoc with that, because individual genes don't always "coalesce" in a simple way back to gene-specific, or even consistent species-specific Adams and Eves. Different fragments of each gene, ultimately individual nucleotides, go back to different genes and different common ancestors, that may even be in different ancestral species (Adam and Trog?). When we try to reconstruct the ancestry of present life, we have to be aware that it is reticulated rather than a Tree with a single trunk.

Random Mutation

The critical evolutionary point about mutation is that it must be random relative to function; specifically, the needs that arise during an organism's life do not induce mutations to satisfy those needs. We rightly struggle mightily against any Lamarckian challenge to this fundamental tenet, which at present seems relatively secure; but there are a few cracks. Mutations and the equivalent variation-generating processes of gene conversion and recombination are not random along the genome. The reasons are not all known, but there are suggestions that genes may sometimes be arranged in ways that protect some regions of the genome from change, leaving others specifically more vulnerable to change, for functional reasons. We know of systems in some species, especially bacteria, in which relevant parts of the genome are actively made more mutable in the presence of stressful environments, which allows the organism to generate diversity that may enable it to survive. "Adaptability" systems of that sort don't lead to purely Lamarckian inheritance of *specifically* acquired traits, but they approach it, and the assumption of the randomness of mutation relative to function is so fundamental to evolutionary theory that any experience-directed phenomena need to be looked at seriously.

Population History

Evolutionary change at the gene level is affected by population size and structure, migration and mating patterns, and the time and place of each mutational event. When we attempt to reconstruct evolution from patterns of present genetic variation, we have to make assumptions about the unknowable details of that history. We are unable to write an equation for the exact trajectory of, say, the evolution of sparrow flight the way we can for arrow flight. Instead, we create *as-if* models. Real populations have all sorts of structure, which changes every generation. Since we don't know the actual details, we estimate the *as-if* "effective population size," N_e , of a homogeneous population that over very long time periods would generate the

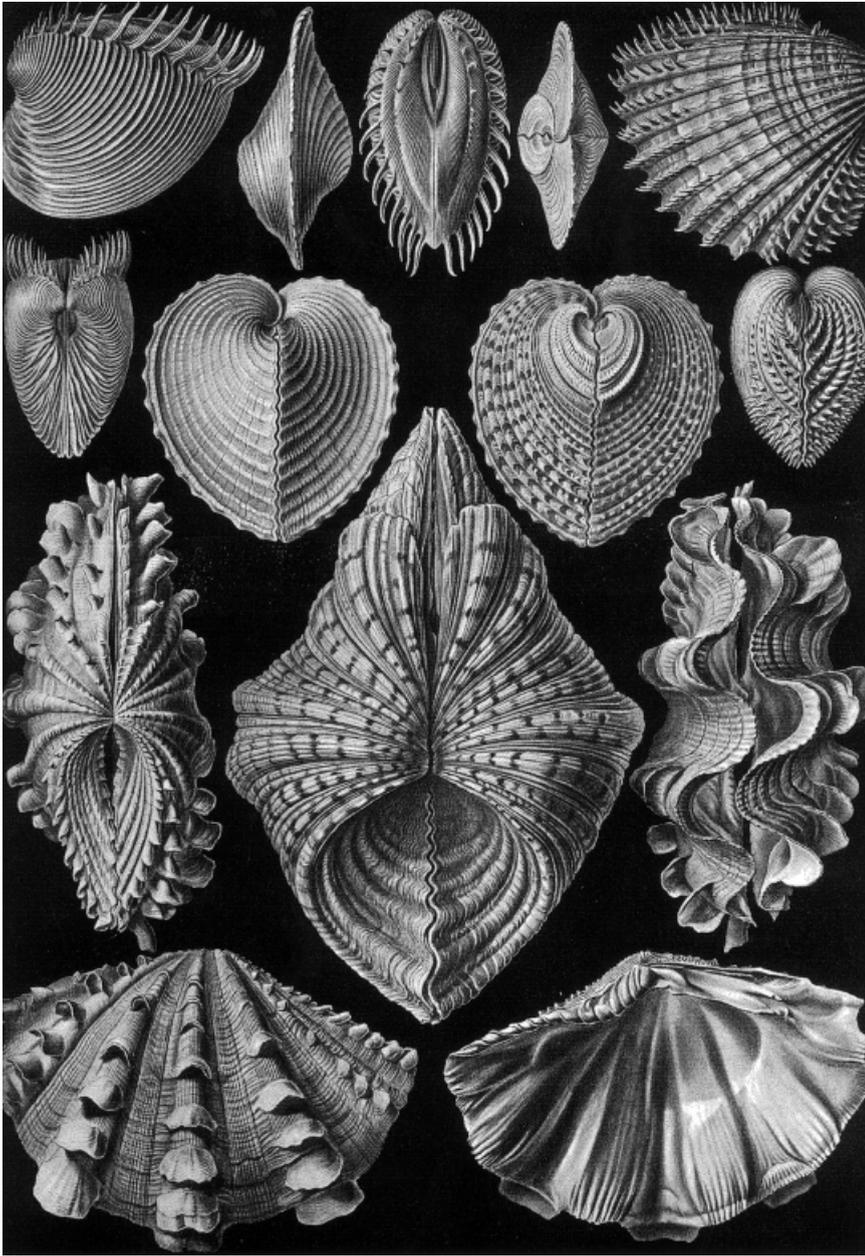


Figure 1. Is any explanation 'true'? A drawing by Ernst Haeckel of natural diversity in seashells. What could be the source of this variation? Does evolutionary theory really "explain" it?

same amount of genetic variation that we observe today. That's where the commonly used value of 10,000 for the size of source population for modern humans comes from. We make similar assumptions about average mutation, recombination, and migration rates, and selective coefficients. The resulting theory has built-in non-identifiability issues, because different sets of plausible parameter values can yield the same result. We face ad-

ditional problems when we try to reconstruct the evolution of complex morphological or behavioral traits, because we typically have no idea how many genes are involved or the selective and stochastic forces that acted on them. Yet it is routine to describe morphology *as-if* it evolved in adaptively deterministic ways, and as if that makes the explanations true because they are consistent with population genetics principles (*genes-for*

upright posture were favored in this-or-that environment, etc.).

We construct evolutionary scenarios *as-if* conditions were simple, though we know they weren't and that we usually can't specify a very believable uncertainty range.³ This is different in kind as well as in degree from the approximations introduced in Newtonian theory in making predictions of an arrow's trajectory. Too often, the result is over-determined, largely uncheckable Just-So reconstructions. We may choose to believe our favorite scenario (and of course might be right), but that is not as different as we might fancy from the pat nature of other cosmologies, because we can always reconstruct a plausible story given our axioms. This is one reason we have so much trouble arriving at consensus even about relatively simple, recent events at the core of our discipline, like modern human origins.

Extrapolation, Speciation, and Adaptation

We treat population genetics as a means of explaining darwinian evolution of species, but population genetics does not really deal with the formation of species *per se*; we have to add them *deus ex machina* to our theory. The theory itself is uniformitarian in that it specifies microevolutionary processes that we extrapolate indefinitely over time and space. It may be right to assume that speciation involves genetic divergence produced by population genetics processes acting over long time periods, but that's basically as speculative as when the Synthesis was proclaimed 70 years ago. Genetic divergence can occur without speciation (you and I are different), and speciation can be uncaused by genetic divergence (e.g., behavioral isolation). Surely, also, species can arise by drift rather than adaptive divergence.

Whatever species are, they may or may not arise at a single point in time. Most theory is darwinian (gradualistic and adaptational), but it may not require much genetic change to establish a mating barrier; which anyway need not involve adaptive change. The role of adaptation has if anything

been reopened by recent discoveries of homeotic mutations in laboratory experiments (e.g., the production via a single mutation of extra digits, limbs, teeth, etc.). These experiments are relevant to anthropological concerns like the evolution of primate dental or limb morphology, but there is little useful theory for it.

There are deeper difficulties associated with modeling adaptive evolution that may not be widely perceived. Selection means genetic change *because* of particular traits. Selection is typically treated as a deterministic “force,” in contrast to the randomness of genetic drift. But what could make it a force? A force should have a consistent magnitude and direction, but differential reproduction among genotypes is probabilistic at best and except in the extremes it is difficult to say *why* it happens. Those clear-cut extreme effects (like lethal mutations) are typically rare or biologically uninteresting, and don’t appear to explain most variation or adaptation. It is notoriously difficult to discriminate between selection and drift, based indirectly on existing patterns of genetic variation or on direct observation of differential reproduction.

We face the additional problem that we don’t know how many genes are involved or the genotype-phenotype relationships for traits whose adaptive history we would like to understand. If homeotic mutations do occur—for example to change the number of digits or teeth—they could easily rise to high frequency by drift alone. Adaptive scenarios usually assume stable environmental forces over very long time periods (strong enough to overcome genetic drift), which we usually model as a kind of average, at best, but may be pure guesswork. For example, the human brain may be an adaptively selected structure, but it is no joke to try to reconstruct the events that were responsible over the past million years. Brain size may have grown by an average of 1 mm³ per generation, but how is such change manifest in terms of the actual fitnesses of the beasts that competed day to day on the African plains? Probably by selection at the extremes in each generation, but that’s just my guess.

Many biologists (and biological an-

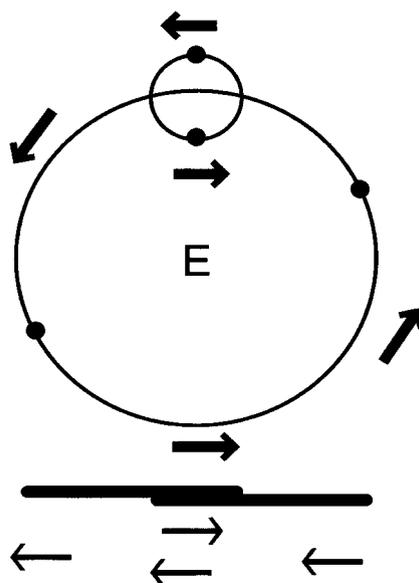


Figure 2. Scientific theory going around in circles? Hypothetical path of an object rotating about the Earth, with an epicycle added to explain apparent retrograde motion as viewed from the Earth. Top shows the hypothesized orbit, bottom the apparent direction of motion. (see Kuhn, 1957).

thropologists) see the world through selection-colored glasses, treating selection as prescriptive or energetically efficient for almost any trait. I think such strong adaptationism leads to excessive genetic determinism—the ubiquitous invocation of *genes-for* explanations. We’re surrounded by manifest evidence that selection is not so prescriptive, because there is substantial variation and inefficiency in most traits, in most organisms, most of the time. Genes are important, and since we develop from a single cell there must in some sense be *genes-for* almost anything. But traits are not always tightly determined by specific genotypes. Given this, it may actually be more difficult to explain the deep phylogenetic *stasis* that we see in some genetic mechanisms (e.g., *Pax6* and eye or *Hox* genes and axial and limb development) and morphology (e.g., horseshoe crabs and cockroaches).

WHEN IS FITTING TOO WELL NOT FITTING WELL ENOUGH?

There are no theory police, but theory does help science by placing con-

straints on what are acceptable assertions. A problem with issues like those I’ve raised here is that they allow evolutionary theory to fit too well, enabling us to evade some of the core constraints by which we judge scientific statements. Evolutionary reconstructions are probabilistic and in a sense not clearly falsifiable. This allows us to cling to favored hypotheses (like *genes-for* disease or various behavioral traits) in the face of repeated negative results. Even to specify the likelihood of our reconstructions we use statistical methods (like significance tests) that assume sampling from replicable phenomena, yet we know that evolution produces unique objects by unique events. Though historical sciences can’t claim the predictive powers of experimental sciences, we counter that at least we can “retrodict” the past. But in making (up?) the kinds of plausibility stories described above, all we usually can assert is that observed data are compatible, via the axioms of evolution, with *some* scenario we can imagine. In these senses, evolutionary theory fits the data too well. But in some senses it does not fit well enough.

In Ptolemaic astronomy, the heavenly bodies circled the Earth. Occasionally, however, one was seen to move backwards. Retrograde motion could be explained by hypothesizing *ad hoc* “epicycles” in individual orbits, as illustrated in Figure 2. This worked for a while until too much of it was needed, Ptolemy was replaced by Copernicus’ Sun-centered model (Kuhn, 1957), and many exceptions fell into place. The realization of evolution similarly changed how we view life, explaining many things at once. Because its essential ideas about common ancestry seem doubtlessly to be right, evolutionary theory has resisted a century and a half of assault,⁵ but some of our basic notions about the processes involved are becoming a bit frayed at the edges in light of recent genetic data, and evolutionary models are loaded with *ad hoc* tinkering and exceptions in order to make them fit what we observe. Are there places where we need to get off our epicycles, because questions we haven’t answered *can’t* be answered adequately with our current premises? Or is the

real truth that only a very permissive “theory” will accommodate the facts, because evolution is messy at its core? If so, by what are assertions to be adjudicated other than shouting contests, ever-recycling the same alternative scenarios? Good for employment, not so good for understanding Nature.

One can debate the exceptions, revisions, or uncertainties in these traditional notions about how evolution works. The importance of things like horizontal transfer of genes may be challenged because they are rare. But mutation is also rare, and much hinges on the relative effective rarity of each evolutionary factor. If we start saying that rare things are unimportant in evolution, do we also have to dismiss selection because most of it is virtually impossible to detect directly? If so, what we’re left with is drift.

The formal axiomatic theory of evolution is about 80 years old. In many ways, recent discoveries simply revisit issues we already knew about. But new data show clearly that genomes are more fluid, complex, and dynamic than the tightly programmed, simply-evolving, one-way semiconductors of protein-coding information we thought them to be. It is healthy to be skeptical even of truths we hold to be self-evident, and to ask: suppose it isn’t true—what would follow? Do we need a theory of evolutionary biology?

What beyond shared ancestry is inviolate? Forthcoming columns will look at where some of these issues stand at the verge of a new century, to see where they still seem sound, and where they may need changing, if we wish to understand evolution more clearly.

NOTES

I would welcome comments on this column: kmw4@psu.edu.

I thank Anne Buchanan, as usual, for doing her best to make this as understandable and responsible as she can get me to be. John Fleagle has been more than forbearing during the iterations needed to get this off the ground.

1. I also liked the word for the sentimental reason that Quine, who was a leading philosopher of logic, preceded me as a math major at Oberlin College (but he was capable enough to make something of it).

2. My purpose is to stimulate ideas. That means being declarative rather than guarded, short on caveats, omitting countless credits to others who already thought the same things. I don’t claim originality.

3. This is as distinct from probabilistic (statistical) means of evaluating data. Evolutionary theory has problems in both.

4. Not all their arguments are entirely trivial (whether they’re right or

wrong). For example, evolutionary reconstructions assume common ancestry *on Earth*.

5. Given a spate of recent anti-evolutionary books, I feel compelled to state that nothing in this column in any way questions the *fact* of evolution, which seems indubitably established, nor supports creationist accounts (one cannot call them “explanations”) for the diversity of life. See Crews references.

TO READ

Most things discussed here can be profitably explored by web searching.

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