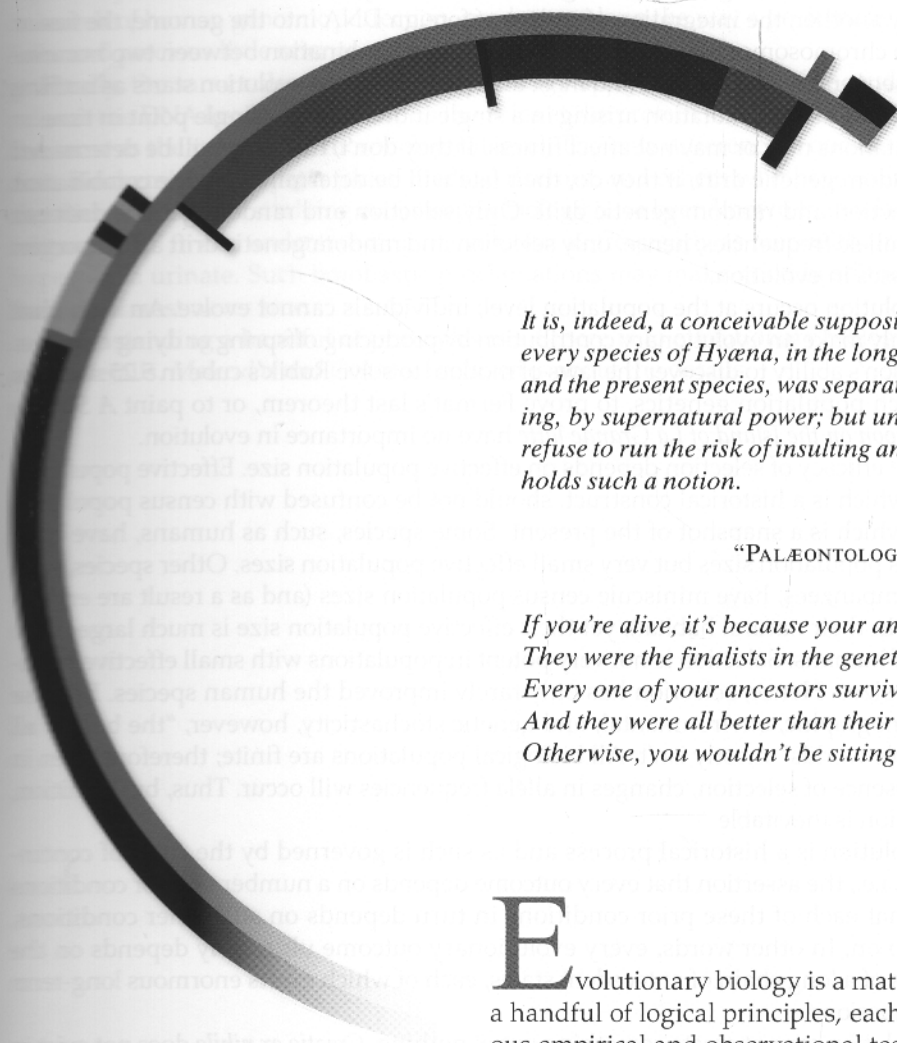


Introduction



It is, indeed, a conceivable supposition that every species of Rhinoceros and every species of Hyæna, in the long succession of forms between the Miocene and the present species, was separately constructed out of dust, or out of nothing, by supernatural power; but until I receive distinct evidence of the fact, I refuse to run the risk of insulting any sane man by supposing that he seriously holds such a notion.

THOMAS HUXLEY

"PALÆONTOLOGY AND THE DOCTRINE OF EVOLUTION" (1870)

*If you're alive, it's because your ancestors were the best survivalists
They were the finalists in the genetic Olympic Games
Every one of your ancestors survived to reproductive age
And they were all better than their competitors at getting laid
Otherwise, you wouldn't be sitting here today.*

BABA BRINKMAN

"DARWIN'S ACID" (2009)

Evolutionary biology is a mature science. It is a coherent discipline with a handful of logical principles, each of which has repeatedly withstood rigorous empirical and observational testing. Evolution is not difficult to define. If one ignores the obfuscations of the creationists, the casuistry of the philosophers, and the ruminations of the sophisticates, evolution is merely a change in allele frequencies. There is no other mandatory attribute to the evolutionary process.

The evolutionary process may or may not be gradual; it may be imperceptibly slow or spectacularly fast. The evolutionary process may or may not be progressive. It may give rise to astonishing biological complexity or it may reduce the organism to a shadow of its former self. The only thing that can be said with certainty about evolution is that change is inevitable.

Evolution does not give rise to perfection or to anything resembling intelligent design; spinning wheels on fixed axles have never evolved in nature. Evolution does not drive the living world toward a better, fairer, more efficient, more honest, or cleverer state. Evolution merely produces changes that are not excessively deleterious. The most we can say about the products of evolution is that they work—some efficiently, some only barely, and some in a manner that is clumsy, plodding, and bureaucratic. If genes, genomes, and organisms were created by a benevolent intelligent designer, the problem of theodicy would never have arisen, and departments of pediatric oncology would never be needed.

The origin of all novelty in nature is mutation. Within the category of mutations, we include all heritable changes in the genetic information that have the potential to be transmitted from generation to generation, be they the substitution of one nucleotide by another, the integration of a piece of foreign DNA into the genome, the fusion of two chromosomes into one, or the reciprocal recombination between two homologous sequences. The greatest and most amazing novelty in evolution starts as nothing more than a single mutation arising in a single individual at a single point in time.

Mutations may or may not affect fitness. If they don't, their fate will be determined by random genetic drift; if they do, their fate will be determined by the combination of selection and random genetic drift. Only selection and random genetic drift can affect allele frequencies; hence, only selection and random genetic drift are important processes in evolution.

Evolution occurs at the population level; individuals cannot evolve. An individual can only make an evolutionary contribution by producing offspring or dying childless. A person's ability to discover the laws of motion, to solve Rubik's cube in 5.25 seconds, to teach population genetics, to prove Fermat's last theorem, or to paint *A Sunday Afternoon on the Island of La Grande Jatte* have no importance in evolution.

The efficacy of selection depends on effective population size. Effective population size, which is a historical construct, should not be confused with census population size, which is a snapshot of the present. Some species, such as humans, have huge census population sizes but very small effective population sizes. Other species, such as chimpanzees, have miniscule census population sizes (and as a result are endangered in their natural habitat), yet their effective population size is much larger than that of humans. Selection is not very potent in populations with small effective population sizes. Hence, selection has only rarely improved the human species. Because of demographic, environmental, and genetic stochasticity, however, "the best of all possible worlds" mostly isn't. All biological populations are finite; therefore, even in the absence of selection, changes in allele frequencies will occur. Thus, by definition, evolution is inevitable.

Evolution is a historical process and as such is governed by the rules of contingency, i.e., the assertion that every outcome depends on a number of prior conditions and that each of these prior conditions in turn depends on still other conditions, and so on. In other words, every evolutionary outcome ultimately depends on the details of a long chain of antecedent states, each of which exerts enormous long-term repercussions.

Evolution cannot create something out of nothing. *Creatio ex nihilo* does not exist in nature. Moreover, there is no true novelty in evolution. Digestive enzymes may evolve into venom, forelimbs may evolve into wings, hindlimbs may evolve into anchors for the muscles that maneuver the penis, and wings may evolve into halteres that function as gyroscopes; however, each new development must have a precedent. Evolution is a process that is constrained developmentally and can only act on what is already present. If a mermaid or a flying pig were shown to exist, we would have to discard the theory of evolution.

During evolution, it is easier to create equivalence than improvement. It is also easier to create functionlessness than functionality. The tens of thousands of genetic diseases that are due to gene death and loss of functionality attest to this fact. Gene death can sometimes be manageable. Thus, all large genomes are strewn with pseu-

dogenes that have no functioning counterparts. Because of gene death, humans have to get their vitamin C from oranges and cats are not tempted by sweets. Interestingly, functionlessness may even be advantageous. Akin to an empty ecological niche, a gene's death may create opportunities for subsequent mutations.

Evolutionary biologists, like most people, have a fascination with *Homo sapiens*. Humans, however, do not occupy a privileged position in that grand scheme of things called "evolution." The human genome is smaller than that of an onion and contains fewer protein-coding genes than cassava. Human biology is infinitely more boring than that of ciliates, human population numbers are dwarfed by those of tardigrades, and human genetic variability is negligible in comparison to that of the nematode *Caenorhabditis brenneri*. Ever since Copernicus, our anthropocentric worldview has repeatedly been shown to be erroneous, yet we continue to spend billions of dollars in search of human genomic perfection, producing along the way a great many headlines and precious little science.

Finally, the same rules of evolutionary biology apply to all levels of its study. The rules at the DNA level are the same as the rules at the protein level, which in turn are the same as the rules at the morphological level. The only difference is one of resolution. Biochemists, computer jocks, medical doctors, and others who have exempted themselves from ever studying evolutionary biology have been known to invoke "paradigm shifts" in our understanding of evolution as frequently as men with prostatic hyperplasia urinate. Such bombastic proclamations may make good headlines, but they are almost never true.

Understanding a handful of principles is all there is to evolutionary biology. The rest is details. *Molecular and Genome Evolution* is about the details.