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The Arrival of Evolutionary Thought

The notion that our planet and its inhabitants have not remained exactly as the Creator was supposed to have made them was in the air long before 1859, when the English natural historian Charles Darwin collected and published his evolutionary ideas in his great work *On the Origin of Species by Means of Natural Selection*. By that time, geologists had long known that the 6,000 years allowed by the Bible since the Creation was vastly inadequate for the sculpting of the current landscape by any natural mechanism; and the biologists who were just beginning to study the history of life via the fossil record were not far behind them. Around the turn of the nineteenth century, the French zoologist Jean-Baptiste Lamarck began to argue that fossil molluscan lineages from the Paris Basin had undergone structural change over time, and that the species concerned were consequently not fixed. Importantly, he implicated adaptation to the environment as the cause of change, although the means he suggested – subsequently infamous as “the inheritance of acquired characteristics” – brought later opprobrium. Soon afterwards, the Italian paleontologist Giambattista Brocchi, also working on marine invertebrates, observed that distinct species tended to replace one another abruptly in the sedimentary record of Tuscany. That led him to the idea that species, just like individuals, had births, histories, and deaths (by extinction). Births occurred when one species gave rise to another, so that lineages of organisms could actually diverge (and thereby eventually form branching trees).

The basic elements for recognizing and understanding evolution as a process of biotic change over time were thus in place almost half a century before Darwin wrote. What was added by Darwin – who devoured Lamarck's work, but may or may not have been exposed to Brocchi's ideas – was nonetheless revolutionary. In his masterwork, Darwin articulated and exhaustively documented his insight that the nested pattern of resemblances we see among organisms in nature is best explained by common ancestry. Physically similar organisms resemble one another not because the Creator wanted them that way, but because they share recent common ancestors. In turn, less similar organisms share remoter ancestry, degrees of difference being due to the accumulation of physical changes in ancestor–descendant lineages as a function of time. Darwin framed his argument for common descent with astonishing erudition and finesse, forcefully bringing his radical ideas to the attention of a largely orthodox Christian scientific community and public that was, at last, prepared to be at least partially receptive. Not that the enterprise would be easy. Darwin delayed publishing his evolutionary thoughts for many years out of a fear of public (and his devout wife's) reaction; and he was particularly at pains not to draw attention to the pretty obvious implication that, as an animal and a primate, *Homo sapiens* necessarily has an evolutionary history too. Indeed, all he said on that subject in the *Origin* was that "light will be shed on the history of man and his origins." Still, although Darwin had correctly foreseen the uproar that would break out when his book was published, the clamor subsided more quickly than he might have anticipated. By the end of the nineteenth century a secularizing British public had largely come to terms with its (broadly) ape ancestry, leaving the scientists to squabble over details of process.

Darwin's own thumbnail characterization of his theory of evolution was "descent with modification." This is a wonderfully succinct summary of the process that gave us the stunning structural diversity we see among living forms today, via the accumulation of heritable changes in a long series of lineages that successively forked out from a single common ancestor. That ancestor probably lived as much as four billion years ago, and its tens of millions of living descendants are as different as bacteria, bushes, and bobcats. Darwin's explanation of how this could have happened – a major selling point in his time, though vigorously debated subsequently – involved what he termed "natural selection": a concept that was so intuitively reasonable as to have (as legend has it) caused his close colleague Thomas Huxley to slap his forehead and exclaim, “How stupid not to have thought of that!”

Darwin knew that all living species are variable, and he came to believe that fact to be critically important. What is more, although he had no idea (or, more correctly, an erroneous one) of how biological inheritance works (he accepted the inheritance of acquired characters), he was very conscious of the fact that most physical features are parentally inherited. Darwin also knew that breeders, by carefully selecting which individuals in a population will reproduce, are able to induce very rapid and substantial changes in lineages of domestic animals and plants. So, why not Mother Nature? Darwin reasoned that in any variable population some individuals are inevitably better endowed than others in hereditary traits that enhance their survival and reproduction; and because those better adapted (“fitter”) individuals will survive and reproduce more successfully than the rest, their descendants and their favorable traits will inevitably multiply in the population with the passage of time and the generations, even as inferior adaptations disappear. Repeated over enough generations, this blind natural process of selection of fitter individuals will slowly and inevitably transform each species/lineage, with only time and circumstance limiting the amount of accumulated change possible. Darwin also knew, of course, that lineage splitting, and not just change within each lineage, had to be important in generating the amazing diversity that we see in the living and fossil worlds.

Genetics and the Modern Evolutionary Synthesis

Darwin’s concept of evolutionary change by natural selection depended on the passing down, from parent to offspring, of inherited characteristics; but it had been formulated in the absence of an accurate notion of how heredity worked. That gap began to be filled at the turn of the twentieth century. Back in the 1860s, the Augustinian friar Gregor Mendel had studied heredity in flowering peas he grew in his monastery garden; and although he published his results in a local journal that was read by few (Darwin is rumored not even to have cut the pages in his copy), he is generally given credit for the principles of “Mendelian” inheritance that were separately worked out in three different European biology laboratories in 1900, following the confirmation in 1883 that the hereditary information was carried in the mother's ovum and the father's sperm. Those principles, which launched the modern science of genetics, included the notion that hereditary features are independently passed along under the control of discrete, paired (one from each parent) hereditary units. Those units do not blend in the offspring, but are passed instead from one generation to the next intact and undiluted. A "recessive" element from one parent will not be expressed in the offspring's "phenotype" (physical appearance) if a "dominant" form is received from the other; but it is always there nonetheless, ready to be passed along in turn. It was not long before those hereditary units had been dubbed "genes" (their alternative forms were called "alleles"), and the term "mutation" had been applied to the spontaneous changes in the genes that provide the variation on which evolution acts.

Various other observations were quickly made. For one thing, rather than being dichotomous, most characteristics vary continuously in their expression in populations (think of physical strength or visual acuity, for example). That is because the development of most characters is controlled not by single genes, but by many of them working together. It was also quickly determined that the environment played an important role in the determination of phenotypes, and in addition most genes turned out to play a role in the determination of many different physical characteristics. Putting all this together gave birth to the science of population genetics, which mathematically models the behaviors of genes in populations; and in 1918 the English quantitative geneticist R. A. Fisher published his "infinitesimal model" that sees most phenotypes as the result of a very complex interplay between numerous genes, on the one hand, and the environment, on the other. At around this time it was also realized that, especially in small populations, random factors (known as "drift") could also play a significant role in the fate of newly appearing variants.

During the first quarter of the twentieth century, biologists vigorously debated the relationship of genetic processes to evolutionary change. It was soon recognized that those spontaneous mutations were copying errors that constantly occurred in the genes as they were duplicated in the production of new cells, including the reproductive ones. Most such errors resulted in weakened function, and hence their bearers could be weeded out by selection. Others

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might be neutral with respect to function, and thus might either quietly disappear, or simply hang around, as a matter of chance. But functionally valuable new alleles can provide the new variation on which evolutionary change thrives; and indeed, "mutation pressure" consequently became a favorite driver of evolution, the speed at which genes mutated controlling the rapidity with which evolutionary change could take place. As such considerations were introduced, natural selection became only one of several contenders for agency in evolutionary change. But things shook out quite rapidly, so that by the end of the 1920s Fisher and other mathematical modelers had laid the groundwork for the development of what would become known as the "Modern Evolutionary Synthesis." Following the lead of the Russian-born geneticist Theodosius Dobzhansky, working in the USA, geneticists, systematists (students of diversity in nature), and paleontologists came together in a tacit agreement that evolution was largely propelled by the long-term action of natural selection on lineages of organisms. Change came as the frequencies of old and new alleles in those populations shifted under selection, with the outcome of keeping them in equilibrium with changing environments, or improving their adaptation to stable ones. Evolution was all about gradual adaptation.

This "neo-Darwinian" perspective threw the emphasis back on to slow change within lineages. And it had the presumably unintended effect of making species recognition problematic in the dimension of time. Species had been recognized since the seventeenth century as the basic "natural" unit in the living world; and the ornithologist Ernst Mayr, in addition to being one of the giants of the Synthesis, was also a leading proponent of the "biological" view of species, seeing them as the largest unit in nature within which interbreeding among individuals may freely take place. In this view, the larger taxonomic units ("taxa"), such as the genera into which species are grouped, the families into which genera are grouped, and the orders into which families are assembled, are simply products of the human propensity to classify, while in contrast the limits of species are determined by the reproductive choices or performances of their own members. There are now some 30 different definitions of the species on offer, partly because it turns out that members of very closely related but nonetheless differentiated species may indulge in reproductive activities if given a chance; but the biological definition would still probably be the choice of most working vertebrate systematists – if they were forced to choose.

Mayr was also a leader in working out the biogeographical implications of the fact that species evolve from other species, and he especially espoused the notion that most vertebrate species can differentiate only when they are in isolation. In other words, a subpopulation can develop the genetic incompatibility with its parental population that will make it a different species only when genetic exchange between the two is interrupted. Such incompatibility might be expressed anatomically, behaviorally, or simply in impaired reproductive performance. Just for the record, early in his career Darwin had thought hard about this matter, too. However, while he recognized that various bird lineages in the Galapagos archipelago had differentiated in isolation on their respective islands, he ran into difficulty visualizing how isolation could have been achieved on the continents. Mayr had no such problem, because by his day it was already well established that instability in past climates and environments, plus what we now call tectonic events, had repeatedly interrupted the continuity of habitats worldwide. But Mayr's paleontological colleagues had to face the awkward reality that, in the dimension of time that was their bailiwick, the Synthesis saw species not as discrete units with reproductive boundaries, however blurry, but as steadily modifying lineages in which earlier stages inevitably evolved themselves out of existence as the years passed.

That made life difficult for the paleontologists, whose job it was to make sense of the fossil record. That was because, if they were both to describe an ancient world comparable to today's, and to adhere to the principles of the Synthesis, paleontologists had not only to diagnose distinct species in the fossil record, but also to recognize that those species were inherently undiagnosable, since there were in principle no boundaries between them. Any division of a gradually evolving continuum was necessarily arbitrary, so that not only was the attempt to do so intellectually unsatisfying, but whatever you chose to do would, even in principle, be subject to endless inconclusive argument. In its early and more nuanced versions the Synthesis was open to recognizing complexities such as this. But – almost inevitably, given the human love of reductionist explanation – it gradually "hardened" to become a dogma, at the center of which lay the slow, gradual modification of lineages by natural selection. Species as "real," bounded, entities took a back seat; and even the paleontologists went along with this as, under the reductive and seductive sway of the Synthesis, they ignored the skimpy nature of the emperor's clothing. And, as we see in Chapter 3, it was in its hardened form that the Synthesis was eventually introduced into paleoanthropology, by none other than Ernst Mayr himself.

Punctuated Equilibria

Given the fact that the Synthesis had relegated paleontologists to the essentially clerical task of clearing up the details of Life's history, leaving to others the more interesting pursuit of discovering its great patterns, it is hardly surprising that the first rumblings of discontent came from students of the fossil record. Long before the Synthesis intruded, Darwin's paleontologist colleague Hugh Falconer had already been impressed by how long distinctive mammal and other species lingered in the rocks of the Siwalik Hills in India, over a total period now known to be around four million years (myr). But so heavy lay the hand of the Synthesis that such observations were ignored, and it was not until 1971 that Niles Eldredge, a paleontologist at New York City's American Museum of Natural History (where Ernst Mayr had spent his early career) upset the applecart. In that year Eldredge published a summary of the conclusions he'd reached in his doctoral thesis on Devonian trilobites (bottom-dwelling marine invertebrates) from the US Midwest and upper New York State. And rather than try to fit his fossil data into the rigid structure of the reigning Synthesis, Eldredge allowed himself to discover a very different evolutionary pattern: one that was similar, as he would later find out, to the one Giambattista Brocchi had discerned in Tuscany a century and a half earlier. The picture he saw was overwhelmingly one of stability (stasis): Over a 6-myr span in the Midwest, there was only a single significant event in his group of interest, the abrupt replacement of a particular trilobite species by a close relative. Eldredge saw basically the same thing at sites in New York; but at one quarry there he found both kinds of trilobite together, and concluded that he had stumbled on a place where an event of speciation had actually been in progress roughly 400 myr ago. The most parsimonious scenario was that, for an extended period, the parental trilobite species had been ubiquitous in the Devonian shallow seas that covered much of what was to become the United States; that a rapid speciation event had occurred close to the eastern periphery of its distribution; and that the descendant species had then spread out to replace its progenitor throughout its range. Not at all what the Synthesis would have predicted!

Eldredge then joined forces with his colleague Stephen Jay Gould to generalize this finding, and at a meeting the next year they jointly presented the notion of "Punctuated Equilibria" to replace the "Phyletic Gradualism" of the Synthesis. Evolution, they claimed, rather than being a gradual affair, was more commonly episodic in nature. It largely involved the interruption of longer or shorter periods of stasis by short-term speciation events associated with morphological innovation; and the changes visible in the fossil record were often driven by abrupt climatic and environmental shifts that made perfection of adaptation irrelevant. All of which meant, of course, that many of the famous "breaks" in the fossil record (i.e., the lack of expected intermediates) might encode real information about evolutionary histories, rather than simply reflecting deficiencies of preservation. It also returned species to the status of "real" entities, bounded in time as well as in space. As Brocchi's early-nineteenth-century observations had suggested, species indeed had origins at speciation; finite but often long lifespans during which descendant species might bud off as peripheral populations were isolated and went their own ways; and, eventually, deaths when extinction came. Once more, paleontologists were at liberty to study objective, bounded entities.

This questioning of a comfortable received wisdom provoked a widespread initial outcry and such mirthful characterizations as "evolution by jerks." But soon evolutionary biologists came to terms with punctuated equilibria as a phenomenon to be dealt with, even though many continued to believe that gradual natural selection still had an important place in evolutionary change. In my case, these findings caused me to reconsider everything I had been taught. I realized that thinking in terms of natural selection had taken the focus away from the species itself, transferring it to characteristics of the individual. And yet, what ultimate good is it to be the most excellently adapted example of your species, in whatever feature, if your entire species is being outcompeted into extinction? Or if your survival or reproductive success will be largely a matter of chance, as they very often are? Still, the force of tradition is strong, and paleoanthropologists continue to speak blithely of the "evolution of the foot," or the "evolution of the brain," or the "evolution of the gut," without properly digesting the fact that all these structures are inextricably embedded in whole functioning organisms, and that it is those organisms, not their individual features, that are triaged by nature. In the real world you succeed or fail as a complete being, not as a foot, or a brain, or a digestive system. What is more, each gene has many jobs to do, so that changing any one feature may lead to undesirable alterations in others.

The bottom line is, then, that selection can only fine-tune a particular feature within a species if that feature happens to be absolutely critical for individual survival or reproductive success. It is almost certainly no accident, for example, that the male chimpanzees who must compete constantly for access to females have huge testicles (almost as big as their brains), while the silverback gorilla males that almost effortlessly dominate their harems do not. And success in competition among related taxa may hinge on tiny differences: The astonishingly rapid replacement in the United States of earlier variants of the SARS-CoV-2 virus by the new variant (Lineage B.1.1.7) first identified in the UK seems to have been due to increased transmissibility attributable to a minor modification to its spike protein.

Of course, nature is a very complex place; and it is always possible to find a striking exception to almost any generalization you might care to make about it. Nonetheless, it does seem reasonably fair to say that, especially among intensely social organisms such as the primates, it is often sufficient to be good enough just to get by. The excellence of your individual adaptation(s) may not be of great relevance in a world where social cushioning exists, and where so much also depends on chance. Your expertise as a climber, for example, will hardly help much in a drying environment in which trees are disappearing. Indeed, it occurred to me very early that, while natural selection is a mathematical certainty in a world in which more individuals are born than survive to reproduce (while I was writing this a robin's nest outside my window, containing four voracious chicks, was rudely raided by a crow that randomly murdered them all), its main function is to trim off the extremes of the spectrum of variability within each species, thereby maintaining the "fitness" of the species itself to survive and reproduce, rather than that of the individuals composing it. To caricature for the sake of effect, if as a biped you are born with one leg or three, you are less likely to survive and reproduce successfully than you are if you have the standard two. This function is known as "stabilizing selection," and it is of critical value in keeping entire lineages viable in the face of the genomic tendency to mutate.

Finally, we need to bear in mind that external events occurring entirely randomly with respect to adaptation have probably been the most critical evolutionary drivers of all. It is, for example, almost certainly no accident that our own genus *Homo* evolved, and very rapidly modified, during the Pleistocene ("Ice Ages") epoch. This was a time when major climatic swings routinely occurred even within individual lifetimes. On the species level, such circumstances not only repeatedly created the conditions for speciation via successive population isolations, but also the conditions for competition when those populations were reunited when conditions swung back. And at a higher level, large excursions in climate and habitat were often associated with major biotic turnovers during which entire faunas were replaced. Specifically in the human case, which involved a cultural, large-brained, and particularly pragmatic creature, such changes may sometimes have favored behavioral rather than physical accommodation – which, as we will see, may have had a lot to do with the remarkable speed with which humans evolved over the last two million years.

A Revolution in Systematics

Right around the time when the notion of punctuated equilibria was beginning to force a rethinking of evolutionary process, an analogous revolution was taking place in systematics, the science that deals with the diversity and classification of organisms. Until the middle of the twentieth century, the business of recognizing and classifying units in nature had largely been a matter of expert opinion. Knowledgeable people declared what they thought; and that was that. It was very tough to challenge the opinion of an acknowledged expert because it was his (very occasionally her) word against yours; and, if he or she was famous, you were usually out of luck. But in 1950 a German entomologist called Willi Hennig challenged all this by proposing a testable approach to systematics, one that unfortunately did not have much international impact until his book was translated into English 16 years later as *Phylogenetic Systematics*. But once the cry had been taken up by the American Museum