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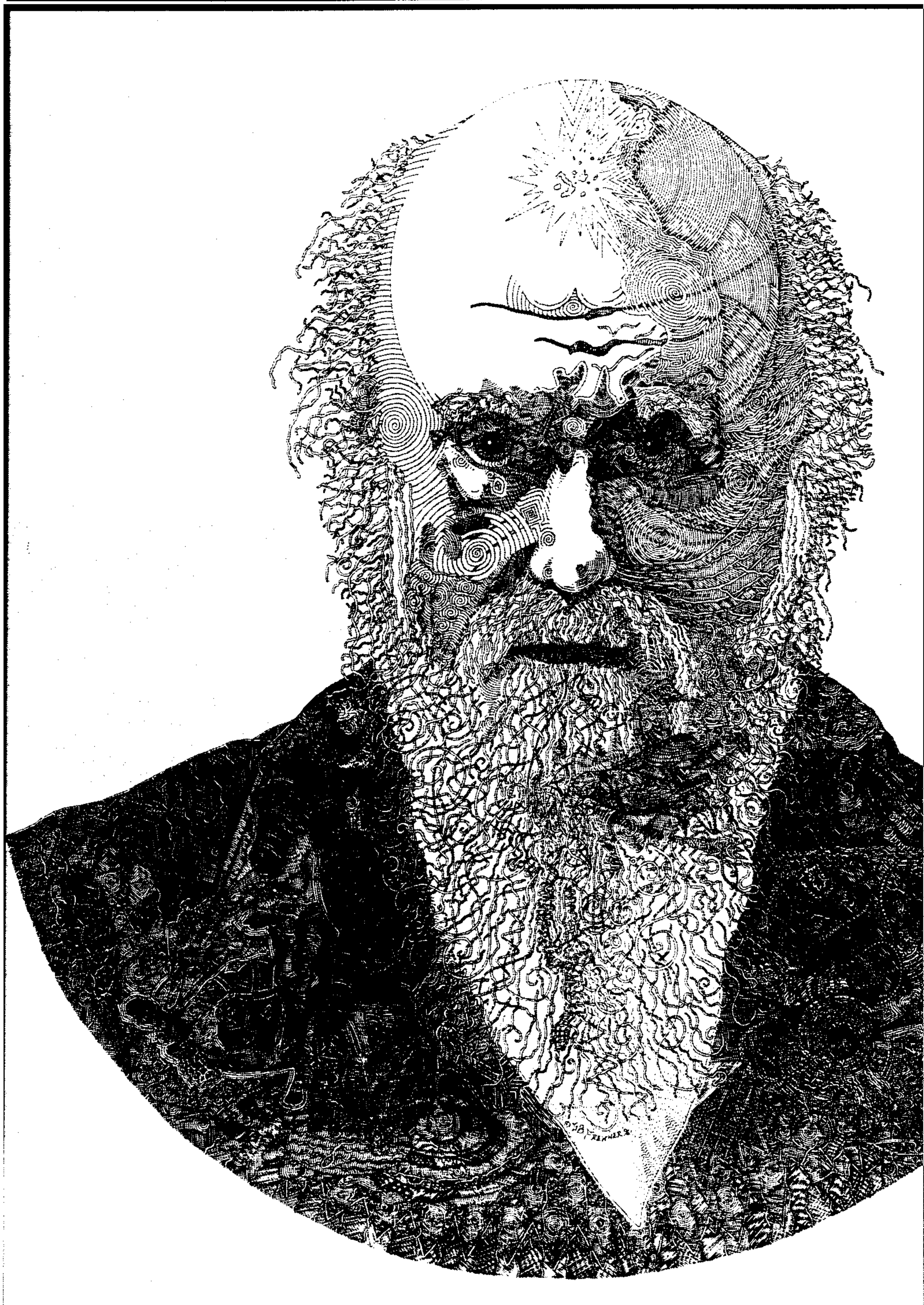

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Darwin Then and Now: Cameo of an Undergraduate Course

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Late in 1995, *Time* published a cover story, "Evolution's Big Bang", that described current work on the explosion of taxa in the course of ten million years of the early Cambrian. Between 543-533 million years ago (MYA; using zircon dating), phyla appeared in sudden profusion. Many were momentary, but the survivors comprise over ninety percent of existing taxa. Multi-cellular micro- and macro-organisms originated then. So did complex ecosystems, complex morphology, the immune system, and the nervous system. For a moment evolution traveled at "supersonic speed", said *Time*. The explosion was unique; nothing quite like it has happened since.

Darwin's contemporaries knew about the challenge that the Cambrian held for gradualistic models of evolutionary change, and Darwin worried how to explain it. More recently the Cambrian stimulated the punctuated equilibrium model of evolution's tempo. "Punc eke" is an oscillation described by nonlinear dynamics. The concluding section of the *Time* essay was devoted to nonlinear approaches to saltations. It is titled "Beyond Darwinism". A leading exponent of chaotic complexity, Stanley Kauffman, said that "these patterns of speciations and extinctions, avalanching across ecosystems and time, are to be found in every chaotic system — human and biological".

The student who showed me the feature article said excitedly "that's what you told us in the Darwinian Revolution course!" Her enthusiasm was catching, and for a moment I congratulated myself on having scooped *Time*, despite the fact that *Time's* science news tends to be on the trailing edge. Still, if such an article could be meaningful to Jenny, it would probably be meaningful to other students; and the graphics aren't bad either. So in deference to the big virtual classroom — the media — I decided to make some color overheads and include the feature in the course materials for "The Darwinian Revolution". We used these materials to illustrate the development of evolutionary thinking and as a way of engaging the students in active learning about the history and complexities of evolutionary theory.

The Setting

"The Darwinian Revolution" is a required course in the History and Philosophy of Science major at Griffith University, an institution which enrolls 21 000 students on six campuses. Staff from the science and humanities faculties collaborate in teaching eight core and elective subjects. Enrollments vary between courses, from 25 to 80, although enrollments are stable in each course.

The Darwinian Revolution enrolls 30-35 students, of whom about a third study science or technology; the remainder are humanities students. I share the teaching duties with Richard Yeo, a science historian and author of *Defining Science: William Whewell, Natural Knowledge, and Public Debate in Early Victorian England*. The prerequisite is completion of one year of university study.

Humanities students do not take university science courses, but many have completed high school biology, and most are keen on natural history documentaries. We boost this background by listing titles of documentaries available in video shops and in the library. For some it is easier just to tape television natural history documentaries, and they do. Lectures are illustrated by video clips and by color overheads. The lecture and assessment pedagogy are humanities-based; the controlling discipline is intellectual and social history.

We identify natural history/zoology as the field covered by the course. The identification provides continuity across the two centuries of scientific growth and links competing natural history theories and interpretations. It invites students to plug in their background knowledge of wildlife, conservation, agriculture, or animal husbandry. Finally, we encourage the use of personal narratives, from Darwin's *Autobiography* to Jane Goodall's *In the Shadow of Man*, as learning prompters in the hope that a good yarn from the field may make zoology more attractive. Creation "science" gets no mention because students don't bring it up. They also don't press us to discuss special creation, but we do anyway because it's integral to Darwin's story.

We divide natural history into Linnean and Darwinian types. Linnean natural history is described as static and taxonomic; Darwinian as dynamic and explanatory. Some in-between things, such as Robert Chambers's speculative *Vestiges of Creation* and Linnaeus's own variation-on-archetype scheme, show that the classification is porous. Nevertheless, dichotomizing helps students appreciate the "revolutionary" conceptual transformation incident to any evolutionary natural history. Lamarck, Chambers, Spencer and Darwin are the four evolutionists considered, but extended attention is reserved for Darwin.

I say "appreciate" deliberately. This fuzzy learning category is our response to the lack of prerequisites and to the variation in student knowledge. We "fuzzify" by not requiring mastery of specific bodies of fact — for example, Linnean binomial classification or Cuvier's theory of archetypes. Instead, assessment by essay permits students to select a topic that matches their interests. There fuzziness stops. The essay questions require close attention to specific factual knowledge and relations among concepts, organized by historical inquiry.

A Dynamic Natural History

Since the transition from static to dynamic natural history is accessible through Darwin's intellectual itinerary, we visit his Cambridge years. Paley's *Natural Theology* and Lyell's *Principles of Geology* are highlighted as formative influences prior to the Beagle's voyage. The *Natural Theology* is a tour of natural history, organized by the apologetic intention to demonstrate the perfection of the Creator from the perfection of his creatures. This "God-in-the-details" was much to the youthful Darwin's taste, as was Paley's moral-aesthetic vision of nature as edifying object of admiration. We dwell on the resonances between Paleyan "perfection" and the mature Darwin's "adaptation". However, the mentor of the Beagle's voyage was Lyell, not Paley. Darwin met him shortly before his departure. Volume I of *Principles*, a state of the art geology and paleontology, had just been published.

Lyell's vision was decidedly Linnean. He rejected catastrophes as significant causal factors in earth history. He concluded that the mechanisms of subsidence and elevation observed in his own day sufficed to explain mountain-building as well as the disappearance of land masses in the past. Lyell was also a sharp critic of Lamarckism, which he equated with evolution. (Lyell wasn't brought over to evolution until shortly before publication of *Origin*).

These teachings sunk deep roots that shaped the mature Darwin. He never departed from gradualist geology, with its corollary that nature does not make leaps. (At bottom this is the principle of continuity, which Leibniz propounded in the idiom of rationalist metaphysics). We emphasize that Darwin applied Lyell's gradualism to species evolution when he finally made his own leap to dynamic natural history. Species are in motion, but very slow motion, like mountain-building, occurring by "infinitesimally small" cumulative steps. Gradualism involves the least possible departure from Linnean stasis, yet it changes the central task of natural history from taxonomy to the construction of a grand scheme of metamorphosis.

In the old scheme, natural history does not explain how each species came to be what it is. It is enough to demonstrate that it could not have come to be by chance. Such was the materialist view that Paley sought to confute by describing the complex functional fit of animals and their parts. The description discloses creatures as sublime artifacts. By contemplating their "perfection" (beauty), our finite minds come to know the divine mind. Natural selection, like Paley's God, is also a unitary causal agency (Darwin once styled it "my deity") but it works in a vast multitude of ways. The task of the naturalist is to discover how it works for each species; and this entails phylogenetic reconstruction, or in Darwin's language, tracing "descent with modification". So, the Darwinian naturalist has a new task unknown to the Linnean: explaining the evolution of each species and taxon.

To prevent students' sleep-walking past this earthquake, we rattle some bones. How many species are there anyway? How many taxa? In 1859, Joseph Agassiz published his count of 129 370 animal species. By 1910, over 522 000 animal species had been named. This is an immense biodiversity. And how many phylogenetic trees did Darwin construct? None; though he worked hard to compile the pedigrees of all domesticates back to the original stock, and Thomas Huxley produced his trace of the evolution of the horse. Our other bone-rattling is co-evolution, illustrated by overheads of color- and form-mimicry, plus descriptions of the amazing life cycles of a few common parasites. That usually boggles their minds. Later in the course we follow up this blunt instrument assault with refined samples from the debate on natural selection (Huxley, Agassiz, Richard Owen, St George Mivart).

In elucidating Darwin's key discovery, we safeguard against two distorting influences. The first is the shadow that neodarwinian thinking casts on the historical "Eureka." Students who know some genetics tend to superimpose recombination and mutation on the insight, which is also common in the secondary literature. We deal with the problem by identifying the undertow in Darwin's thought that pulls toward the modern synthesis. It is his study of artificial selection and his attempt to formulate a theory of inheritance. It is easily said that implicitly he "knew" about recombination and mutation, but lacked the language. We argue instead that he lacked the concepts as well. At the time of the "Eureka" (1838), Darwin had no theory of inheritance; the pangenesis theory lay decades ahead. Even had Darwin thought out pangenesis by 1838, it would have been no help, since it is about as contrary to Mendelian "factors" as it is possible to be. Thus, although Darwin's insight logically requires a correct theory of inheritance, want of one didn't stop him having the insight.

To stouten this fence, we distribute a dozen quotations in which Darwin succinctly describes natural selection. One of the clearest occurs in "Variation of animals and plants under domestication". It begins by recalling a reverie on the Galapagos Archipelago, when Darwin "fancied myself brought near to the very act of creation." Galapagos fauna were variants of mainland species, but it was "inexplicable" how the "modification" occurred. The riddle would have "remained forever unsolved" had he not studied domestication, which gave him "a just idea of the power of Selection. As soon as I had fully realized this idea, I saw, on reading Malthus's *Essay on Population*, that Natural Selection was the inevitable result of the rapid increase of all organic beings; for I was prepared to appreciate the struggle for existence by having long studied the habits of animals" (Porter and Graham 1993, p 264). The thought seems to be this: domestication is near to speciation, but what in nature corresponds to the breeder? Superfecundity and the resulting inevitable struggle for existence form this ubiquitous and inescapable force.

Darwin likened it to "ten thousand sharp wedges packed close together and driven inwards by incessant blows, sometimes one wedge being struck and then another with greater force (Darwin 1968, p 119). To elucidate selection "force", students are challenged to stroll, in imagination, through a botanical garden and find ten wedges pounding away. One class burst into laughter when a student answered triumphantly: "ten gardeners". My alternative is nestling competition among ospreys because I have a stunning video showing how the stronger nestling, with the concurrence of parents, kills its weaker sib in competition for food. Here is nature "red in tooth and claw" sure enough.

Historical and Social Contexts

The next distorting influence arises from stress lines generated by the Internalist versus Externalist interpretation of the insight. Did Darwin know his own mind when he instanced animal "habits" to confirm ubiquitous competition? Or did he bring the capitalist economic vision of social relations to bear on the animal kingdom? And if the latter, is Darwin's theory at bottom ideology? Such questions are warranted in the course pedagogy, which considers Darwin as preserver and innovator in a specific cultural milieu. The milieu includes political economy.

Malthus's *Essay on Population* polemicized against utopian justice as violating the no-free-lunch premise of political economy. His novel knock-out punch was that the nasty law of population growth made resource competition inevitable. To read Malthus is to be exposed to the grim world of political economy, so it's implausible to argue that Darwin didn't have contemporary society in mind in the moment of his creative leap. But in preserving Malthus's insight, Darwin extended it to make differential mortality the force of evolutionary change — something that didn't occur to Malthus. Darwin never wrote a political tract but he did cultivate natural history for the next forty years. Therefore, his theory belongs to natural history, not political advocacy.

This might resolve the matter were it not possible to be an evolutionist without being a naturalist as well. Yet Chambers and Spencer were evolutionists without natural history, and so were the vast majority who accepted evolution in the last century. While Darwin labored to husband his evidence, non-scientists accepted evolution simply as a yarn. Chambers' speculative *Vestiges of Creation* drew scorn from naturalists, but Spencer's prestige was enormous among the learned and among general readers. His evolutionary vision proclaimed the principles of political economy — the "great god of competition" as Daniel Simberloff calls it (Simberloff 1988). Indeed, Spencer's trumpeting of capitalist progress reached its zenith even as natural selection was "eclipsed", as Peter Bowler puts it, by Mendelian genetics and by reconsideration of the natural history evidence (Bowler 1983).

Clearly many wanted to believe in evolution, and the will to believe was as marked among socialists as among liberals. But why? There is no want of answers. We suggest to students that a conceptual tidal wave of this magnitude locks in quite heterogeneous motives, for example, popular enthusiasm for technology, justification for European world dominance, justification for social reform and so on. If there is a common thread, it is probably that evolution provided ostensible scientific validation for the belief in the inevitability of social progress (thus reversing Malthus!). Meanwhile among naturalists, evolutionary progressivism was only a hypothesis and a contentious one at that. Darwin didn't endorse it.

This outcome, circa 1900, completes our elucidation of the difference between science and ideology. Social myth-makers co-opted the ensigns of science because together with nationalism it had emerged as the credible authority rivaling religion. While scientists were not immune to mythologizing — we instance Karl Pearson and Ernst Haeckel as makers of socially opportune evolutionary myths — still TH Morgan's development of chromosome theory in his Columbia University laboratory occupied a completely different cultural milieu — experimental science.

In a course constructed to exclude retrofitting history to today's concerns, how does trendy nonlinear dynamics get in the door? It gets in because we relax the ban on retrofits. It isn't good pedagogy to imply that the Darwinian revolution stopped at 1900. We have an extensive menu of update items: Lynn Margulis on symbiosis, the discovery of the ecosystem, the structure of eusocial cooperation, the emergence of cladism and molecular-based taxonomy; current debates on hominid evolution; jumping genes, somatic hypermutation, the new catastrophism, the new evolutionary timetable, self-organization theory. A different mix of updates is chosen on each passage of the course. The updates are presented as compare-and-contrast exercises that sometimes highlight continuity with Darwin, sometimes discontinuity.

An item that illustrates both the continuity and discontinuity of current evolutionary research is the discovery of somatic selection (sometimes called "evolution in a day") by the Australian scientist Ted Steele (Steele, Gorczynski, and Pollard 1984). Molecular biology is discontinuous with Darwin's natural history, which did not incorporate the cellular biology of his time. Nevertheless, Steele considers himself emphatically a Darwinian selectionist, even though somatic hypermutation is a directional (non-random) mutational process among variable region genes that he and his collaborators contend interprets Lamarckian acquisition of characters, such as acquired immune responses (Steele, Gorczynski, and Pollard 1984).

How can this be? Everyone knows that Lamarck and Darwin are antithetical! Ah, but they aren't! In pangenesis, Darwin acknowledged Lamarckian inheritance as a crucial supplement to natural selection. Absolute separation of the two modes of inheritance is the doctrine of neodarwinism. Steele and his collaborators make much of this historical quirk in contesting neodarwinian "dogmatism". They turn the tables of the "heresy" reproach by claiming to be the true paleodarwinians.

Somatic hypermutation comes with a misconduct option: two priority disputes. The story features David-sized Australian scientists battling in the columns of *Nature* and *Science* with titans at Harvard and Rockefeller Universities. Steele and collaborators were really steamed up. For nearly a decade their discovery was derided as a theoretical impossibility. Then, as its experimental reality came to be recognized (perhaps together with its Nobel potential), those titans rushed into print with claims of a "new" discovery. Steele countered with a plagiarism charge. *Nature* editor John Maddox eventually resolved the dispute by brokering a joint letter in which Steele withdrew the plagiarism charge while the Harvard scientist, John Cairns, acknowledged Steele's prior discovery (Steele and Cairns 1989; Steele 1989).

In the second priority dispute, a Rockefeller University scientist wrote in *Science* a history of the discovery that omitted any reference to Steele and colleagues (Thaler 1994), even though they published the first and the most research in this field. Those who credit that history will not know that there was a dispute about the authenticity of the process and hence will not know that the "Central Dogma" once ruled out somatic hypermutation (Temin 1989). Thus is revolutionary scientific change domesticated to normal science.

The priority dispute is a window on how heresies are sometimes normalized as consensus science. The pattern was ten years of resistance, then sudden expropriation of the contraband evidence under the auspices of "Big Science". A similar thing has occurred with the normalization of catastrophism. Recognition of continental drift and asteroid impacts, together with massive destruction and climatic change that they visited and five mass extinctions apparently correlated with impacts, are conventional wisdom today. Volcanoes are also known to be more destructive than was previously imagined. The flood basalt variety ooze lava for months, centuries, or millennia, creating large land masses (the Daccan Traps) and changing the mix of atmospheric gases. Some scientists promote the concept that flood basalt eruptions correlate with one or more mass extinction.

The normalization of the new catastrophism is very recent. The continental drift controversy, and later the Cretaceous-Tertiary (K-T) mass extinctions controversy, are among the most acrimonious in recent science history (LeGrande 1988). According to David Raup, who survived at the epicenter of the K-T row, it wasn't the scientific issues that got people mad. It was the Old Guard's refusal to give up uniformitarianism. He writes that "even an idle mention of the possibility that something in the history of the earth could be called catastrophic can produce showers of denial and abuse from many geologists" (1986, p 29). He reports a French colleague as saying that French scientists were reluctant to propose new theories in paleontology and evolutionary biology because "they have never gotten over the humiliation of the defeat of Cuvier's catastrophism" (Raup 1986, p 29). It is difficult to fathom that great scientists can cast so long a shadow — unless we remember that uniformitarians were defending a principle that Darwin absorbed from a geology text published 170 years ago!

Revising The Revolution

The course also addresses the retrofit that "synthesizes" Darwin with population genetics and its successor, self-organization theory. The population genetics generated by RA Fisher and Sewall Wright is an elaborate structure that supports an enormous range of "selections" that have slight foundation in Darwin's theory — balancing selection, selectively neutral mutations, random walk, r/K selection, kin selection, linkage disequilibria, and so on. These processes are inaccessible to those lacking mathematical aptitude, including Darwin himself.

Darwin's blending theory of inheritance could scarcely have been formulated by a mathematician because its basic idea poses an insuperable quantitative difficulty. If parental traits blend in the offspring, parental variation is halved in the first generation, quartered in the second, and so on until the favorable variation is lost. Blending, if it occurred, would quickly reduce all diversity in a population to a monotonic set of traits; there would be nothing for selection to work upon. The muddle compounds when we notice that the theory doesn't account for the persistence of recessive traits that Darwin's own experiments with snapdragons confirmed (Oldroyd 1980, p 143). To extricate himself from this difficulty, Darwin postulated inheritance of acquired characters as the source of new variation. In this scenario, environmental variation induces somatic or behavioral changes, which are assimilated to the germ line.

I suggest to students that pangenesis is a typical muddle due to a qualitative approach to a phenomenon whose order is mathematical. Mendel, whose pea experiments were very similar to Darwin's snapdragon experiments, guessed at the unit character of inheritance and formulated the statistical rules of trait segregation. Although Mendel had read the *Origin of Species*, he did not speculate on how natural selection might operate on his laws of inheritance to generate new species. The probable reason, as we may guess from the criticisms of Darwinism by TH Morgan, August Weissman, Fleeming Jenkin and others, is that new species will not arise from recombination (Bowler 1983). Species genomes are extremely conservative. The velvet worm *(Peripatus onychophoran)*, which has remained unchanged for 500 million years, seems to be the champion survivor.

The synthetic theory rescued Darwinism from eclipse by redefining evolution as any change in the frequency of alleles within a gene pool from one generation to the next. Darwin's "infinitesimally small" changes are now precisely defined. His error regarding fitness is corrected. It is not the slight advantage possessed by a few individuals that imparts competitive edge, but the mean value of an adaptation in a population. This "microevolution" is basically a gene pool in equilibrium, and it is not what Darwin imagined to be happening — constant accumulation for change that is driven toward speciation by a continuously applied selection pressure.

At the celebration of the centennial of the *Origin of Species*, there was, according to Ernst Mayr, "complete unanimity" that neodarwinism was "internally consistent and firmly established" (Mayr 1963, p 8). The picture is dramatically changed today. In 1972, Stephen Jay Gould and Niles Eldredge published their classic paper, "Punctuated equilibria: An alternative to phyletic gradualism" which gave direction to a thorough reassessment of paleontology that continues today (Eldredge and Gould 1972). During the same period, the Mendelian theory assumed by Fisher has been revised so far that it continues to be called Mendelian only by courtesy (Milkman 1982; Ho and Saunders 1984).

Mendelian genes are featureless except for the trait they determine. They recombine and occasionally mutate. Today's genes carry out a prodigious number of complex developmental and repair operations. They can split, transpose, amplify, excise, invert, back transcribe, and even hang themselves at the right time (the apoptosis gene). Genes acting on genes and gene products amount to endogenously controlled power of organisms to alter themselves, or to maintain a steady state. In a review of the implications of the molecular evidence for the interpretation for species stability and rates of evolutionary change, Thomas Schopf argued that the ensemble of actual and potential emergent properties of a specific genome organization, its latitude for self-organization, may be a nonselectionist source of evolutionary change (Schopf 1981; see also Thoday 1975).

But the adoption of these concepts were blocked until there was an alternative to Fisher's linear equations. This new non-Darwinian revolution is now running at full steam. I describe the revolution as consisting in the development of a genuine theory of emergence, in contrast to the "building blocks" model of development by serial accumulation of change. This concept is illustrated by videos of computer-generated fractals, cellular automata, and the like. We also refer students to a PBS documentary on the application of self-organizing theory to evolution. So the course concludes on a bright note. The great adventure in understanding the immense diversity and beauty of life has been revised and relaunched into an exciting future.

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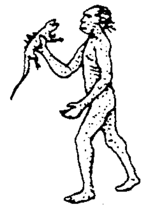

Contemplating human origins in North Carolina (see story pages 5-6). Originally published in the Raleigh (NC) *News and Observer*, April 4 1997. Reprinted with permission.