

A Question of Individuality: Charles Darwin, George Gaylord Simpson and Transitional Fossils

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Throughout his long career, Charles Darwin tended to think of himself primarily as a geologist. He had, after all, devised a theory of mountain uplift—as well as its inverse, the formation of coral atolls, while on the *Beagle*. He had also described and analyzed the geology of South America. And, to my mind, what also made Darwin a geologist is that he used South American paleontology, beginning with his early experiences at Punta Alta and Monte Hermoso in Bahia Blanca (Argentina) as early as 1832, to begin exploring the idea of transmutation (see Eldredge 2009a; Brinkman, 2009, for extensive discussion). Paleontology, of course, is a perfect example of a hybrid field—variously called “biogeology,” or nowadays, “paleobiology.” To find a fossil, and to understand the biology—especially the evolution and ecology—of extinct species, you need to know your geology.

Historians have tended to overlook or even to consciously minimize Darwin's explorations of South American paleontology as a (I would say “the”) crucial early component of his transmutational thinking. Though Darwin had said, in the opening lines of his *Origin of Species* (Darwin 1859), that it was the “geological relationships of the present to the past inhabitants” of South America that in part had thrown “some light on the

origin of species,” readers remained for the most part skeptical until relatively recently. After all, Darwin hardly mentions these fossils in the *Origin*, writing disparagingly of the fossil record as too incomplete to reveal much about the nature of the evolutionary process except in the broadest possible terms.

In my view, the reason scholars have tended to miss the significance of paleontology in the development of Darwin's thinking while on the *Beagle* is that their vision of Darwin's ideas of evolution has been based largely on the theory he published in 1859: a theory that stresses the adaptive modification of anatomical features through natural selection. Though most serious Darwin students are well aware that he did not come to the idea of natural selection until the late 1830s—some two years after he had returned home to England from the *Beagle* voyage—they still, I think, tend to assume that any sign of transmutational thinking (on Darwin's or anyone else's part) would primarily have to take the form of thoughts on the adaptive modification of the features of organisms.

This equation of transmutation with the transformation of anatomical features is also rooted in earlier, pre-Darwinian thinking. In particular, it is the very essence of Lamarck's theory of transmutation—the best known and most fully articulated pre-Darwinian set of ideas on what we now call “evolution.” Lamarck stressed the continuity of all species: if our knowledge of the living world (and by extension, the fossil record of extinct species) were totally complete, the discontinuities between species would disappear, as species would appear to gradually meld into one another in time and in space. That species appear discrete as they occur around the globe, and as fossils, is an artifact of our incomplete knowledge—or so Lamarck's thinking went.

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On the *Beagle*, Darwin was asking a very different question: Are there secondary (natural) causes underlying the births of species—or are species, as was conventionally assumed in his day, strictly the products of direct creation by God? He was invoking what historian Giuliano Pancaldi (1983; see also Rudwick 2008) has aptly called “Brocchi’s analogy”: the Italian geologist Giovanni Battista Brocchi had suggested (Brocchi 1814) that species have births and deaths just as do individuals. Darwin was asking what patterns of species distributions in space and time might look like if species are born—of other, “congeneric” species—through natural causes, rather than solely through direct Divine creation. Darwin was looking for appearances and disappearances of species, *not* striking adaptations—which is what most biologists (with historians and philosophers closely following suit) think of when they think of Darwin, or even of evolution in general (see also Eldredge 2009b).

The strongest signal of Darwin’s active testing of transmutational ideas while in South America (beginning in the Fall of 1832—nearly three full years before he reached the Galapagos in August 1835) is his focus on the replacement of discrete, “closely allied,” “congeneric” species—as seen especially clearly in his zoology (Keynes 2000) and geology notes (still largely unpublished—but available online at www.darwin-online.org.uk/). Some instances involved extinct fossil species replaced by living species (his best example being the extinct cavy at Bahia Blanca replaced, he thought, by the mara—the living Patagonian cavy; Eldredge 2009a; Brinkman 2009). Others involved the replacement of congeneric species living allopatrically in different parts of South America; Darwin’s best example of the latter pattern was the two extant species of rheas (Eldredge 2009a). In all instances of replacement, Darwin’s focus was steadily on endemic taxa: he was interested in native South American groups of birds and mammals, simply to be sure that the patterns of replacement—of births and deaths of species, as he put it in his essay *February 1835* (Darwin 1835)—reflected real events occurring in South America. This way, he avoided the possibility that extinct species would be replaced by species migrating in from faraway places.

As the trip wore on, Darwin began to insist that there was no intergradation between the closely related species he was comparing and seeing as replacements of one another. Rather, he saw species as discrete individuals—Brocchi’s analogy coming to the fore. Perhaps the earliest example came in his zoological notes on the Falkland Islands fox, written during his second visit there in April 1834 (Keynes 2000, p. 209–210). Darwin says the Falkland fox is restricted to the Falklands—“indisputable proof of its individuality as a species.—It is very curious, thus having a quadruped peculiar to so small a tract of country.” He

appends a note saying that Lowe (a whaling captain) states that “all from this island [West Falkland Island] are smaller & of this shade of colour.” In his later notes, Darwin puts it this way: [Mr. Lowe]...“asserts that this difference between the Foxes of the two Is^{ds} is invariable & constant” (Darwin’s *Animal Notes*—<http://darwin-online.org.uk/content/frameset?itemID=CUL-DAR29.1.A1-A49&viewtype=text&pageseq=1>; 1836), inverted to read “constant/asserted difference” in the famous passage in the *Ornithological Notes* (Barlow 1963) also written near trip’s end—the one passage, nearly all agree, which is overtly transmutational in Darwin’s notes written while still on board the *Beagle* (Kohn et al. 2005; Eldredge 2009a).

And so too with the mockingbirds on the Galapagos—of which Darwin says in his contemporaneous notes “each variety is constant in its own island” (Keynes 2000, p. 298). The mockingbirds, closely allied with mainland South American species, are nonetheless also *consistently* different from island to island in the Galapagos. No matter how finely the distinctions are drawn, the species (or “varieties”) that replace one another in time, space, and even on nearby islands in an archipelago, show “constant” differences, one from another. They are individuals. They have births and deaths.

In his *Red Notebook* (see Eldredge 2009a; Herbert 1987), where Darwin is overtly and fully a transmutationist, Darwin revisits the rheas, claiming that they, too, do not intergrade into one another (he merely hints at this in his notes on the *Beagle*). His theory here is saltational—one species abruptly gives rise—“birth”—to a descendant species, the two living side by side, much as a human mother usually lives alongside the children to which she has given birth.

Though this is indeed Darwin’s first transmutational theory, it is very different from Lamarck’s notions of smooth intergradation between species. Lamarck predicted a “smear” of variation if one examined nature closely enough. In the end, as far as Lamarck was concerned, species are not discrete individuals. It is very much as if Darwin were testing Lamarck—and rejecting his ideas—at the very same time he was developing his own first transmutational notions based on Brocchi’s analogy—and the underlying ethos of contemporary British science: that secondary (natural) causal explanations should be sought for natural phenomena—no matter to what extent God may be involved as the primary (ultimate) cause.

Think of it this way: the creationist position was that God created species as discrete entities. Darwin was exploring the possibility that secondary causes underlay the discrete creation—now rendered as “births”—of species. On the *Beagle*, and through his writing of the explicitly transmutational passages of the *Red Notebook* (probably in March, 1837) after he had been home for

nearly a half year, Darwin never wavered from seeing species—and even their subdivisions, “varieties”—as discrete individuals, and as far as “transitional” fossils were concerned, Darwin’s early thoughts on the matter saw similar, yet always discrete, congeneric species replacing one another—as in the example of the extinct cavy that he thought had given rise to the modern Patagonian cavy.

Historians are not the only ones to misconstrue or ignore the nature and significance of Darwin’s focus on the replacement of closely related species in space and time while he was in South America. The renowned paleontologist George Gaylord Simpson—who made more important contributions to evolutionary thinking than any other mid-20th century paleontologist—traveled to Patagonia in 1930 (when Simpson was 28; Darwin was 23 when he first arrived in Patagonia; for that matter, I was 65). Simpson’s focus was on early Tertiary mammal fossils—trying to come to grips with the origin of the unique, endemic South American fauna, but at the same time depriving himself of the advantage that Darwin had in comparing much younger fossils with still-living species.

Simpson’s first book, *Attending Marvels* (Simpson 1934), is a popular account of his adventures (fossil collecting and otherwise) in Patagonia. Astonishingly, Simpson makes little or no mention of Darwin’s visit nearly 100 years earlier. But Darwin’s ghost is there, not so much with the fossils, but with what Simpson made of the living species. A particularly instructive example comes in a passage Simpson wrote on the martineta—one of the larger species of tinamous, a family of birds also endemic to South America. Martinetas, unlike rheas, can fly. But Simpson foresees an evolutionary future that will one day render the martinetas flightless—as the rheas already are. Conversely, of course, Simpson is describing his imagined version of the evolution of flightlessness in rheas. Simpson (1934, p. 207) writes that the “martineta is a curious bird that can fly but does not like to. It normally stays on the ground all the time and runs when startled. Only in extremity will it fly, and then low, heavily, and only for about a hundred yards.”

He then compares martinetas with rheas—and looks into the evolutionary tea leaves:

The most peculiar thing about the martineta, however, seems to me to be its resemblance to the ostriches [i.e. rheas]. In size and build it is very different, yet the points of similarity are numerous and important. The feet, for instance, are exactly like ostrich feet (the three-toed, rhea kind, of course) in miniature and the tracks are like those of the charitas [juvenile rheas] although still smaller. The preference for running is also a point of similarity, and seems graphically to illustrate the first stage in the development of a

flightless bird. Only a little more emphasis on this habit, and the martinetas would cease to fly altogether. Then their wings would quickly degenerate and the mass of breast muscles disappear, and within a few generations the possibility of flying again would be lost. And once they were flightless, there would almost surely be a steady increase in size.

I predict that the martinetas of a few hundred thousand years from now, or a million or two, if they survive that long, will be ostrich-like in every way. Or, put it another way, it seems highly probable that the ancestors of the Patagonian ostrich in the remote past were very martineta-like. Quite possibly the ostrich and the martineta are actually relatives, the ostrich merely being a little more advanced in its evolution.” (Simpson 1934, p. 208).

Simpson goes on to speculate on the adaptive reason for flightlessness—at least in Patagonian birds: the strong winds so prevalent there—useful to soaring eagles, but a hazard for birds that make their living on the ground who still do a bit of flying.

I have had a shortened version of this quotation hanging on my office wall at the American Museum of Natural History for over 35 years. It is the very quintessence of Darwinian gradualism—the predominant image Darwin left us with his *On the Origin of Species*—where evolution is in largest measure a matter of the slow steady linear—gradual—adaptive modification of the features of organisms. In Simpson’s passage, there is even a sense of the inevitability of this change given the passage of time, the survival of the species involved, and the persistence of the environmental or other signal to which natural selection is reacting given the existing genetically based anatomical features and the basic ecology of the organisms in question. Simpson’s passage on martineta and rhea evolution, past and future, is indeed the very essence of what Steve Gould and I much later came to call “phyletic gradualism” (Eldredge and Gould 1972).

Though he does not say so here, this was the image that Simpson had of the evolutionary process generally—including the evolution of his fossil mammals. Simpson had a late-Darwinian picture of gradual, phyletic evolution in mind when he wrote those words—not the births and deaths of discrete species that Darwin was thinking about when he collected his Argentinian fossils. Small wonder, then, that Simpson once proclaimed that “Darwin’s collections of fossil mammals could not and did not lead directly to evolutionary conclusions” (Simpson 1984, p. 36—quoted in Brinkman, 2009)—“with the possible exception of the tucutucu-like rodent” which alone among Darwin’s mammalian fossils struck Simpson potentially “as ancestral, in an evolutionary sense, to any living species.” (After returning home in 1836, Darwin learned from Richard

Owen that the fossil cavy was actually a “tucutucu”). Simpson, as astute an analyst of the written word I have ever encountered in the evolutionary literature, also grasped the significance of Darwin’s focus on endemic species, scoring “a point in favor of evolution” when he discussed the fossil glyptodonts and the living armadillos—as well as the sloths—all native to the Americas (see above, and Eldredge 2009a for more on the significance of endemism to Darwin’s “experiments” with transmutation while on the *Beagle*). But by and large, Simpson (along with nearly everyone else until recently) dismisses Darwin’s *Beagle* experiences with fossil mammals as critical to the development of Darwin’s evolutionary ideas.

But then, sometime during World War II, if not before, Simpson had something of an epiphany regarding the relative paucity of examples of transitional fossils in the geological record. Simpson wrote a brilliant, idiosyncratic book he entitled simply *Tempo and Mode in Evolution* (Simpson 1944). In his introduction, Simpson says that “... experimental biology in general and genetics in particular have the grave defect that they cannot reproduce the vast and complex horizontal extent of the natural environment and, particularly, the immense span of time in which population changes really occur. They may reveal what happens to a hundred rats in the course of ten years under fixed and simple conditions, but not what happened to a billion rats in the course of ten million years under the fluctuating conditions of earth history.”

In his text, Simpson specifies what he calls the “determinants” of evolution: variables such as rate and “character” of mutations, population size, etc.—all the familiar components of population genetics. His point is to establish that while population genetics has a handle on the basic factors of the evolutionary process, nonetheless, novel theory is required to specify just how these genetic determinants, together with natural selection and Sewall Wright’s concept of genetic drift (see Eldredge 2008b) can best explain evolutionary patterns in true “evolutionary time” only seen in the fossil record.

Simpson provides such novel theory. At the heart of the matter lies the common pattern of the relatively abrupt appearance of higher taxa—such as turtles, bats, armadillos, rabbits, and whales (Simpson 1944, p. 126). Simpson sticks by his conventional Darwinian guns, affirming his conviction that species and genera evolve gradually through time—and that the reason why good examples of such gradually evolving lineages are hard to find is to be chalked up to vagaries of the fossilization process. But the amount of evolution required to transform, say, a terrestrial mammal into a whale, Simpson reasoned, was too great to happen in the slow, steady pace that Darwin taught us to expect for the evolutionary process. Otherwise we would find transitional fossils galore.

Simpson concluded that the typical absence of transitional fossils between major groups reflected true evolutionary “signal” in addition to the “noise” of the missing data of a poor fossil record. New groups must evolve relatively quickly, in restricted areas in the world, and often in environments not typical of the habitats of either the ancestors or the fully-fledged, adaptively modified descendants. Think of it: terrestrial artiodactyls have a rich fossil record from the basins in which they lived; likewise, whales have a good fossil record in marine sediments. But perhaps the species transitional between terrestrial artiodactyls and fully aquatic whales lived along the strand line, sometimes in, and sometimes out of, the water. Beach deposits are not unknown in the geological record—but they are far less common than both fresh water basinal and marine deposits. Those transitional species must have existed (*Archaeopteryx* establishes that much insofar as bird evolution is concerned), but the sheer rapidity of the evolutionary transition in marginal environments virtually ensures that good sequences of transitional fossils will remain hard to come by, or so Simpson reasoned.

Simpson would have been delighted to see the many examples that have been discovered since his day that are highlighted in this current issue: he knew they must have existed. But his suspicion that transitions typically involve rates of above-average evolutionary change is by no means automatically invalidated simply because the hard work of paleontologists has paid off with such rich dividends, with so many well-documented sequences of transitional fossils now on the table—and in this issue.

Simpson devised his own special blend of “evolutionary determinants” to account for the rapid evolution underlying the abrupt appearances of new, higher taxa. He called it “Quantum Evolution”—borrowing the term “quantum” from physics. As he later explained, the term “quantum” was meant to imply, not so much (or only) rapid rates of evolution, but rather the “all or nothing” change of state, from ancestral taxa to highly modified descendant, that Simpson thought the paleontological patterns implied.

Simpson constructed his theory of quantum evolution around geneticist Sewall Wright’s (1932) “adaptive landscape” imagery (see Eldredge 2008b, for a discussion of adaptive landscapes and their use in evolutionary theory; Simpson 1944, sometimes shifted to his own terminology, talking about interzonal shifts on an “adaptive grid,” but the essence of the imagery is the same as Wright’s). In brief, imagining genetic variation displayed on a topographic map, Wright depicted the more “harmonious” gene combinations (i.e., better adapted organisms within a population) as residing at or near the “peaks,” and less well-adapted organisms to occupy positions on the slopes—or even in the valleys, between peaks. The problem of evolution, as Wright saw it, was for a species to maximize the number of

its individuals occupying the peaks of adaptive fitness. Wright and others (e.g., Dobzhansky 1937) soon extended the metaphor to talk about entire species (and even higher taxa) occupying adaptive peaks, separated from related taxa by inadaptable valleys.

Seizing this approach, Simpson saw the origin of new higher taxa as a matter of rapid, all-or-nothing movement from one major adaptive peak to another, occurring in three phases. In Simpson's own words: "(1) an inadaptable phase, in which the group in question loses the equilibrium of its ancestors or collaterals, (2) a preadaptive phase, in which there is great selection pressure and the group moves toward a new equilibrium, and (3) an adaptive phase, in which the new equilibrium is reached" (Simpson 1944, p. 207).

Nine years later, in his *The Major Features of Evolution*, Simpson retreats from his earlier version of quantum evolution—now calling it "a special, more or less extreme and limiting case of phyletic evolution" (Simpson 1953, p. 389). At issue had been his earlier discussion of the "inadaptable phase"—where populations were seen to have lost previous adaptations prior to acquiring their new ones. By 1953, in other words, Simpson had largely come back into the pure Darwinian fold of seeing evolution as an essentially linear process of adaptive change always under the guidance of natural selection—though Simpson did still hold out for an all-or-nothing transition between adaptive zones or peaks and still saw the bursts of evolution of entirely new groups as involving exceptionally rapid rates of change.

But though Simpson's original formulation of quantum evolution has for the most part been lost sight of (in no small measure because he himself later watered it down), nonetheless, his insistence that patterns in the fossil record hold evolutionary meaning lives on. For example, the theory of punctuated equilibria (Eldredge 1971; Eldredge and Gould 1972; see Eldredge 2008a) combines the notion of geographic speciation with the empirical pattern of stasis in the fossil record—in effect applying Simpson's ideas of rapid evolutionary change down to the level of species.

Punctuated equilibria (see Eldredge 1985; Eldredge 1989), in turn, helped resuscitate the notion that species are indeed like individuals: with births (speciation), histories (longevities), and ultimately deaths (extinction). From time to time, a species may give rise to other, descendant species. Viewed as individuals, the possibility arose that species could themselves be "selected" or simply "sorted" (see Vrba 1980, on the "effect hypothesis" and related concepts).

When the "species as individuals" discussion and debate erupted in the 1970s and 1980s (started by Ghiselin 1974), no one linked it to Brocchi and Darwin. Darwin had long since abandoned the metaphor—after discovering natural

selection, coming to see species in space and in time as at least approaching Lamarck's predicted pattern of a continuous smear, a gradual melding of organismic characteristics. At least that is the main message that came down to succeeding generations of biologists from Darwin's *On the Origin of Species*.

So our last question is: Why did Darwin abruptly drop the Brocchi's analogy and the view that species are individualized entities with discrete births and finite lives?

The still-dominant interpretation of Darwin's "conversion" to evolution (Sulloway 1982) holds that it was not until Darwin returned home from the *Beagle* voyage in the Fall of 1836—and soon thereafter started hearing the results of the analyses of his specimens from the likes of Richard Owen (fossil mammals) and John Gould (birds) as well as other distinguished London-based naturalists, that he became "converted" to evolution. This can no longer be seen as literally correct—Darwin had used patterns of replacement of species in space and in time to take him to transmutation in the general sense while he was still on the *Beagle*.

But in the narrower sense of the origin of Darwin's vision of evolution as predominantly a matter of adaptive modification of organismic phenotypic features—the beginnings of his evolutionary theory that have come down to us today—I believe a slightly emended version of Sulloway's (1982) thesis is basically correct. It had nothing to do with Richard Owen's identifications of the fossil mammals. Rather, it had everything to do with John Gould's conclusion that the Galapagos finches—all the finches, not just the mélange of ground finches—constitute a diverse array of phylogenetically interrelated species. *That*, I believe, was the actual trigger that sent Darwin off in an entirely new direction.

It was not until the second edition of the *Journal of Researches* (aka *The Voyage of the Beagle*; Darwin 1845) that Darwin would write, under a John Gould-produced image of four profiles of Galapagos finch heads showing great diversity in bill shape and size, that "one might really fancy that from an original paucity of birds in this archipelago, one species had been taken and modified for different ends." It is a lead-pipe cinch that Darwin had precisely those same thoughts in the Spring of 1837 when he first learned of Gould's analysis of the Galapagos finches.

Now Darwin needed a theory of adaptive change. In the Fall of 1837, he opened his "Transmutation Notebooks," first revisiting Grandfather Erasmus' *Zoonomia* (Kohn 1980) and within a year discovering natural selection. With a mechanism of adaptive change achieved, Darwin could then slip entirely away from the patterns of geologic and geographic replacement of discrete species that had brought him to transmutation in the first place.

Gone was the notion of individual species, with discrete births and finite lifetimes. Only to be rediscovered in the 1970s—in part through the theory of punctuated equilibria—which reads a lot more like Darwin on the *Beagle* than Darwin in 1859.

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