

## f28 Punctuated evolution < Gould, Eldredge; allopatric >

But I do not pretend that I should ever have suspected how poor a record of the mutations of life, the best preserved geological section presented, had not the difficulty of our not discovering innumerable transitional links between the species which appeared at the commencement and close of each formation, pressed so hardly on my theory.  
—Darwin, 1856.<sup>1</sup>

If therefore it be a general law (as I have much reason to believe is actually the case) it could be said truthfully in many cases that genera do arise suddenly, geologically speaking, and not by slow and gradual process of evolution.  
—Henry S. Williams (1847-1918), ca. 1890.<sup>2</sup>

**Stephen Jay Gould** focused, in numerous of his published essays, on the undeniable fact that the fossil record rarely shows evidence of gradualism in the evolution of the species. This is at odds with Darwinian thinking.

But in *Origin*, Darwin does not appeal to the fossil record. What he knew of it, second hand in the years following the *Voyage*, was that some species in many levels of strata remain essentially unchanged, numerous species are not present in later beds because of extinctions (on the authority of Cuvier), and species at any level, not present at lower levels locally, have either migrated in from elsewhere (as Lyell would have it) or, according to his own theory, they evolved *gradually* from different species at lower levels. However the existence of numerous new species at one level required intermediate forms leading from some fewer numerous, different, species at a lower levels. Not being found, these “missing links,” which add to thousands and ever more as new species are located, can only mean that at every level, the stratigraphic record is far more absent than present. So, pointless to dwell on. And circular reasoning wins the day.

**Stephen Jay Gould** (1941-2002)<sup>3</sup>

“We are here because one odd group of fishes had a peculiar fin anatomy that could transform into legs for terrestrial creatures; because the



earth never froze entirely during an ice age; because a small and tenuous species, arising in Africa a quarter of a million years ago, has managed, so far, to survive by hook and by crook. We may yearn for a ‘higher’ answer—but non exists



In the 1960s, Gould and **Niles Eldredge**<sup>4</sup> both graduate students in paleontology at Columbia University and the American Museum of Natural History in New York City, for their doctoral theses, looked for gradualism in the fossil record. Gould, under the guidance of Norman D. Newell, Curator of Invertebrates at the Museum, studied *Poecilozonites* snails which, like the West-Indian land snail *Cerion*, a genera of gastropods that he later concentrated on, “manages to generate unparalleled diversity of form without parceling its population into true species.” He could discern in each no evolutionary trends. Niles Eldredge looked for gradualism in a *Phacops*, a genera of Devonian trilobites. Specimens for his study were available from a site he worked in America and from collections from around the world. The genera had existed for 18 million years. Try as he might he could find no evidence of evolution. Finally he found at his collecting site one feature that was possible evidence of vertical evolutionary change: the number of lenses in the compound eyes of the trilobites in stratigraphically higher layers are 17 from 18 in lower layers.

However, he learned that at the time his species had 18 cones to an eye, elsewhere, at the same stratigraphic level, existed species with 17. Thus what he had observed could be explained as lateral

migration of outlying populations when those in his area went extinct (or had left). What he came to learn was that the variability of the genera of trilobites that he studied was from 15 to 18 cones to an eye and that this group had appeared with this variability, had persisted and had gone extinct.

In 1972, Eldredge and Gould coauthored a paper that laid bare their dawning understanding of known fossil record.<sup>5</sup> Their description of evolution's workings which can account for the fossil record as it is found, is called *punctuated evolution*. This powerfully combines *two* statements that derive from Ernst Mayr's allopatric (*see* Topic f29) theory of species evolution:

*The mode of change*—isolation of a small population, which does not die out, or rejoin the larger parental mass, can evolve undiluted novel features that become substantial enough to constitute a new species.

*The rate of change*—rapid spread of genes throughout the small population and an aggressive selection for favorable genes by natural selection.

Neontologists see uniformity of form of organisms within their home ranges. Paleontologists see no sensible change of form for several millions of years for mammal and reptile species and upward of 5 or 10 million years for marine species.<sup>6</sup> Darwin in his 1844 *Essay* had correctly explained the former as due more to crossbreeding than to selection. Huxley, simply named the latter “persistent types.” Such horizontal (spatial) and vertical (temporal) stases are naturally embodied by the punctuated-evolution hypothesis that: speciation will occur in a region of limited extent (as we easily can envisage); in a tribe isolated from the parental population (many scenarios suggest themselves); and, in a geological instant (maybe only a bedding plane but, by our mortal standards, incredibly long—say five- to fifty-thousand years).<sup>7</sup>

A corollary of punctuated evolution is that saltations apparent in the fossil record of species' evolution are likely illusionary. The sorites puzzle (**Footnote f28.1**) of how to determine a species in the fossil record is solved not by stratigraphic unconformities (the old explanation) so much as it is by the sampling unlikelihood of finding a fossil of a species' population for the time of a punctuation event. Gingerich clarifies: “Generational change is so rapid that stability comes soon, but the stability is often perturbed and then new microevolutionary and macroevolutionary patterns begin.”<sup>8</sup> A prediction of punctuated evolution is that evolutionary trends (more complex sutures in ammonites, larger sizes in horses, bigger brains in humans) are not snippets of a continuum but *are* a succession of real species. So most importantly, punctuated evolution can be tested! Of the many ingenious studies already made and passed by peer review (**Footnotes f28.2,3**), all agree that punctuated evolution explains at least a good part of the real evolutionary story.<sup>9</sup> And indeed, in all but coining a name for it, the same interpretive explanation of the found fossil record was first apparent, in pre-geneticist terms, to Thomas Henry Huxley. Its new dusting off has value in revealing clearly, for debate, two views of evolution both of which should be weighed (**Footnote f28.4**) in any explanation of specific examples of evolution.

### Form follows function

The phrase “form follows function” is best known as Louis Henry Sullivan's dictum for explaining the naturalness of style in architecture down the ages.<sup>10</sup> He urged his dictum as guide for good *conscious* design. Sullivan's thinking reflected the (mostly muddled) effect on his milieu of Darwin. Darwin himself was urging the thesis that form follows function in evolution of organisms without any conscious design at all but as the result of natural selection. Sullivan's problem was to hurry that dignified process consciously so as make a skyscraper natural in the rush of Chicago's loop. For Darwin, good form of an organism evolves as a gradual adjustment of its parts to the constrains, and allowed freedoms, of a setting.

The ability of our species for cognition and art builds on our ability to share our thoughts aided by speech. Robert J. Richards reviews:<sup>11</sup>

In the standard account of hominid evolution as functions of incipient language use and requisite mental representations would provide the pressure for consequent molding of the voice box and

improved cerebral connections. Individuals who were slightly more efficient in communication and understanding would have advantages in hunting, child rearing and surviving. Such selective processes would gradually improve the cognitive capacities of those hominid lines whose previous adaptations allowed such traits, finally producing creatures that could cleverly and finely depict animals in caves.

In *The Descent of Man*, 1871,<sup>12</sup> Darwin argued, and in post-genetic times, neo-Darwinists in their reductive genetic arguments agree, that human anatomical and cognitive traits gradually arose in tandem. Divergence arose in our species from faint distinctions in our common ancestors with African great apes, with the greater capacities being in our more proximate relatives.

Parallelism and relay evolution allows a future, as the present, preordained in its broad outline by likenesses and separation of forms in earlier ages. The physical world, which is also molded by the organic world, is not a dictator but to the extent that the realities of its control determines life's course, form has followed function.

### Function follows form

Huxley was more of the opinion that human beings (his "Psychozoa") emerged by a dramatic split from morphologically and behaviorally stable great-ape populations due to circumstance that selected for the attributes which, thence forward, kept the species separate. In a punctuated evolution scenario, the new form can be a preadaptation, which once utilized, is marked in its consequences. In his book *Becoming Human*, 1998, Ian Tattersall finds evidence for punctuated evolution of humans who, after hundreds of thousands of years of being, suddenly became symbol-making humanity.<sup>13</sup> We may yet regress to that time of wonder by moving with a flickering light into the dark low recesses of the Combarelles cave in France where 13,000 years ago the first of our kind delicately engraved images of the then animals (horses, lions, mammoths, woolly rhinoceroses) and others, then later, overlay these with geometric patterns of undeciphered significance. Tattersall finds for punctuated evolution, in the sudden start, in the record of unprecedented behaviors beginning in our late-Pleistocene ancestors, some 30,000 to 50,000 years ago, that imply wholly new properties of the human brain: self-reflection and symbolic consciousness. Cognitive function of the brain evidently did not emerge gradually with the growth of brain size. The large brain that allowed for tool design remained static during the evolution of many hominid species. Speech, that we have, arose in Cro-Magnon even when it could have been inhibited in Neanderthals by their slightly different throat anatomy. But even if articulated speech was denied them, their humanity is recorded by evidence of their ritual life (burials and veneration). If true, the emergence of humanity was not, in that case, dependent on speech. The traits, the "exaptations," that together allowed for speech were: a lengthened larynx, enlarged prefrontal lobes, and cerebral wirings. Punctuated evolution occurred when articulated speech emerged from their unprecedented coordination. Gould and Richard (Dick) Charles Lewontin in 1979 coined the term "spandrel"<sup>14</sup> (mischievous for its encouragement of just-so tales)<sup>15</sup> for biological structures or traits that are accidental byproducts of history and not the result of natural selection but upon which natural selection can then busily operate.<sup>16</sup> Their referent for the word spandrel (literally: the space between the curve of an arch and the right lines inclosing it) is an incidental by-product of construction that the architect is free to embellish. For hundreds of thousands of years before our ancestors could have been a morphologically and behaviorally stable species, several of the genus *Homo* separated from each other as novel behaviors emerged that were sufficient to keep the newly derived ones distinct. Gould (1991) points out: "The current 'out of Africa' versus 'candelabra' debate on human evolution represents a claim for speciation and punctuated evolution [versus gradualistic divergence of races slowed by cross-linking hybridization] in our own origin."<sup>17</sup>

Exaptations (Tattersall's synonym for preadaptations) are features that evolved independently and had very different functions prior to being coopted collectively for a new role in which they cooperate. That exaptations can erupt upon the scene and best the drama of sudden climate or geography change that would otherwise kill, is a neo-Darwinian argument for selection operating on a species rather than on the individual.

The hypothesis of punctuated evolution is an explanation for living fossils (*Lingula*, alligators, snapping turtles, aardvarks, the dawn redwood) that belong to narrow, long existing, lines with almost no spin-off species. Divergence in punctuated evolution is the sudden disappearance of an ancestral species and appearance of many species that, by descent, replace it. Long-lived narrow segments of phylogeny with living fossils at their present end are those whose chances were never either survival through speciation or extinction.

Punctuated evolution is a story of contingencies and is favored wherever a case can be made that function has followed form. □

**Footnote f28.2 1996 news release headline: “Snails Caught in Act of Evolving.”**

A genus of marine snail *Cerion* on the Bahamian Island, Great Inagua, is found as living *C. rubicundum* (a large and ribby species) and recently extinct *C. excelsior* (the largest of all *Cerion* species). *Cerion* shells that graduate quite smoothly in form between these two species were found and collected from a mudflat in the southeastern corner of Great Inagua by Gould and David Woodruff. Later, a dating technique based on changes in the composition of amino acids in the shell over time allowed Glenn A. Goodfriend to show that the sequence of forms were also a record of time. The time spanned when keyed to radiocarbon dates for some of the shells was some 10,000 years. That, Gould pointed out, “represents a geological eye-blink in the fullness of evolutionary time; whereas this transformation in our snails marks a full change from one species to another, not just a small decrement of leg length or a change in the timing of breeding within a single species.”<sup>18</sup>

**Footnote f28.3** An extension of punctuated evolution, for which Gordon Baird in 1992 coined the term “coordinated stasis,” is equilibrium acting at the level of communities. This could be when the involved species interact so closely they cannot evolve, and when, to counter a local environmental change, the group can relocate. Apparent in the middle Devonian and Silurian fossil record ocean-bottom mud dwelling animals is: certain groups of species persist unaltered for tens of millions of years, and then undergo an episode of rapid extinction and the formation of new species.<sup>19</sup>

**Footnote f28.4** Neither form nor function clearly follow each other in Southeast Asian *Rafflesia* (discovered by Stamford Raffles in 1819) contemplation of which at best reminds that the defining character of the Plant Kingdom is not photosynthesis but is that a plant-cell has cellulose walls. This nonphotosynthetic parasitic flowering plant lives as a thin strand “infection” within a photosynthetic host—*Tetrastigma* (a vine in the grape family). For furtherance, each occasionally puts through the vine-bark a reproductive out-growth of a cabbagelike bud that after some ten months of growth using vine-nutrients, opens to last a few days as a leathery five-petaled (orange in color and spotted with cream-colored warts) single flower (variations of these account for the 17 described species of the genus) notable as the world’s largest (some measuring 90 cm across) and for its foetid (carrion-like to rotting-vegetable) stench. Flowers are either male or female. Pollinated (possibly by flies, ants or by means yet to be described) female flowers set seeds that only tree shrews have been observed to eat. Exactly how *Rafflesia* infections are inoculated has yet to be determined.<sup>20</sup>

**Footnote f29.1** Plants hybridize (mate with plants from different species) commonly in the wild. Many do then prosper and evolve. This, in stark contradiction, Verne Grant noted in *Plant Speciation*, 1977, to the vulgar notion that nature’s hybrids are maladjusted evolutionary dead-ends. For example, sunflower species *Helianthus anomalus*, *H. deserticola*, and *H. paradoxus* grow in extreme habitats of sand dunes, dry-desert floors, and salt marshes respectively. They are hybrids of *H. annuus* and *H. petiolaris* which live in temperate climates. All have been in existence since *H. annuus* appeared 60,000 years ago. (*H. petiolaris* appeared 200,000 years ago.) **Loren Rieseberg** has shown, by direct demonstrations beginning 1988 that the ordinary parent sunflower plants can be mated to yield hybrid offspring with hardier combinations of the same genes—for alleles combinations determine phenotypic traits as: succulent leaves, leaf shape, salt tolerance, and seed size. “Hybridization is important in larger, or difficult, evolutionary transitions,” Rieseberg explains. “The idea is that hybridization generates variation at hundreds or thousands of genes simultaneously.”<sup>1</sup>

