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Darwin's Gradualism

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We protest the inaccurate accusation made against us by Penny (1983) in his recent comment on Darwin, gradualism and punctuated equilibrium. He cited a quotation from Darwin as we rendered it (Eldredge and Gould, 1972:87), saying that we "apparently" took it from the first edition of the *Origin*, then claiming: "However, this is not a verbatim extract." As evidence, he reproduced a passage from the sixth edition of the *Origin*, in which the words cited by us are interspersed amidst a variety of other sentences that supposedly alter their meaning. Contrary to Penny's charge, the quotation as given by us is an accurate verbatim extract from the first edition of the *Origin* (1859:342), except that the words "is" and "this fact," which we interpolated, should have been given in brackets, but were not (by typographical error) in our original paper (1972:87).

Penny argued that, because Darwin acknowledged in several places the potentially highly variable character of evolutionary rates, he was not a committed gradualist and, if not actually the father of punctuated equilibrium, he at least veered sufficiently close to it to deprive us of any marked originality. One simply cannot do history by searching for footnotes and incidental statements, particularly in later editions that compromise original statements. As with the Bible, most anything can be found somewhere in Darwin. General tenor, not occasional commentary, must be the criterion for judging a scientist's basic conceptions.

If Darwin historians agree on a single point (for example, see Gruber [1974] and Mayr [1982]), it is the importance and pervasiveness of Darwin's gradualism—a

commitment far stronger than his allegiance to natural selection as an evolutionary mechanism. After a brief and early flirtation with saltation in his 1837 notebooks, Darwin never wavered in his support of gradualism (of course, with the possibility of marked variation in rate). He wrote in the section on geology from the 1842 sketch of the *Origin* (Darwin, 1909:23): "Our theory requires a very gradual introduction of new forms, and extermination of the old The extermination of old may sometimes be rapid, but never the introduction. In the groups descended from common parent, our theory requires a perfect gradation not differing more than breeds of cattle, or potatoes, or cabbages in forms." This commitment to gradualism underlies the most striking imaginery of the *Origin* itself, particularly the famous passage (Darwin, 1859:84): "It may be said that natural selection is daily and hourly scrutinising, throughout the world, every variation even the slightest; rejecting that which is bad, preserving and adding up all that is good; silently and insensibly working We see nothing of these slow changes in progress, until the hand of time has marked the long lapse of ages." Most striking is Darwin's continual conflation of gradualism with natural selection, the very point that inspired Huxley's major criticism: "You load yourself with an unnecessary difficulty in adopting *Natura non facit saltum* so unreservedly." Darwin (1859:189) wrote, for example, making his usual conflation: "If it could be demonstrated that any complex organ existed, which could not possibly have been formed by numerous, successive, slight modifications, my theory would absolutely break down." To deny Darwin's strict

allegiance to gradualism because he acknowledges marked variation in rate makes about as much sense as claiming that he was not really committed to natural selection because he attributed the two eyes on one side of a flatfish to inheritance of acquired characters, while advocating selection for the camouflage of their coloration. Darwin was a complex and subtle thinker; historians must assess general tenor amidst acute arguments and exceptions for specifics.

Penny (1983:74) did concede that our papers may have done some good "if they free paleontologists from expecting to find speciation leading to 'insensibly graded fossil series.'" But Penny's claim that only paleontologists have descended (unmodified) from Darwin with gradualism fixed firmly in mind is false. Simpson (1944:203) did write: "Aside from isolated discoveries that contribute less directly to the study of evolution, nine-tenths of the pertinent data of paleontology fall into patterns of the phyletic mode"—a statement from a paleontologist who, despite his justified fame for viewing evolutionary rates as variable, was plainly thinking "gradually" as he penned these words. But consider Mayr's (1942:153) *only* reference to patterns of evolutionary change through time in his *Systematics and the Origin of Species*: "Hitherto we have spoken only of the delimitation of contemporary (synchronic) species. The delimitation of species which do not belong to the same time level (allochronic species) is difficult. In fact, it would be completely impossible if the fossil record were complete. The species of each period are the descendants of the species of the previous period and the ancestors of those of the next period. The change is slight and gradual and should, at least theoretically, not permit the delimitation of definite species." Simpson and Mayr were not alone, of course; the general theme of the early synthesis (especially Dobzhansky [1937, 1941] and Mayr [1942]) was the integration and reconciliation of the twin themes of *gradual* genotypic and phenotypic transformation with

the very existence of gaps—that is, species—among elements of the modern biota. Paleontologists neither invented nor lay special claim to evolutionary gradualism.

Finally, the denial of originality to colleagues is a potentially destructive game that some scientists love to play. We simply submit that if Darwin said it all before and everyone knew about it, our original paper on punctuated equilibrium would have been treated as a crashing bore. Punctuated equilibrium is the attempted integration of speciation theory with patterns of morphological stasis and change commonly observed in the fossil record. After all, as Mayr (1942:147) pointed out long ago, Darwin never really discussed the "origin of species" in any modern sense. If many of our colleagues saw some value and originality in what we said, they must have discerned a difference between our contentions and those traditionally and correctly attributed to Darwin's own concept of the fossil record.

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