Commentary

Stephen Jay Gould

On May 20th the world lost a major thinker in the field of evolutionary biology and its foremost historian of ideas in this field. Stephen Jay Gould's prodigiousness, breadth of knowledge and grandiloquence sometimes made him seem more like a figure of the 19th century than the 20th, but his work was critical in the transition from the neo-Darwinian synthesis to the more developmentally-influenced concepts of evolution of the present period.

Gould was a keen observer of natural phenomena, and fearless in pursuing the consequences of his observations even if they led to unorthodox conclusions. Notwithstanding his many talents, he did not involve himself in the molecular approaches that emerged as the mainstream of evolutionary and developmental studies during his lifetime. This worked to his advantage, however, in that it freed him to consider large scale macroevolutionary events through the telescope of paleontology, to which he brought a new glamour, rather than the microscope of molecular genetics, where the big picture is frequently missed. Punctuated equilibrium – the fits and starts of the fossil record – was elevated by Gould and his colleague Niles Eldredge to a phenomenon that required rethinking the neo-Darwinian orthodoxy (Gould and Eldredge 1977). So was the "Burgess Shale effect", the finding that most, if not all, the major animal body plans burst forth in a relatively narrow span of time between 500–600 million years ago (Gould 1989).

The standard neo-Darwinian view (deriving primarily from theoretical work of R A Fisher) was that sudden morphological change (saltation) cannot be characteristic of evolution and there must thus be something incomplete about observations of morphological discontinuity – a consequence of gaps in the fossil record, and so forth. Most viable genetic changes in modern organisms are of small effect, leading to incremental phenotypic change. Mutations of large effect, seemingly needed for both punctuated equilibrium and the Burgess Shale phenomenon, are typically pathological and so, Fisher argued, won't be fixed (established) in natural populations.

While neo-Darwinism had ways of explaining the emergence of genetically distinct populations, such as geographic isolation (Ernst Mayr) and genetic drift on multipeak adaptive landscapes (Sewell Wright), and therefore could accommodate the "punctuated" character of the fossil record, all such models had more difficulty with the "equilibrium" aspect. Why is morphology so static in the face of large-scale external changes? Gould and Eldredge's insight concerning the tempo and mode of evolution pointed to the need for different kinds of answers.

Gould typically used metaphors rather than mechanistic analyses to argue his case. The spandrels of San Marco, the entry point into a famous critique of adaptationism by Gould and his colleague Richard Lewontin (Gould and Lewontin 1979), are structural side effects of architectural necessities that later can be used for other purposes. This phenomenon in the evolution of organisms was subsequently generalized as the concept of "exaptation" by Gould and Elisabeth Vrba (Gould and Vrba 1982). Another metaphor Gould was fond of was "Galton's polyhedron" (Gould 1986). A sphere will roll along a surface by making incremental changes in its position of contact. A polyhedron, however, if prodded, will make a quantal change in its contact with the surface. By such didactic means Gould sought to establish that there were alternatives to incremental Darwinism.

In search of predecessors in his approach to macroevolution, and with characteristic intrepidness, Gould revisited the work of such unjustly scorned figures in biology as Jean-Baptiste Lamarck, the first scientific thinker about organic evolution (Gould 1979, 1999a, b), D'Arcy W Thompson, who believed that biological forms bore the imprint of physical forces (Gould 1971), and Richard Goldschmidt, coiner of the term "hopeful monster", a shorthand for certain saltationist views now coming back into fashion (Gould 1977a). But the fact that his own scientific speciality afforded him

no causal means for accounting for the macroevolutionary phenomena that drew his attention made him a ready target for neo-Darwinist critics. His remoteness from the contemporary cellular and material sciences that might yield such explanations also kept him from attaining the status of revolutionizing evolutionary theorist to which, from the evidence of his writings, particularly his last book (Gould 2002), he clearly aspired.

Gould's most serious attempt to deal with the actual underlying basis of macroevolution was in his first book *Ontogeny and Phylogeny* (Gould 1977b) where he drew on 19th and early 20th century analyses of comparative anatomy and embryology to show that subtle changes in timing of developmental process can lead to morphological novelty through a process termed "heterochrony". This work was neglected by the mainstream of developmental biology, which was then embarking on a productive but narrow fascination with genetic mechanisms of development. But Gould's view that developmental mechanics (not just genetics) was important for understanding morphological evolution was taken seriously by some working at the interface of evolutionary and developmental biology, and the book had a surreptitious career as an important spur to the new field of "evo-devo" that has emerged over the last decade. This field also has its share of what Gould termed "Darwinian fundamentalists" (Gould 1997) but that style of thought is losing force as extensive discordances between genetic and morphological evolution are coming to light, and nongenetic determinants of phenotypic evolution (physical properties of tissues, emergent properties of complex systems) are entering into the mix.

Stephen Gould's intellectual audacity was undoubtedly tied to his political progressivism. An avowed Marxist, he took on the role of public citizen in opposing the misuse of biology in social thought and policy (Gould 1981) and the corruption of science education promoted by religiously motivated creationists (Gould 1999c). As with his scientific work, his public role was informed by an historical appreciation of the origins of received doctrines, along with a unique capacity to see what they left unexplained and to imagine better possibilities.

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