Commentary

Stephen Jay Gould
(1941–2002)

S J Gould died last May from a cancer, at the age of 60. I first encountered him in 1982 at an evolutionary meeting in Dijon (France). The aim of this workshop was to confront paleontologists and population geneticists. S J Gould and his friend N Eldredge were somehow a focus in the meeting, due to their evolutionary theory of punctuated equilibria (Gould and Eldredge 1977). Discussions were sometimes tense between biologists and paleontologists. I remember Gould repeating "our theory is not a theory on speciation, but on the appearance pattern of species in the fossil record". Even now, many people have problems in distinguishing anagenesis and cladogenesis.

S J Gould is probably the most influential evolutionary biologist since Charles Darwin, having written, in his monthly column of Natural History magazine, 300 consecutive issues starting in 1974 and ending in 2001. Many of these articles have been further published in books.

After a doctorate in Paleontology (1967) at Columbia University, S J Gould went to Harvard where he spent the rest of his career, becoming the Alexander Agassiz Professor of Zoology in 1982. As a paleontologist, he was a specialist of gastropod molluscs from West Indies. But he soon became involved in broader and more general subjects concerning biological Evolution. Still now the punctuated equilibria theory is a controversial but a reference concept. In 1977 he published *Ontogeny and Phylogeny* (Gould 1977), a book emphasizing the need to incorporate developmental biology into the evolutionary theory. In this respect he was a pioneer in a now rapidly growing interdisciplinary field, Evolution and Development (Evo-Devo).

In 1982 with E Vrba, he drew attention to the fact that many traits having now an obvious function were not initially selected for that function (Gould and Vrba). For example the anterior limbs of penguins, which are very efficient flippers, were first selected for flying. They called such changes 'exaptations' but, for unclear reasons the paper and the new term went forgotten. A similar idea was developed with R C Lewontin (Gould and Lewontin 1979), telling that "the Spandrels of San Marco" are an architectural constraint, not an aesthetic choice from the architect, and that similar phenomena do occur frequently in the course of evolution. Biologists must always be cautious against adaptive Panglossian interpretations.

Coming back to paleontology, S J Gould (1989) developed the idea that, in early Cambrian, a spectacular and rapid diversification occurred in Metazoa, resulting in numerous distinct phyla, many of them now extinct. As might be expected, this thesis is now controversial but again remains as a reference for further analyses.

S J Gould has recently published (Gould 2002) what will remain a masterpiece and now a scientific testament of more than 1400 pages: *The Structure of Evolutionary Theory*. As a scientist, S J Gould was an opponent to other widespread theories. For examples he was against the *selfish gene* concept arguing (rightly to me) that natural selection often acts at more integrated levels than the gene, such as populations, species and even clades. He also was against the development of sociobiology, fearing possible dangerous and excessive interpretations about human evolution. Fortunately, sociobiology is now a mature scientific discipline, having shed most of its possible ideological implications.

How can we define a general trend in such a huge work of scientific reflections and writings about evolution? To me, the general, recurrent theme is that biological evolution is a well proven fact, which has produced an extraordinary diversity of forms, but never with any kind of general direction, any tendency toward a general progress. Of course, Darwinian natural selection remains the main mechanism for improving populations and species, permitting their persistence in a very competitive

world. But their improvement is not a long term objective: stochastic processes acting at very different levels play an important, sometime decisive role, in shaping evolutionary trends. This is true at the molecular level (Kimura 1983) but also at more complex integrated levels. Evolution proceeds from a permanent interaction between adaptation and stochasticity. For example S J Gould has repeatedly argued that, without the meteorite impact which, at the end of Cretaceous period, was probably responsible of the extinction of most dinosaurs (only bird survived), mammals would have remained a group of tiny and not remarkable species. The mammalian radiation which followed, and then the appearance of man himself, is an unpredictable and remote consequence of a cosmic accident, 60 million years ago.

References

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JEAN R DAVID
Lab. Populations, Genetique et Evolution,
Avenue de la Terrasse,
Bat 13-BP1, CNRS,
91198 Gif sur Yvette Cedex, France
(Email, david@pge.cnrs-gif.fr)