Commentary

Gould's intellectual ontogeny

When I first met Stephen Jay Gould in Cambridge on a December day in 1969, I encountered an energetic, young, highly articulate professor fascinated by shell shape in land snails. By that year, Gould had published almost ten papers whose major themes were adaptation, the relationship between shape and size, and the linkage between adaptive characters and non-adaptive tag-along traits. For Gould, physical conditions such as the availability of calcium carbonate (the mineral component of shells), changing surface-to-volume ratios as body size increases during growth, and water loss through evaporation by way of the shell's opening were the dominant targets of selection and adaptation. The laws of growth provided constraints on evolution and required many traits to change in ways that should not be interpreted as adaptive. As objects of study, Gould settled first on Pleistocene land snails of Bermuda, and later on the marvelously varied shells of the West Indian land-snail genus *Cerion*, on which generations of German and American naturalists had lavished their attention earlier in the century. Gould saw these shells as works of architecture, as signposts of evolution, as objects whose formal analysis would reveal principles of form, function, ontogeny, and phylogeny.

But then, like all great scientists, Gould underwent an intellectual transformation. With his background in the German school of formal morphology – the mathematical description of shape and size – he was predisposed to be influenced strongly by several up-and-coming colleagues – David Raup, Thomas Schopf, and later his own students Daniel Fisher and John Sepkoski among them – whose orientation to the productions of nature was abstract in an entirely different direction. With these friends, Gould embraced the view that complex patterns of evolution could be generated without reference to adaptative thinking. Forces larger than individual-level adaptation were at work, forces affecting the susceptibility of lineages and evolutionary branches (clades) to extinction and proliferation. Gould was equally affected by Niles Eldredge's apparent discovery that fossil trilobites from the Devonian period of New York remained morphologically static for millions of years, there evidently being no evolution despite environmental variation and change. By the late 1970s, Gould had become thoroughly convinced that the kind of adaptation which Darwin had taught biologists and paleontologists to expect was only part – and a small part, at that – of the rich tapestry of the history of life. Adaptation is, in his view, temporary and local; much of the morphology we see is non-adaptive, the necessary consequence of deeply engrained rules of biological architecture, carried as baggage and as raw material for potential future use while great geological forces caused species to arise, proliferate, and die out. Gould's evolutionary world became a turbulent place in which historical events hinged on chance occurrences, unique contingencies, and historically burdened life forms. In this world, the course of history was at the mercy of climates and calamities whose timing and effects were dictated by geological and extraterrestrial phenomena. Other than changes in variance, or the range of permissible sizes and shapes, the record of life revealed no patterns in history to Gould.

Gould prolifically and forcefully communicated his world view to his paleontological colleagues and to the wider educated public. Besides inspiring much research on stasis, his power lay in creating and guiding the evolutionary *Zeitgeist* for twenty years, rendering some lines of inquiry fashionable – the study of hierarchy, of the evolutionary behaviour of clades, and mass extinction, for example – and others much less so. Gould had little patience with studies on how fossil organisms worked, and he largely skirted ecological questions after his early period. For years, many paleontologists and a few biologists were reticent about proposing adaptive explanations for the phenomena they observed, in fear of being accused of telling "Just-so" stories that could not be tested. There were always

exceptions, of course, but those who engaged in adaptationist study and rhetoric were on the whole relegated to the lunch counter while those closer to Gould's world view were comfortably situated at the head table.

Strongly held views Gould surely had, but in my experience Gould welcomed rational disagreement. Though my views diverge significantly from Gould's on the relative importance of adaptation in history, the nature and origins of morphological constraints, and the existence of large patterns in history, we remained life-long friends, openly and honestly discussing our differences. Gould was a man of scientific honor who, after weighing the evidence and arguing from his background and interests in abstract morphology, ontogeny, and intellectual history, came to his conclusions and perspectives thoughtfully. Like most of us, Gould came to modify (some would say soften) his positions as he accommodated new evidence and arguments into his superstructure of evolutionary thought. Evolutionary change became less bound up with the formation of species than it was in Gould's early conception of puncutated equilibria; and Gould acknowledged the importance of biological agents, and therefore of long-term adaptation, in the evolution of antipredatory defenses and sexually selected traits, even if he clung to the views that forces shaping extinction and diversification were in the end more powerful. In the final analysis, he may not have persuaded many of his colleagues that stasis is widespread, that adaptation pales in importance compared to contingency and accident, or even that baseball is in any way interesting, but he certainly forced everyone to re-examine their views and to think much more precisely about historical phenomena, which before Gould's career had been largely excluded from the orbit of scientific inquiry.

Contrary to Gould, I hold that adaptation is a universal process and outcome in all economic systems, including the biosphere and all its species; and I believe that first principles of economics provide the basis for a large-scale, general trend in the history of species and other economic units toward greater economic control by increasingly powerful agents. Contingencies and accidents abound, to be sure, and the timing of steps in historical development depend on external triggers and other boundary conditions; but the major features of history, including evolution, transcend these particulars.

GEERAT J VERMEIJ
Department of Geology,
University of California at Davis,
Davis, CA 95616, USA
(Email, vermeij@geology.ucdavis.edu)