

Steven J Gould – an appreciation

It is rare that the death of a biologist reverberates throughout the World's media, such as the New York Times, Times of India, Toronto Globe and Mail and Neue Zürcher Zeitung, as it happened when Stephen Jay Gould died on 20 May 2002. This kind of reaction by the public has traditionally been awarded rather to physicists, if to scientists at all. Gould belonged to a minority among contemporary biologists also in another aspect: He was an evolutionary biologist interested in macroevolution.

In several of the many obituaries and appreciations that have been written in response to Gould's death, it was alleged that his scientific output was unexceptional. The crux of this observation lies in what was implied, namely that only his empirical studies (mainly on West Indian land snails) count as scientific studies. None of the writers felt that it was necessary to evaluate his empirical work. Empirical studies in non-experimental areas of biology (e.g. paleontology, morphology, systematics), once published in peer-reviewed periodicals, are generally and tacitly assumed to represent "data" (i.e. essentially facts) and are of interest only to colleagues working on the same subject. It is fair to assume that Gould's death would have barely caused a ripple had he concentrated on empirical research like the overwhelming majority of biologists. But Gould wrote also on theoretical issues in biology and engaged, even indulged, himself in conjectures, theories, and speculations. And it is this part of his work, which he presented and defended in essays and books, that earned him fame and admiration from a broad section of the educated public.

Gould joins a long list of biologists whose fame rests on their non-empirical work and whose often significant empirical work is remembered only by specialists. Étienne Geoffroy de Saint-Hilaire, for example, produced substantial empirical studies, including path-breaking studies in teratology and embryonic development, but his fame and veneration among the intelligentsia of Paris was based on his theoretical writings regarding the unity in the basic construction plan (bauplan or blueprint) of all living organisms (see Appel 1987; Gould 2002). Geoffroy was able to capture the imagination of the educated public with his vision of the broader significance of his empirical observations. Not altogether surprisingly, Geoffroy won the famous debate with Cuvier in 1831 according to the vote of the contemporary European intelligentsia, while Georges Cuvier, whose exceptionally prolific work encompasses solid studies in paleontology, functional morphology, and systematics, won the debate according to the votes of scientists. Even today, Cuvier's name is highly respected among practicing biologists (e.g. Rudwick 1998), whereas Geoffroy is remembered mostly by those interested in theoretical issues and the history of science (e.g. Panchen 2001; Gould 2002). Ernst Haeckel represents another example of a biologist, whose early empirical work is largely forgotten and eclipsed by his theoretical writings, which addressed not only biologists but also the educated public at large and which are the basis of his often controversial fame to this day (e.g. Richardson *et al* 1997). In contrast, Haeckel's colleague and friend, Carl Gegenbaur (Nyhart 1995), was regarded more highly as an exceedingly capable, knowledgeable and solid comparative anatomist, but was hardly known beyond the boundaries of academic biology. Today, his name is all but forgotten, a development that was accelerated when the fields of comparative anatomy and evolutionary morphology lost their former preeminence in contemporary biology. Charles Darwin, represents the exception that confirms the rule: Although immortalized by his "Origin of species" (1859), even though his empirical studies on barnacles, earthworms, human behaviour, and many other subjects are equally groundbreaking, his enduring popular fame remains firmly tied to the highest respect among practicing biologists.

While the Geoffroy–Cuvier debate was fought with Gallic emotionality, we know little about how Gegenbaur, whose Germanic restraint from public display of emotions was well known among his

contemporaries, felt about Haeckel's greater fame. In Gould's case, the reactions to his fame are addressed by Gould (2002) himself in his last book, are apparent in the writings of rivals elaborating the theory of evolution (e.g. Smith 1992), and are part of the collective consciousness of contemporary practicing biologists (see, e.g. Briggs 2002; Fortey 2002; Wake 2002). It is well known that Gould has been far more appreciated by non-biologists than by biologists.

Biology, however, does owe a debt to Gould. For one, in a time, when biological research is viewed by tax payers and politicians mainly as a tool for medical progress and economic growth through biotechnology, Gould tenaciously held fast to his abiding interest in macroevolution, a field that is of purely intellectual concern. Through his popular writings, he ensured that interest in this fascinating and relevant research area was maintained and nurtured in a broad cross-section of the population, at least in North America.

Biologists in general are imbued by a deep mistrust of theoretical work in biology, which is often dismissed as "mere speculation". Decades after Kuhn (1962), Popper (1968, 1983), and more recently Mayr (1988, 1997), generations of aspiring biologists are still being taught to "let the data speak for themselves" and to refrain from any theorizing. Editors of scientific journals still receive a large number of manuscripts that present data without any discussion or interpretation beyond a comparison with previous studies on the subject. This attitude among biologists seems to persist even though conjectures and metaphors have been integral parts of landmark discoveries throughout the history of biology, such as William Harvey's (1653) conjecture, prior to the actual discovery of capillaries by Marcello Malpighi (1661) four years after Harvey's death, that blood flows from arteries through tissues to veins; and Barbara McClintock's conjecture of the existence of "jumping" genes (Comfort 2001). Studies in macroevolution, by their very nature, always entail conjectures.

Macroevolution is defined as evolutionary change that is responsible for the large-scale morphological differences that are observed between supraspecific taxa, such as fishes and tetrapods, or parrots and storks. It is a historical process that is acting over very long time spans. Hence, macroevolution can be recognized as having occurred only *post factum* and must be inferred from indirect evidence and certain premisses. The nature of these premisses and the validity of certain inferences have been a source of controversies, in which Gould chose to involve himself.

One premiss of macroevolutionary research posits that the basic mechanisms of macroevolutionary change are the same as those observed at microevolutionary levels, but accumulated over longer time spans. Microevolution represents evolutionary change at the population and species levels, can be documented by direct observation and experimentation (see, e.g. Weiner 1994), and, therefore, can be explained as resulting from known, observable mechanisms and processes. Gould, having been a graduate student at Columbia University and the American Museum of Natural History, the intellectual centers of the Modern or Evolutionary Synthesis (see Dobzhansky 1937; Mayr 1942, Mayr and Provine 1980), was naturally imbued by microevolutionary theory. Like many paleontologists and comparative anatomists, however, he questioned whether a mere accumulation of microevolutionary changes would result in the large-scale morphological differences that are observed among fossil and extant taxonomic groups above the species level. In hindsight, it seems logical that Gould would try to explain the disjunctions in the fossil record as consequences of actual microevolutionary processes, instead of artifacts of the fossil record (see Gould and Eldredge 1971; Gould 2002). But for a paleontologist it seems also logical that he was searching for special macroevolutionary mechanisms, and he decided that natural selection among species in addition to that at the individual level would fill the perceived gap in the current theory of evolution (see Gould 2002).

Evidence for macroevolution is derived mainly from structural differences at all levels of organismal organization from an organism's morphology to its molecular components. Gould was clearly aware that morphological differentiation is the touchstone of macroevolution, but he questioned the validity of what he assumed were pervasive practices among morphologists. In his famous paper on the spandrels of San Marco (Gould and Lewontin 1979), he attacked the practice of determining the adaptive significance of a particular structure by trying to correlate its presence or absence in different taxa to the presence or absence of particular environmental factors. Such an approach tends to deal only with structures that are related to particular environmental factors and, hence, tends to view all structures as being adaptive. However, classically trained anatomists have

known at least since Galen's times that individual structures are generally part of integrated organ systems and that their function is apparent only within the context of the organ system to which they belong.

Gould also questioned the assumption that individual variability of the genotype, combined with the selective actions by the environment in the broad sense, were sufficient as a motor for morphological change, and he called attention to the existence of constraints and contingencies that limit the possibilities for morphological change. In this, he joined the ranks of many earlier and contemporary biologists, including Darwin himself, who have been keenly aware of the limitations that are imposed on any change of a highly integrated, complex system, such as the eye, and of the "difficulties" inherent in explaining how such changes could have proceeded in actuality; while the evolving system must remain fully functional at all times and cannot be closed for renovation. These problems, however, are long-standing and perennial, and have been explored and discussed under various concepts, such as "holism" (Dullemeijer 1974), "internal selection" (Gutmann and Bonik 1981); "structuralism" (Resnik 1994), and many others. Similarly, his concept of "exaptation" (Gould and Vrba 1982), which explains that certain features may evolve in response to a particular selective regime, only to become subject to a different selective regime, has been explored and discussed previously under the term of "Funktionswechsel" (Dohrn 1875) and "pre-adaptation" (e.g. Bock 1959). Gould (1976), in a tiny note, also challenged the validity of the current, almost exclusive focus on homologies and genealogical relationships in comparative morphological studies, and he pleaded for the recognition of the importance of analogous structures, particularly as models to understand functional aspects of organismal structures. Again, this insight is not Gould's alone, as the use of non-homologous models was common among pre-Darwinian comparative anatomists (Homburger 2000), and still is among modern physiologists in their quests to understand functional properties of organisms.

Gould's main contributions to macroevolutionary theory, and biology in general, may turn out to have been his questioning of the value of common practices and his calling attention to the importance and relevance of neglected issues. Being primarily a paleontologist and not a morphologist, Gould was not in a good position to develop solutions to problems that require expertise in classical morphology, the science of complex structures. However, by having had a fine sensorium for identifying problems that hinder a better understanding of macroevolutionary processes, and by being able to communicate their relevance to a broader audience, he managed to kindle an interest in macroevolution in a broad section of the public. His service could not have been more urgently needed than during the last quarter of the 20th century, when organismal biology was being marginalized by the behemoth of molecular biology and biotechnology; when teaching and research in anatomy and morphology was deemed irrelevant and old-fashioned by biological areas competing for time, space, and funding; and when the median age of practicing anatomists and morphologists was inching dangerously higher and higher.

In the course of contributing monthly to "*Natural History*", the magazine of the American Museum of Natural History, he was able to deploy and hone his gift for communicating ideas evocatively also to non-specialists and to link his scientific visions to ideas from a broader part of the human experience. This expertise was invaluable when, in the early 1980s, the Theory of Evolution came under attack from outside the scientific establishment. A coalition of politically and morally motivated citizens have viewed the morally neutral Theory of Evolution and its support by secular humanists as responsible for the moral disintegration of contemporary civil society and have been seeking a return to a more wholesome society through a stricter adherence to Judeo-Christian precepts. One approach towards that goal was to try to force schools to teach the creation account of the Bible as an alternative to the evolutionary reconstruction of the origin and development of the organic world. When Gould was asked by the courts to testify in support of the Theory of Evolution, he was more convincing and effective than other biologists, because he did not simply trot out well-worn examples of fossil and indirect evidence to try to convince the public that the gradual morphological changes observable during microevolutionary events are also visible in the fossil record. He knew that such gradual morphological changes are not demonstrable at the supraspecific level, at least in vertebrate and anthropoid fossils, which are the focus of concern of those opposed to evolutionary biology. Instead, he spoke about ideas and about the broader context of biological

observations and theories. And he spoke eloquently, and dazzled and spell-bound the audience. There are relatively few people who are genuinely interested in the minutiae making up the body of knowledge of biology, but almost all people are interested in ideas and narratives that can be related in some fashion to the most basic concerns of humanity: Who am I? Where did I come from? How did my surroundings come about, and how are they controlled? Gould did address these concerns by establishing bridges between biology and other areas of human interest and by stimulating the audience to adopt an integrative world view.

Recently, functional and evolutionary morphology has experienced a renaissance with an increasing number of publications, graduate students, faculty members, conferences, and university programs, at least in the United States, as exemplified by the recent hiring of three morphologists to professorial ranks by Harvard alone. Morphology, the science of complex structures, faces an embarrassment of riches with respect to open questions that need to be addressed. The recent resurgence of challenges to the teaching of evolutionary biology in American schools in the guise of support for the theory of “Intelligent Design” is a measure for the inadequacy of current biology to provide a convincing explanation for the process of macroevolutionary change, especially since the reality of microevolutionary processes has been accepted even by the staunchest believers in the biblical account of the origin of the organic world. Furthermore, it needs to be remembered that morphologists did not participate in generating the Evolutionary Synthesis (see Mayr and Provine 1980), so that an integration of modern morphology with neo-Darwinism is still in the offing. Yet, as Gould pointed out throughout his career, still too little is known and understood about the mechanisms of morphological change that underlie macroevolutionary processes.

It is impossible at this point in time to even guess whether there could be a possible causal relationship between Gould’s success as a science popularizer and the recent renewed interest in macroevolution and morphology. Similarly, it is uncertain whether Gould’s (1977) first tome has contributed to the recent renaissance of developmental biology and its use in trying to address macroevolutionary questions. But in any case, morphologists may find it easier to get a sympathetic ear from those holding the purse-strings in academia and funding agencies because of the consciousness raising effects of Steven Jay Gould’s popular writings.

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DOMINIQUE G HOMBERGER
 Department of Biological Sciences,
 202 Life Sciences Building,
 Louisiana State University,
 Baton Rouge, LA 70803-1715, USA
 (Email, zodhomb@lsu.edu)