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Stephen J. Gould's Legacy: Nature, History, Society

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Individuals, hierarchies, and the levels of selection.
A chapter in Gould's evolutionary theory

Abstract

To follow Gould's distinction between microevolution and macroevolution, Charles Darwin's theory of natural selection was a theory about microevolution, selection being the differential reproductive success eventually obtained by individual organisms among which there is competition for access to vital resources, reproductive partners included in the case of sexual selection. This theory implies (1) that individuals organisms can be unambiguously recognized, (2) that what identifies the level, or levels, of selection is interaction rather than inheritance, and (3) that levels of selection other than the individual organism are either nonexistent, or of little relevance.

In Darwin's gradualistic view of evolution there was no scope for macroevolution as a distinct phenomenon, as everything was explained as the product of the steadily accumulation of microevolutionary modifications. In this context, even the distinction between simple intraspecific variety and 'true' species is distinctly blurred.

However, if Gould & Eldredge's (1971, 1977) model of punctuated equilibria represents the actual, or prevailing mode of evolution, species boundaries become less arbitrary and species eventually emerge with an individuality that turns them into potential candidates to the status of units of selection.

Eventually, the individual organism and the species were singled out by Gould as the most important levels of selection, in a conventional hierarchy that begins with the gene and proceeds through the cell, the individual organism, the deme and the species, up to supraspecific clades of any age and size. In this expanded view of natural selection, the species becomes the unit of macroevolution, similar to the role played by the individual organism in microevolution.

In his magnum opus on *The Structure of Evolutionary Theory* (2002), Gould explained at length (1) why the units of selection must be identified, *contra* Dawkins, in the units of interaction rather than in the units of inheritance, (2) why Williams' (1966) and Dawkins' (1976) efforts to construe all selection processes as inherently reducible to selection at the level of gene are based on a faulty reductionism where 'bookkeeping' takes the place of causality, and (3) why the whole theory of selection (and evolution) can be developed by reference to a single hierarchy of levels, or units, of selection, rather than to parallel hierarchies of units of interaction and inheritance as suggested by Eldredge (1985) and Williams (1992).

In a couple of passages, Gould (2002) admitted that "the current evolutionary hierarchy in styles of individuality arose both historically and contingently", that "nature presents some exception to the principle of a fully nested hierarchy for evolutionary individuals", and cited

with full approval Buss' (1987) insightful remark, that "the major features of evolution were shaped during periods of transition between units of selection".
Recent advances in fields as diverse as symbiosis, lateral gene transfer and the evolution of development suggest that to shoehorn biological systems into the levels of the so-called evolutionary hierarchy is an oversimplification of the complexity of many systems and, especially, of the way they are generated throughout ontogeny. Even the concept of individual organism, as a physically independent unit with its precise origin in time does not apply so easily and universally as generally accepted. Evolution, indeed, is not simply matter of change of 'individuals,' at any and all levels of the gene-to-clade hierarchy, but also matter of change of the units (or levels) of selection and of the rules of change themselves.