

## Letter to the Editor

# Species *versus* gene selection

S.C. Tsakas

*Agricultural University of Athens, Department of Genetics, Votanikos, 118.55 Athens Greece; and University of California at Irvine, Department of Ecology and Evolutionary Biology, Irvine, CA 92717, USA*

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Species selection has been recently promoted (Gould & Eldredge, 1988a, 1988b) as the driving force in macroevolution, and viewed as an explanation for the variability in rates observed, both temporally and spatially, at the phenotypic level. This has rekindled the contention between microevolutionists (Maynard Smith, 1987, 1988) and macroevolutionists, which has existed since Darwin's era.

One of the main differences between micro (molecular) and macro (phenotypic) evolution, is the stasis stage possible for the latter, while the molecular evolution proceeds on as far as the lineage continues. Stabilizing selection (Charlesworth *et al.*, 1982), proposed by microevolutionists to explain this, is countered by the proposal of species selection by macroevolutionists. Further complicating the matter, are the existing exceptions which weaken both concepts. As Gould & Eldredge so imaginatively put it, "Can we really hope to explain why the world holds more than a million species of insects and only a dozen or so of priapulids by relative adaptive success of their equally complex morphology alone?"

It is a pleasant surprise to find that we are able to propose an answer to this and other difficult evolutionary questions, such as: Why, for example, do limpets, lingula, depnoi fishes, horse shoe crabs, dragonflies, orthoptera, tortoises, crocodiles, platypus, and bats remain in comparative evolutionary stasis, even though they live under variable environments, compete with other species and have such long existences? Is this the result of sampling or does a common denominator exist? The answer can be found in the speciation burst hypothesis (Tsakas & David, 1986), and the common characteristic is that their most sensitive stages are protected or less exposed to ultraviolet light and/or cosmic rays and consequently experience low mutation rates, especially chromosomal. Chromosomal aberrations have long been proposed as being responsible for speciation events (White, 1978), and then for macroevolution. However, it is necessary to clarify what less exposed means here: the limpets are less exposed by having a short larval stage and by the shielding of their shell; the depnoi fishes, by being aquatic and burrowing into the dry lake bed; the dragonflies, by having aquatic and covered larval forms; the orthoptera, by developing in the earth and/or living there; the crocodiles, tortoises and platypus, by burying their eggs and being semiaquatic; in addition, the former two have thick

external protection; and bats are less exposed by being nocturnal or inhabiting caves.

Thus species, with lower exposure during their sensitive stages, and/or less exposure to their gametic material finally, will be expected to show lower diversity and macroevolutionary rates. Evidence of the same kind is found in the plant world. Such a case occurs between phanerogamic and cryptogamic plants, wherein the latter whose gametic material is much less exposed, shows a significantly lower phenotypic diversity than the phanerogamic. Ultraviolet light is experimentally used as a mutagenic factor on pollen for artificially produced mutations.

Microevolution, therefore, through its variability in mutation rate, appears to affect macroevolution, in addition to the already known influences through genetic drift and natural selection. It is important to notice that higher mutation rates may "trigger" natural selection by providing more variability and genetic drift there by increasing genetic isolation. Another outcome, is the increased genetic load (genetic deaths), especially in species with small effective population size (Kimura *et al.*, 1963), and thus, an increased risk of extinction (Tsakas & David, 1987). From this point of view, the advantage of the insect kingdom is evident. The sustained high level of diversity in insects, comparative to the priapulids, can be due to their generally greater exposure, while they are able to bear the consequent genetic load due to their enormous population size.

It seems apparent that macroevolution is probably more related to microevolutionary processes than ever before considered, and population genetics may provide surprisingly useful answers if the correct questions are addressed and there is a willingness to listen.

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