

Problems in evolution

Mark Ridley

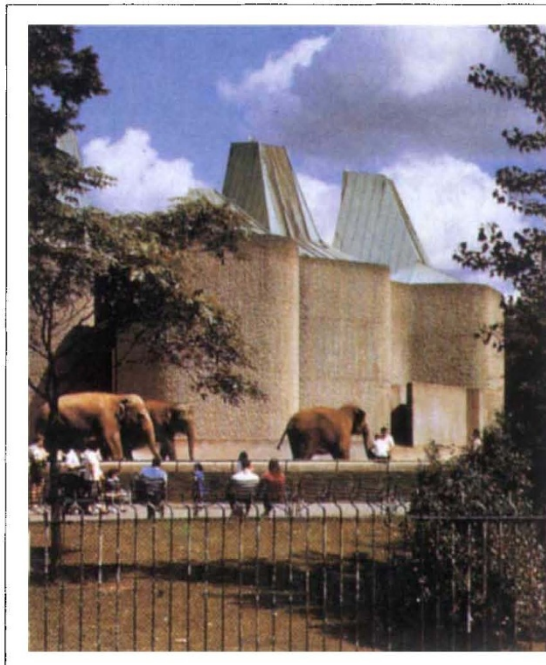
Natural Selection: Domains, Levels, and Challenges. By George C. Williams. Oxford University Press: 1992. Pp. 208. £35, \$55 (hbk); £14.95, \$24.95 (pbk).

WITH *Adaptation and Natural Selection* (1966) and *Sex and Evolution* (1975), G. C. Williams released a pair of books that have influenced evolutionary biology in the late twentieth century perhaps more than any other pair of books by any other biologist. *Adaptation and Natural Selection* destroyed the theory of group selection so comprehensively that woolly headed group-selective arguments have vanished from the professional literature. In *Sex and Evolution* he argued so persuasively that sexual reproduction is the outstanding evolutionary puzzle that evolutionary biologists now discuss sex more than perhaps any other topic.

Williams's new book is less monolithic than either of its predecessors, and combines the argumentative style of both. It contains a series of reflections on controversial topics in modern evolutionary biology, together with suggestions about some further unsolved problems that ought to be receiving more attention. It ranges widely, and many kinds of specialist could sample it for inspiration and fresh thinking. Only the future can reveal whether it will have as much influence as his previous books, but it does contain several ideas that are big enough to make it a possibility.

Williams's explanation for "stasis" (that is, fossil lineages that do not change in form for long periods) is probably the biggest new idea in the book. There are three main existing ideas, and he disagrees with them all. S. J. Gould has suggested that species have "genetic and developmental coherences that resist selective pressures"; but Williams reasons, from microevolutionary evidence, that this "is clearly not true". Others have suggested that species stay the same because, when conditions change, they migrate; but Williams dismisses this as a "fable [that] will not bear close examination" — the selective forces almost certainly alter when the biogeographic range of a species shifts a few thousand miles. Williams also doubts whether stabilizing selection, at least in its simplest form, is the reason because there is so much evidence of rapid change in modern populations.

So why is the form of fossils so often constant through time? Consider the evolutionary pattern of the modern three-spined stickleback. In North America, it is primarily a coastal species, but innumer-



LONDON Zoo's architecture is an exhibit in its own right. Building and rebuilding has taken place almost continuously since 1827, revealing as much about the history of design and construction as that of animal display. The wittily zoomorphic Elephant and Rhino Pavilion of 1962–5, pictured here, was one of a succession of large buildings erected between 1958 and 1976. As an exercise in New Brutalism, it broke with international orthodoxy in zoo architecture, combining "the fantastic with the functional". This photograph is taken from *The Buildings of London Zoo* by Peter Guillery (Royal Commission on the Historical Monuments of England, £12.95 (pbk)).

able forms have evolved as the fish have migrated upstream into individual freshwater tributaries. Williams suggests these derived forms may be evolutionarily short-lived, as their niches will soon disappear; but the main coastal niche, and its ancestral form of the stickleback, will persist for longer. An imaginary series of fossil samples through time would be most likely to draw out the unchanging ancestral lineage, as it occupies its enduring, and little changing, niche. "The appearance of stasis in the fossil record would result from an enormous variability in the persistence of ecological niches."

The explanation is an instance of what Williams prefers to call "clade selection": the process by which different lineages survive better or worse through evolutionary time. It is more familiar as "species selection", but Williams dislikes that expression because (he suggests) the process is no more typical of species than of lineages (or clades) at higher and lower taxonomic levels. In the exemplary sticklebacks, clade selection would be operating among lineages within one (at least conventionally recognized) species. Williams also rejects any connection between clade selection and the theory of punctuated equilibrium, and argues that evolutionary change is not particularly concentrated in speciation events (indeed he concludes that "speciation in the usual [Mayrian] sense has no special significance for macroevolution"), and that "the peripheral isolate theory would seem to be of little use". But the general thesis of the book should warm the hearts of palaeobiologists: "the microevolutionary process that adequately describes evolution in a population is an utterly inadequate account of the Earth's biota". The uncoupling of microevolution and macro-

evolution in Williams's theory is not, as in the orthodox view, due to speciation, but to that "enormous variability in the persistence of ecological niches". Much of the microevolution we observe takes place in ephemeral niches, whereas the enduring niches determine evolution on the grand scale.

Williams discusses many other questions. He argues that "Haldane's dilemma" (the problem of genetic load) was never solved, even though interest in it has faded away; he raises questions about unobserved adaptations that might reasonably be expected — viviparous turtles, more facultative sex determination, more flexibility of metabolic temperatures; and has a wonderful section in which he argues that female pheromones in moths are not sexual signals at all. There are short asides, about topics such as cultural evolution or play, that I suspect would be better places to start new research than the whole monographs that have been written on them. There are so many ideas that no reader will agree with them all. Thus I am sure the question Williams raises about the comparative method really *has* been answered, and I believe his criticisms of M. T. Ghiselin and D. L. Hull's species-as-individual concept are beside the point. But these are small matters in a delightful book. As with any frontier investigation, it will attract some scoffers — the citation police, the factually fixated, anal-retentive equation-processors, and dullards and philistines generally. But they can all be ignored. And — who knows? — the book could free some of them from their vices. □

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