ical compositions, spatial and temporal distributions, and field relations, separate chapters are devoted to the classic localities such as those at and around Kaiserstuhl, Phalaborwa, Ice River, Arusha and Oldoinyo Lengai. The well-known arguments of origin via immiscibility versus fractionation versus direct partial melting; melt versus fluid metasomatism as related to fenitization; and the iron and alkali enrichment versus depletion schemes are displayed with blunt force. Fortunately, new experimental data are given that help to resolve some of these issues, but even

the experimentalists stand their separate ground on details. Whether there are direct or indirect links of carbonatites to kimberlites, nephelinites, melilitites and phonolites is another issue not taken lightly. Because of the economic importance of many elements in carbonatites, the debate will no doubt increase as new data are acquired. Keep your score card handy. □

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Hybrid mystery

Mark Ridley

Speciation and Its Consequences. Edited by Daniel Otte and John A. Endler. Sinauer Associates, Sunderland, Massachusetts: 1989. Pp. 679. Hbk \$50, £40; pbk \$29.95, £23.95. Distributed in Britain by W.H. Freeman.

JOHN Herschel, in a grand phrase that Darwin knew well, described the question of how new species arise as "the mystery of mysteries". The mystery has now been cut down to size. We know the general mechanisms by which it must take place; but the exact circumstances and processes of speciation still remain rather too mysterious, given that it is probably the most researched area of evolutionary biology. It is characteristic that a multi-author book on the subject should contain not only a suggestion (by Coyne and Orr) that the biological species concept (see below) and allopatric theory of speciation are "the only two real advances in our understanding of speciation", but also several persuasive criticisms of the biological species concept including one (by Lynch) which concludes, from evidence that cannot just be brushed aside, that "peripheral isolates speciation" (the most popular allopatric model) "may be even rarer than sympatric speciation among vertebrates".

Lynch supports his conclusion with a combination of biogeographical and phylogenetic evidence. He has picked several vertebrate taxa whose phylogenies are well known and looked at the geographical ranges of closely related (sister) species pairs. He classifies the pairs according to whether their ranges are substantially overlapping (suggestive of sympatric speciation), non-overlapping with one much smaller than the other (peripheral isolate speciation), or have little overlap and similar sizes (vicariance — either allopatric speciation by subdivision, or parapatric speciation). For a sample of 66 speciation events, "the vicariant model explains 71%, the peripheral

isolates model initially explains 15%, and sympatric speciation explains 6%".

Reinforcement has now emerged as a question almost as big as geography. The idea is that if two populations have evolved some way towards speciation, hybrids between them may be disadvantaged, and selection will favour assortative mating within each population (each is selected to mate only with its own type, to avoid producing hybrids). It is an old idea, dating back to Wallace, and has been more or less taken for granted in the literature. The theory seemed sound, it had been illustrated by artificial selection experiments, and it explained various lines of field evidence. But in the past ten years, this has all been turned on its head. In his chapter, Butlin reviews the developments. The theory has been so undermined that he can remark: "since theory suggests that reinforcement is improbable, the evidence must be very strong before a putative example can be accepted". He explodes the artificial selection experiments and finds all sorts of alternatives to reinforcement in the field evidence, leaving the conclusion that reproductive isolation only ever evolves as a consequence of other evolutionary changes. I feel rather reactionary about these developments. It is one thing to pick holes in an interpretation, but another to show it is wrong; reinforcement still seems to me the most natural explanation of such phenomena as character displacement and artificially selective reproductive divergence. The counter-theory, moreover, presupposes either unstable polymorphisms or special genetic models of choice that may not be the only possibilities. But reinforcement has at least been turned back into something to be argued for, and not taken for granted.

Coyne and Orr show, from comparative data and ingenious breeding experiments in the fruitfly *Drosophila*, that the early stages of speciation result from changes in X-linked genes, and divergence at genes on other chromosomes follow. They explain this tendency by the more rapid evolution of recessive genes on the sex chromosomes than on autosomes (where recessive genes are less often expressed).

The difference between sex chromosomes and autosomes does not exist for dominant genes, and Coyne and Orr conclude that speciation is genetically peculiar, being initiated particularly by recessive genes.

Templeton and Cracraft both criticize Mayr's biological species concept in a manner that I believe distorts the concept in a subtle but crucial manner. Mayr defined a species as a group of "interbreeding populations reproductively isolated from other such groups". The definition mentions two properties: interbreeding and reproductive isolation. Templeton (following H.E.H. Paterson) renames this the "isolation" species concept and treats it as if it defined species only in terms of evolved isolation mechanisms. For example, it is possible that two recently diverged populations, living in separate geographical areas, could form two interbreeding groups, even though there was no evolved isolating mechanism between them (such as a difference in reproductive behaviour). Templeton produces this case as a damaging counter-example to Mayr's definition, and a reason to prefer a concept that defines a species by interbreeding, regardless of whether it possesses any isolating mechanisms. The argument, however, hypostatizes one part of Mayr's definition and ignores the other. Mayr defined species by interbreeding too — he put it first, before reproductive isolation. Moreover, the "reproductively isolated" in Mayr's definition need not mean an evolved isolating mechanism. The allopatric populations of Templeton's would-be counter-example do satisfy Mayr's definition: they are reproductively isolated, even if only by a geographical barrier.

There is more to the dispute, however. Templeton argues for a "cohesion species concept" to include asexual as well as sexual species; here there is a genuine disagreement. And some statements of the biological species concept have explicitly mentioned isolation mechanisms, rather than mere reproductive isolation. But the biological species concept has always explained species integrity by gene flow, and to oppose it on the grounds that it is an "isolation" rather than an "interbreeding" species concept is, I believe, bogus.

The 25 chapters comprising the book are all by experts, and (with, to my taste, only two exceptions) attain a consistently high standard. They cover all research methods — population and ecological genetics, systematics and ecology: only the palaeobiologists are left out, but even they should find as much to interest them here as the rest of us. □

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