

from outbred Swiss Albino stock for their respective high and low antibody responses to immunisation with sheep red blood cells (Biozzi *et al.*, *Annls Immun. Inst. Pasteur, Paris*, **115**, 965; 1968). Since the original studies with sheep erythrocytes, a number of reports has shown that this separate responsiveness is maintained when using just about any other antigen, including a few which do not require T cells to give a good response. This has gradually led to the view that the genetic difference in the two strains resides at the level of the B lymphocyte, resulting in a relative inability of Ab/L B cells to differentiate and proliferate to antibody-producing cells following contact with antigen.

The results of Howard *et al.* would seem to put this notion to rest. These authors showed that the antigens levan and dextran B1355, both of which do not require T cells (and both being highly branched polysaccharides), give equivalent antibody responsiveness in the two strains. Furthermore if a haptenic chemical grouping, DNP, was coupled to an antigen which normally gives separate responsiveness (polymerised bacterial flagellin or POL, in this case) then high and low responses to DNP were also obtained, whereas equivalent responses were obtained if the DNP was chemically coupled to levan. This indicates that there is nothing intrinsically defective or different in the ability of B cells with anti-DNP specificity to proliferate and make anti-DNP antibodies in the Ab/L strain. The 'defect' rather is, as the authors say, extrinsic to the lymphocyte population.

What then is the nature of this extrinsic difference? The paper by Weiner and Bandieri suggests that it may reside in the way antigens are handled by macrophages. When peritoneal macrophages were isolated from the two strains and cultured overnight, a striking difference in the morphological appearance of the cells became apparent: the majority of Ab/H macrophages were well spread out, with an irregular cytoplasmic outline and many extensions, whereas most of the Ab/L macrophages assumed a spherical conformation and lacked the many prolongations or extensions so characteristic of macrophages cultured on plastic surfaces. When the authors looked at the way macrophages handled a number of antigens which always give separate responsiveness in the two strains they found these antigens were taken up faster by Ab/L macrophages. Furthermore membrane-bound antigen disappeared rapidly from Ab/L macrophages whereas it persisted in Ab/H macrophages. Intracellular digestion of antigen was more rapid in the Ab/L macrophages and

this may be related to their containing higher levels of lysosomal enzymes.

Thus macrophages from the 'low' responders seemed, if anything, hyperactive. These differences were, however, not observed if the antigen tested with the macrophages was levan. The authors therefore speculate that this hyperactivity might render various antigens more poorly immunogenic in the Ab/L line. Whatever the explanation, it seems that macrophages can express genes which help control antibody responses in these strains.

It also may be of considerable interest to those studying the roles of macrophages in cellular immunity that the Ab/H and Ab/L strains give equivalent responses for virtually all types of such reactions thus far tested, including allograft responses, contact sensitivity to chemicals, and graft-versus-host reactions.

Species richness in geological time

from Peter D. Moore

A CONCEPT which has received widespread support among ecologists is that the species richness of a stable habitat increases steadily through geological time. The justification for such support can largely be traced back to the work of Southwood (*J. Anim. Ecol.*, **30**, 1; 1961) who demonstrated a positive linear correlation between the number of Quaternary subfossil records of various British tree taxa and the number of insect species associated with them. If one assumes that the antiquity and persistence of a tree is reflected by the abundance of its subfossil occurrences, then Southwood's work implies that the longer a tree has been present in these islands in any quantity, the more likely it is that many insect species will be associated with it. The finding suggests that the Quaternary time span has not been sufficient to saturate any tree's resources as an invertebrate microhabitat.

Other data have suggested that the relationship between species richness and time is asymptotic, richness rising rapidly at first, then levelling off. The time scale involved before saturation may be reckoned in decades or centuries rather than millenia. For example, Simberloff and Wilson (*Ecology*, **50**, 278; 1969) exterminated the invertebrate fauna of mangrove islands off the Florida coast and observed that reinvasion occurred in an asymptotic fashion over a relatively short period.

Since Southwood's results are so often used to justify the concept of geological time as a critical factor determining richness, Strong has now attempted to re-analyse Southwood's

data (*Proc. natn. Acad. Sci., U.S.A.*, **71**, 2766; 1974). Strong points out a logical inadequacy in Southwood's basic assumption, in that he confounds the antiquity of tree taxa with their past abundance and distribution. To resolve this confusion, Strong plots each of Southwood's tree taxa on a graph relating the logarithm of taxon range (estimated by the number of kilometre square samples in which it is now found) to the logarithm of the number of associated species (using Southwood's figures). The graph shows a strong positive linear correlation. He also found that the distribution of recently introduced taxa about the regression line is not significantly different from that of the native species. Thus recent introductions are saturated with insect species to the same extent as the natives: otherwise they would have fewer insect species than would be expected from a consideration of their area of occupation.

The conclusion from this work is that the area of distribution of a tree is more important as a determinant of its insect species richness than is its antiquity. Evidently the more abundant a tree species is now the more likely it is to have left many fossils in recent Quaternary sediments; since Southwood did not take into consideration the age of subfossil finds, it is not surprising that he found a positive correlation between fossil abundance and insect species richness.

It is unfortunate that Strong did not use more up to date information concerning the insect species richness of certain trees. For example the estimate for larch of about 15 species is far too low, but most values are probably underestimates and the general form of the relationship would probably not have been altered. Strong is wrong, however, on this basis to deny the assertion by May (in *Stability and Complexity in Model Ecosystems*, Princeton, 1973) that although species richness is well regulated on an ecological time scale the regulated level will increase in geological time. Strong has provided no information on what happens to species richness on a geological time scale except that any change in richness is of little statistical significance in comparison with short-term changes. The variation of species richness over geological periods remains an area for conjecture.

Correction

An error was introduced in the final drafting of the article "Oppression or Altruism in Insect Unions?" (*Nature* **251**, 101; 1974). The (female) workers are of course diploid, like their sister queens, and not haploid as stated.