COMMENTARY

Wu's genic view of speciation

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Professor Wu deals almost exclusively with the 'situation in *Drosophila* and more specifically the *melanogaster* branch of the genus'. To what extent these findings can be generalized and extended to all animals and all eukaryotes remains a question. I for one am impressed by the extraordinary diversity of speciation phenomena in animals and plants. At one extreme are the African cichlid fishes in which reproductive communities, that is biological species, are seemingly kept isolated by a few male preference genes of the females; at the other end are such cases of slow speciation as that of two diverse groups of plants. One in eastern North America, the other at the Pacific coast of eastern Asia which became geographically isolated at least 8 million years ago and yet remain members of a single species without the development of cross sterility or of taxonomic differences.

Postmating isolating mechanisms are important in *Drosophila* but seem to be absent in certain groups of birds. Species of the duck genus *Anas* seem to be perfectly fertile with each other and in backcrosses although they coexist over much of the northern hemisphere with about one hybrid in 20 000 collected ducks.

Considering how many different definitions of the species concept we now have, one might expect a number of different speciation processes. I have commented on this problem in two of my recent papers (Mayr, 1988, 1996).

Most of the so-called species concepts are simply ways of delimiting species taxa. There really are only two species concepts, the typological one, species status determined by degree of difference, and the biological one, the species denoting a reproductive community. With the typological species concept having been abandoned for sexually reproducing populations by all knowledgeable authors the question becomes, how is a new reproductive community established?

The answer is by the acquisition of one or several isolating mechanisms. It seems to depend on the type of organism which is the favoured isolating mechanism. In birds and many other animals it is apparently behaviour. In some groups of grasshoppers it is chromosomal rearrangements (post-zygotic) mechanisms. In *Drosophila* it is behaviour and sterility genes. Let me now after this preamble, pick up specifically some of Wu's statements. If I understand Wu correctly he seems to think that the genic cohesion of a biological species serves as a whole as its isolating mechanism. This is not the traditional concept of the biological species. The reproductive isolation (RI) between two species may be effected by a few genes that prevent interbreeding or by a module of genes doing this. Such genes or modules must fit harmoniously into the total genotype, but this does not make the genotype as a whole an isolating mechanism. I believe this is where Wu and I would disagree.

Wu correctly recognizes the enormous importance of sexual selection in the speciation process of many kinds of animals. This means that an extremely limited number of genes may play a decisive role in establishing a new reproductive community. The recent work on speciation in fishes (cichlids, sticklebacks, whitefishes, etc.) excellently illustrates this phenomenon. It is this which permits sympatric speciation in these groups. All it needs is a strict correlation between a niche preference and a mate preference character. A completely consistent scenario can be inferred without any reference to the genic basis. The sudden occurrence of interspecific hybrids among cichlids of Lake Victoria in east Africa when the water became too opaque for the ready recognition of male-specific characters illustrates this well. Even within a single genus or family different environmental factors may induce or facilitate speciation. Isolating mechanisms may be merely a by-product of (ecological) adaptation to a new niche or they may be a meiotic accident resulting in an incompatible chromosomal restructuring or be the product of a female preference for a new male variant. For most animal groups, particularly the marine ones, we have no clues whatsoever what facilitates speciation. Here even the nature of the separating barriers between different water masses is unknown.

I am not sure that Wu fully understands that the isolating mechanisms are only a small portion of the total genotype. Wu suggests as one possibility 'one may insist on the strict application of BSC is complete reproductive isolation across the whole genome'. But why would one postulate 'a complete reproductive isolation across the whole genome' when one knows that the isolating mechanism comprises only a very small portion of the genome? But then I do not understand the claim on page 8: 'thus the very essence does not have to include RI'. How important the RI is, is well demonstrated by hybrid zones where two well-balanced well-adapted incipient species meet, produce hybrids of reduced fitness which are in time eliminated and replaced by new immigrants from the parental semispecies. This shows the importance of RI.

In my discussions of the cohesive nature of the genotype of a biological species I have nowhere suggested, so far as I remember, that the genotype as a whole serves as an isolating mechanism.

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Yes, the genetic basis of each isolating mechanism must fit harmoniously into the rest of the genotype. But it serves as a module with a specific objective. I for one cannot see any justification for modifying or abandoning the biological species concept (BSC) because the isolating mechanisms are only part but not the whole genotype.

A naturalist like myself has trouble with the question whether 'the gene or the genome is the unit of speciation' (p. 14). For me it is the population that is the unit of speciation (even in cases of sympatric speciation).

I gather that Wu feels that there is some conflict between the adaptational process, which is at all times continuous in a population, and the speciation process. I cannot see such a conflict, particularly in cases where speciation is driven by sexual selection. Adaptation and speciation are controlled by different portions of the genotype and the only restriction there is that the interaction of these two components must be harmonious.

Let me not get lost in detail. Wu has conveniently summarized his conclusions in two sentences. 'The process of speciation is gene-based but RI is fundamentally a genomic concept. Speciation defined by the criteria of RI, as does BSC, would be inconsistent with the process of speciation itself' (p. 23). This is a strictly reductionist claim. One could say equally well, speciation is a population phenomenon and the RI is carried out by the phenotypes of individuals. The RI of species may develop as a by-product of the genetic restructuring of populations during the process of adaptation. However, RI can also be the result of sexual selection and be limited to a very small portion of the genotype. Nothing in the recent genic analyses has weakened the BSC in which the species is seen as a reproductive community. There is an enormous diversity in the genetic foundation of new species. The genetic control of RI of two species may occupy only a very small portion of the total genotype, but it must fit harmoniously into this genotype. At the present time we have no knowledge yet of the genetic nature of the isolating mechanisms of most phyla of animals.

References

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