

COMMENTARY

How do chromosomal changes fit in?

J. BRITTON-DAVIDIAN

Laboratoire Génétique et Environnement, Institut des Sciences de l'Evolution, Université Montpellier II, Montpellier Cedex, France

Wu's (2001) review on the process of speciation brings to my mind several comments that I would like to make as to what is accomplished by the approach he advocates. Wu's (2001) proposal is to update the biological species concept (BSC) by in fact revising what he considers as a consensual notion of reproductive isolation (RI), i.e. complete reproductive isolation. Many interpretations exist of the BSC and I am not convinced that the adherence to this particular definition has been as strict among biologists as Wu (2001) contends. It is clear that few biologists would argue against the designation of taxa as species when they occur in sympatry and between which the barrier to gene exchange is absolute. But, as this is an end product in the process of speciation, it does not tell us much about how the process originated. That incipient species can and do exchange genes is evident from the numerous studies on hybrid zones and examples of horizontal transfer through introgression between what appear to be full-fledged species (Hewitt, 1988; Hardies *et al.*, 2000). However, Wu's (2001) strongest contribution is to provide a conceptual framework of the process of speciation based on a mosaic nature of incipient species genomes, although the task is no less arduous experimentally. This should spur additional empirical and theoretical studies on gene flow taking into account the selective differential in permeability of genomes.

Wu (2001) wishes to refocus the concept of speciation away from RI and onto the process of differential adaptation. In doing so, I find his argumentation sometimes confusing leading to statements such as '...the very essence (of speciation) does not have to include RI...' (p. 8). In fact, implicit in his definition of species is that they are differentially adapted groups that upon contact are not able to share genes controlling the adaptive characters. Given this, how will they maintain this divergence if not by a barrier to gene exchange?

The extensive discussion on the nature of the barrier to gene exchange in Wu's (2001) paper is worthwhile, in that it emphasizes the shift in focus that has occurred in recent studies from models of speciation by mutation and

drift to those analysing the contribution of differential adaptive traits to RI. However, a potential drawback of this shift in emphasis as argued by Wu (2001) may be the setting aside of the role of chromosomal rearrangements in reducing gene flow. This issue is somewhat dodged with an analogy dealing with the status of lineages differing solely by the presence a toxin gene and its repressor in one and their absence in the other, leading to hybrid inviability of their progeny. What then of karyotypically divergent taxa such as the chromosomal races of the house mouse, the interbreeding between at least some of which can produce sterile hybrids (Johanisson & Winking, 1994; Britton-Davidian *et al.*, 2000). It is evident as stated by Wu (2001) that the study of RI and its consequences are required to assess the extent of the barrier to gene exchange, and this applies to this case as well. However, these chromosomal races clearly illustrate three aspects of karyotypic change: (i) chromosomal divergence can have an effect on hybrid fertility and thus on the extent of gene flow, (ii) this type of change can occur very rapidly over a short evolutionary time scale, and (iii) it is not genic, which means that it would have been completely overlooked in any gene-based study of reproductive isolation.

The point I would like to make is that this type of change exists and may have consequences for the rates of evolutionary pathways to speciation. Because this process includes RI leading to differential adaptation which Wu (2001) wishes to de-emphasize, does not mean that it should be minimized as a field of research. Although the emphasis has moved away from models of chromosomal speciation as expounded by White (1978), interest in the consequences of chromosomal change as a barrier to gene flow has been renewed by the exciting studies on sunflowers and *Drosophila* (Rieseberg *et al.*, 1999; Noor *et al.*, 2001). Such analyses argue for a role of chromosomal rearrangements in reducing gene flow through suppression of recombination (see Rieseberg, 2001). When linked to some chromosomal rearrangements, isolation genes decrease gene flow in larger regions of the genome than in those where the former are absent. Although additional data are required to assess the relative importance of this role of chromosomal rearrangements, these results are totally germane to the mosaic genome view of species of Wu (2001). Who knows, future research in this field may even indicate that rearrangements are isolating mechanisms in the sense that they would be selected for by their effect on recombination, or that they are adaptive traits in that a change in structure may modify gene expression during interphase (Capanna & Redi, 1994; Auffray *et al.*, 2001; Rieseberg, 2001).

Correspondence: Janice Britton-Davidian, Laboratoire Génétique and Environnement, Institut des Sciences de l'Evolution (UMR5554), Université Montpellier II, Pl. E. Bataillon, cc65, 34095 Montpellier Cedex 5, France. Tel.: +33 4 67 14 39 10; e-mail: britton@isem.univ-montp2.fr

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