Genetics of Speciation

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The American Genetics Association (AGA) is a nonprofit membership society whose mission is to promote the study of genetics. To meet this obligation, the AGA publishes the Journal of Heredity and promotes research in all fields of genetics. The latter is accomplished through an annual meeting and symposium, as well as by sponsorship of special events, such as workshops and symposia in areas of interest to the AGA.

In 2006, the annual meeting and symposium of the AGA was held from 21–24 July in Vancouver, British Columbia. The symposium, cosponsored with Molecular Ecology, was titled “Genetics of Speciation” and attracted close to 300 participants. Allen Orr was the recipient of the 2006 Wilhelmine Key Lectureship and gave the keynote lecture on “Speciation in Drosophila: from Phenotypes to Molecules.”

Six articles from the symposium, which focus mostly on the genetics of postzygotic isolation, are published in this issue; another six more ecologically orientated papers will appear in Molecular Ecology.

The lead article was authored by Allen Orr, J. P. Masly, and Nitin Phadnis, who review what we know about the genetics of intrinsic postzygotic reproductive isolation, at least with respect to genes underlying hybrid incompatibilities. Based on the 4 such genes that had been published by the symposium date (July 2006), Orr et al. note several striking patterns. In particular, most of these genes are evolving rapidly due to natural selection, a finding that supports the neo-Darwinian contention that reproductive isolation typically evolves as a by-product of adaptation. Given the seeming unity of these results, Orr et al. ask the provocative question “Is the genetics of postzygotic isolation wrapped up?” That is, will more work in this area likely yield any truly novel results?

Fortunately, new results discussed by Orr et al. suggest, in fact, that we are in for some real surprises. Most startling is the discovery that genetic conflict may frequently be the cause of rapid evolution of genes underlying intrinsic postzygotic barriers rather than adaptation to a new environment. Second, there is now evidence that microchromosomal rearrangements may sometimes be the cause of hybrid incompatibilities rather than the traditional Dobzhansky–Muller model.

Another of the symposium speakers, Mohamed Noor, has been a leader in exploring nontraditional mechanisms for the evolution of intrinsic postzygotic barriers. In particular, he has developed and empirically tested a model in which genomic regions with low recombination (such as chromosomal inversions) allow Dobzhansky–Muller incompatibilities to accumulate despite ongoing gene flow. In this issue, Cirulli and Noor localize the break points of an inversion between two Drosophila species. Contrary to most other studies, there were no shared repetitive sequences between the 2 break point regions. Thus, the cause of the inversion remains a mystery.

Most attempts to localize hybrid incompatibilities have employed experimental crosses, in which associations between molecular markers and sterility or inviability are used to identify chromosomal segments or genes that contribute to hybrid disorders. Although this approach has been highly successful, it is difficult to apply to nonmodel organisms, which can be challenging to rear in the laboratory or greenhouse. Thus, a number of authors have explored the possibility of using patterns of introgression in natural hybrid zones to localize genes or chromosomal rearrangements that contribute to isolation. In “Searching the Genomes of Inbred Mouse Strains for Incompatibilities that Reproductively Isolate Their Wild Relatives,” Payseur and Place successfully employ this strategy to identify pairs of loci that may contribute to reproductive isolation between 2 mice species.

One of the early conclusions (above) from studies of the genes causing hybrid incompatibilities is that postzygotic isolation often appears to be a by-product of adaptation. Thus, Leonie Moyle asks whether quantitative trait loci (QTLs) underlying putative prezygotic isolating traits in tomatoes, which presumably have been shaped by natural selection, colocalize with QTLs for hybrid sterility. Unfortunately, there is little evidence for a causal association between prezygotic and postzygotic isolation.

Intrinsic postzygotic isolation may also arise through genome doubling or polyploidy. However, polyploidy has other genetic and phenotypic consequences beyond reproductive isolation. One of the most interesting of these (and potentially most important) is the observation that large shifts in gene expression may accompany polyploidization. Because polyploidy may involve both interspecific hybridization and genome doubling, the effects of these two processes on gene expression often are confounded. In “Evolution of Duplicate Gene Expression in Polyploid and Hybrid Plants,”
Keith Adams reviews the rapidly expanding literature on this topic. He reports that large numbers of genes exhibit shifts in gene expression in hybrids and polyploids; that some of the changes appear to be repeatable, whereas others are seemingly stochastic; and that hybridization has a more profound effect on gene expression patterns than does genome doubling.

The final paper by Brouillette et al. represents a departure from the other studies in that its focus is on the genetics of extrinsic postzygotic isolation, in this case adaptation to sand dunes by a hybrid sunflower species, *Helianthus anomalus* (see cover photo). They ask whether traits important to the survival of *H. anomalus* are controlled by QTLs with large effect; large QTLs will respond more quickly to selection and might have facilitated the rapid adaptation of *H. anomalus* to the dune habitat. The results were mixed. Two major QTLs for leaf nitrogen uptake were identified, but Brouillette et al. failed to detect QTLs for leaf carbon isotope discrimination.

These studies illustrate the rapid progress being made toward understanding speciation—Darwin’s “Mystery of Mysteries”—and foreshadow future discoveries. As concluded by Orr et al., “it is . . . encouraging to realize that future work in the genetics of speciation may demand considerable changes in our views, not minor and inconsequential modifications.”