

Genetics and the origin of species: the continuing synthesis a symposium in honor of Richard G. Harrison

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This is a special issue of *Genetica* that has its origins in a symposium held in honor of Richard G. Harrison at Ithaca, New York on July 22–23. Former students of Rick Harrison organized the symposium and most of the speakers were former students, as well. The quality and breadth of the talks were a testament to Rick's influence as a thinker, synthesizer, and mentor and it is only appropriate to reflect on Rick's contributions to the fields of evolutionary ecology, systematics, and genetics in this preface to the symposium articles.

Although R.G. Harrison began his scientific career as a biochemist studying the structure of myosin (Cohen et al. 1970; Harrison et al. 1971); an interest in natural history, ecology, systematics, and evolution brought him to Cornell University in the mid-1970s where he pursued his Ph.D. in the Section of Ecology and Systematics under the guidance of Peter Brussard. This was an exciting period in the field of evolutionary biology. Allozymes, which were the first molecular genetic markers that could be easily studied in

most living organisms, were being used by evolutionary biologists to measure levels of genetic variation in natural populations, to reconstruct phylogenies and patterns of genetic differentiation, and to explore species boundaries and patterns of gene exchange in hybrid zones. Recognizing the utility of these markers for reconstructing the evolutionary history of insect groups that contained cryptic species, Rick studied allozyme variation in eastern North American field crickets and demonstrated that a compelling model of allochromic speciation could not be true (Harrison 1979a).

At the same time, Rick was intrigued by the flight polymorphisms of crickets and how these dispersal polymorphisms were maintained in natural populations (Harrison 1979b). While this interest did not lead to a major research program, it did lead to a major review and synthesis paper (Harrison 1980), which would establish a pattern that has characterized Rick's career—a quick and critical mind that cuts through clutter, sees patterns, can construct models to explain the patterns, but at the same time accepts that the models may not be true and does not cleave so strongly to a model or a hypothesis that he ignores contrary evidence.

After finishing his Ph.D. work, Rick was offered an assistant professorship at Yale University, where he began the work on hybrid zones, for which he may, perhaps, be best known. Once again, this interest was spurred by what he discovered in field crickets—a hybrid zone between the sister species *Gryllus firmus* and *G. pennsylvanicus*. Work on this hybrid zone led to a series of papers in the 1980s (Harrison and Arnold 1982; Harrison 1983, 1985, 1989; Rand and Harrison 1989a) that provided a description of the zone as well as insights into the factors that might partially isolate the two taxa. One important finding to emerge from this work was that the hybrid zone appeared

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to have a mosaic, rather than clinal structure (Rand and Harrison 1989a, b; Harrison 1989). Rick and his student, David Rand, developed the implications of this finding in some detail, noting that hybrid zones with such a geographic structure would be expected to form when interacting taxa are ecologically or behaviorally distinct and when the structure of the environment, which will often form a patchwork of habitats, determines the structure of the zone. This model countered the prevalent model in the literature; namely, that hybrid zones are clines maintained by the balance between selection against hybrids in the zone and gene flow into the zone, and that hybrids are intrinsically less fit than parental individuals. One consequence of mosaic structure noted by Harrison and Rand (1989) is that extinction of one or the other interacting taxa in a zone is unlikely and that reinforcement is more likely.

Rick's work on hybrid zones in the 1980s culminated in the most widely cited (more than 600 times) paper he has yet written, a synthesis of the hybrid zone literature titled—*Hybrid Zones: Windows on Evolutionary Process* (Harrison 1990). In this article, Rick provides the definition of hybrid zones that has since been adopted by virtually all hybrid zone workers:

“Hybrid zones are interactions between genetically distinct groups of individuals resulting in at least some offspring of mixed ancestry. Pure populations of the two genetically distinct groups are found outside the zone of interaction”.

The paper is a *tour de force* that provides advice on distinguishing primary from secondary intergradation, ways to study the fitness of hybrids (he advocates cohort analysis), and the means by which patterns of introgression in hybrid zones can be used to dissect the genetic architecture of reproductive barriers. Moreover, in this paper, Rick persuasively argues that genetic isolation must be considered a property of individual genes (or chromosomal segments), not a characteristic of entire genomes, and that reinforcement lacks a strong evidentiary basis. It is not that Rick was opposed to the idea that reinforcement can occur in hybrid zones, he simply wanted better evidence. Indeed, he pointed out at the close of the paper that reproductive character displacement, the outcome of reinforcement, has the potential to give rise to a hybrid zone population that is not only isolated from the species with which it is interacting, but from its allopatric parental populations. Thus, hybrid zones can be the source of new species.

The Harrison laboratory has continued to publish seminal papers on hybrid zones over the course of the past 20 years, on both *Gryllus* and other model systems, such as *Limenitis* butterflies (Mullen et al. 2008). The work on *Gryllus* has demonstrated that the *G. firmus*-*G. pennsylvanicus* zone is bimodal; that is, the majority of crickets in

the zone are not hybrids, but instead appear to be similar to the parental species, and that many other hybrid zones present the same pattern (Harrison and Bogdanowicz 1997). This bimodality appears to be attributable to strong behavioral premating barriers between *G. pennsylvanicus* females and *G. firmus* males, as well as to the failure of *G. pennsylvanicus* males to induce normal oviposition in *G. firmus* males after mating (Maroja et al. 2009b). An emphasis on careful ecological studies, which has been a hallmark of the Harrison laboratory since the 1980s (Howard and Harrison 1984a, b) continued to provide insights into distribution patterns of crickets and the geographic structure of hybrid zones; namely, that the spatial scale at which a hybrid zone is sampled affects its apparent structure. A hybrid zone may appear clinal at one scale and mosaic at another (Ross and Harrison 2002).

Mitochondrial DNA

Rick's interest in mitochondrial DNA was initially motivated by his search for markers that could do a better job than allozymes of differentiating *G. firmus* and *G. pennsylvanicus*. However, very soon after he began the foray into mitochondrial DNA, he and his students made a surprising discovery that helped establish his reputation as a leading molecular evolutionist—individual crickets harbor mitochondrial DNA size variation and heteroplasmic mothers give rise to heteroplasmic offspring (Harrison et al. 1985). This paper was soon followed by others, which described the transmission genetics and molecular population genetics of mtDNA size variation (Rand and Harrison 1986a, b), and which demonstrated that *G. firmus* and *G. pennsylvanicus* have distinct mtDNA lineages (Harrison et al. 1987). In 1989, Rick published one of the definitive reviews and syntheses of mtDNA as a genetic marker. In this paper, he noted that rates of evolution are heterogeneous across the mtDNA molecule, that rates of evolution vary across taxa, and that properties of mtDNA defined for one group of organisms cannot be assumed to be properties of the molecule in other groups. He also voiced a theme that was to become familiar to his readers—allele phylogenies are not equivalent to organism phylogenies, and species boundaries and species relationships may need to be defined gene by gene.

By the early 1990s, Rick's laboratory was widely regarded as one of the leading mtDNA laboratories in the world. Over the course of the next two decades, he and his students and colleagues would use studies of mtDNA to assess evolutionary relationships, population genetic structure, and species delimitations of a variety of different animal groups (Normark et al. 1991; Brown et al. 1994; Nummerger and Harrison 1995; Harrison et al. 2003; Hatch

et al. 2006; Maroja et al. 2007; Nydam and Harrison 2007). They also used studies of mtDNA to test the avian constraint hypothesis (Stanley and Harrison 1999), models for the origin of hybrid zones (Willett et al. 1997), the impact of past glaciations on population differentiation and speciation (Sperling and Harrison 1994), the origin of the genus *Schistocerca* in North America (Lovejoy et al. 2006), hypotheses of Pleistocene speciation in copepods (Thum and Harrison 2009), and the origin of invasive beetle populations (Carter et al. 2009, 2010).

Molecular changes at speciation

In 1991, Harrison wrote his second great review and synthesis article, *Molecular Changes at Speciation*. In this review, he examines the question of whether speciation leaves a distinctive signature on patterns of molecular genetic variation and whether variation in DNA sequences (or allozymes) can provide an understanding of the geography of speciation or the evolutionary forces that operated during a speciation event. Although he concludes that speciation events do not leave unique signatures and that molecular genetic variation cannot provide unequivocal evidence in favor of a particular sequence of events, nevertheless such evidence together with a detailed knowledge of the biology of organisms will make it possible to at least assign high probabilities to some scenarios and low probabilities to others. Continuing the theme that allele phylogenies are not equivalent to organism phylogenies, he also emphasizes that unlinked markers will sort independently at divergence events. Therefore, one must generate sequence data from many unlinked genes in order to increase the probability of recovering the true phylogeny of a group of organisms. Moreover, data from many genes allows one to distinguish between reduction in variation due to selective sweeps and reduction in variation due to population bottlenecks and to evaluate patterns of introgression across the genome. Although the focus of the paper is what evolutionists can learn from studies of genetic differentiation, Rick ends the paper by noting that the ultimate goal of evolutionary geneticists studying speciation is to map and eventually clone the genes responsible for reproductive isolation between closely related organisms.

The genetics of reproductive isolation

The pursuit of this ultimate goal is evident in the work of the Harrison laboratory on the European corn borer and its recent focus on fertilization proteins in *Gryllus* and other model organisms, including *Heliconius* butterflies (Walters

and Harrison 2010). In the United States, three races of the European corn borer that differ in pheromone communication and life history have been described. Through QTL mapping, the Harrison laboratory has been able to map the factors that control pheromone production and male behavioral response (Dopman et al. 2004) and show that strain exclusivity occurs at the Triose-phosphate isomerase (*Tpi*) locus (Dopman et al. 2005). Moreover, through a candidate gene approach, the Harrison lab has demonstrated that pheromone binding protein and the $\Delta 11$ desaturase gene are not responsible for the reproductive isolation (Willett and Harrison 1999a, b; Geiler and Harrison 2010). The work on fertilization proteins in *Gryllus* has been even more fruitful. Here Rick and his students have demonstrated that seminal protein genes evolve more rapidly than housekeeping genes and that the rate of fixation of nonsynonymous substitutions is three times higher in the seminal protein genes than in the housekeeping genes (Andrés et al. 2006). Moreover, proteomic studies and studies of differential introgression across the *G. pennsylvanicus* and *G. firmus* hybrid zone have identified two seminal proteins, AG-0005F and AG-0334P, that are divergent between the two species and show near-zero introgression across the zone (Andrés et al. 2008; Maroja et al. 2009a). Thus, after more than 30 years of work the Harrison lab now has two candidate genes to work with that may account for some of the reproductive isolation between *G. pennsylvanicus* and *G. firmus*.

Species concepts

The third great review and synthesis paper written by Rick Harrison, *Linking evolutionary pattern and process: The relevance of species concepts for the study of speciation*, was published in 1998, in the book, *Endless Forms: Species and Speciation*. In this paper he explains, critiques, and organizes species concepts and definitions and considers how they might provide a context for studies of speciation. He suggests that each species or lineage has a distinctive life history and that different groups of biologists tend to focus on different parts of the life history of a species, which is one of the reasons they often talk past one another. What characterizes this chapter, and so much of Rick's work, is the clarity of thought, the willingness to be generous and critical at the same time, and the ability to give credit for the insightful aspects of concepts and definitions while not shying away from criticizing their limitations. He cuts through the confusion and obfuscation in a manner that illuminates without over-simplification. It is a rare gift and one that we can only hope that he continues to share with us. It has been too long since Rick last found the

time to really organize and publish his thoughts on an important evolutionary topic.

Concluding remarks

Although Rick's contributions as an evolutionary biologist are sure to have a lasting impact on the field, his contributions as a teacher and mentor may be even more significant. There are few evolutionary biologists in the world who have trained more undergraduate and graduate students and postdoctoral fellows than Rick Harrison. Indeed, his influence as a mentor and colleague is so far-reaching that it is difficult to identify anyone in the field who has not had some kind of meaningful interaction with him, whether through a visit to his laboratory or through a conversation at a conference. That influence was on display in the symposium held in Rick's honor at Cornell in July of this year and in the papers that follow. We believe they are a fitting tribute to one of the most admired and inspirational figures in the field of evolutionary biology.

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