

The Status of Scolytid Genetics—A Reductionist's View¹

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As biologists considering studies of scolytid genetics we are fortunate that an insect model exists that has been the target of genetic analyses on both the individual and population levels for most of the twentieth century. The knowledge base associated with *Drosophila melanogaster*³ and congenics is staggering, and it is a tribute to scientific inquiry that so much is known about organisms of such little economic importance. The goal of the classical genetic crosses of *D. melanogaster* begun in the lab of T.H. Morgan in 1909 was to infer the genetic basis of the phenotype (phenotype → gene). The development of P-element-mediated transformation (Rubin and Spradling 1982) allows "reverse genetic" studies where the gene of choice is placed into the organism and the resulting individual is assayed to infer the phenotypic product of the gene (gene → phenotype). During the period between the advent of each of these approaches with *Drosophila*, serendipity and intensive screening procedures revealed a wide array of morphological, developmental, and behavioral mutants; biochemical studies characterized nucleic acids and proteins; genetic studies led to the development of physical, cytological maps of polytene chromosomes; and, soon, the entire genome will be sequenced (Merriam and others 1991). The phenomenon of transposition ("jumping genes") has been actively investigated in *D. melanogaster* (Green 1980, Engels 1983), and the transposons themselves have been the targets of studies of population genetics (Charlesworth and Langley 1989). In addition to the biochemical and molecular work, the drosophilids have been the subject of studies of population biology, phylogeny, and pheromone production (Bartlett and others 1986, Kaneshiro 1988, Singh 1989).

In the Scolytidae, no mutants have been isolated, prospects for long-term culture have not been developed, most crosses have been performed to determine species status of wild populations rather than to assay for intraspecific phenotypic variants, and few biochemical reactions have been characterized. When evaluated against the background of *Drosophila* genetics, the status of scolytid genetics can be described as primitive at best. Thus, it is in an area of enormous opportunity, where,

because of the stature of the insects in forest management, minor scientific gains may have large economic impacts.

However, rather than repeat the past 80 years of *Drosophila* genetics with the Scolytidae, we should apply the *Drosophila* knowledge base to scolytids as often as possible. No scolytid is likely to become a model for eukaryotic biology, but by applying the tools used with *Drosophila*, we may discover some interesting and perhaps unique biological phenomena in the Scolytidae.

For the purposes of organization, it is useful to divide scolytid genetics into the reductional and holistic approaches. By reductional I mean the analysis of biochemical, morphological, or behavioral traits of individuals and the interpretation of the results from a molecular or mechanistic perspective. By holistic I mean the analysis of the same traits from pooled samples of individuals and the interpretation of the results from an ecological or population perspective. The following are several reductional areas of study that seem relevant to scolytid genetics.

1) **Genetic analysis of morpho- and chemosystematic characters:** A variety of useful morphological characters have been identified for distinguishing scolytid taxa (Bright 1976, Bright 1992, Bright and Stock 1982, S.L. Wood 1982). However, mutations in these characters have not been studied in a systematic fashion [e.g., red vs. white eye color, vestigial vs. wild-type (normal) wing morphology in *Drosophila*]. Recently there has been considerable interest in establishing chemical phenotypes for some species in the Scolytidae, and using the newly discovered chemosystematic characters in constructing phylogenetic relationships (cuticular hydrocarbons—Page and others 1990a, b, 1992; Bright 1992; chirality of pheromone components—Seybold and others 1992b; and migration of metabolic enzymes in starch gels—Cane and others 1990b, and other studies).

However, while typical chemical phenotypes have been characterized, nothing is known about the genetic regulation leading to these phenotypes and possible mutations that might lead to altered chemical phenotypes. Furthermore, because of the insensitivity of the chemical assays, the chemical phenotypes have often been determined on pooled samples of individuals, whereas we ought to evaluate the phenotypes of individuals. It will be important to standardize laboratory and statistical procedures used to evaluate a range of individual normal chemotypes so that mutants can be recognized when they are encountered. This is not an easy problem. For example, the cuticular hydrocarbon profile from a species typically contains 60 to 80 hydrocarbon components which vary in presence,

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³An organization called the *Drosophila* Information Service catalogs and communicates biological (mostly genetic) data about *D. melanogaster* and related species. In addition, there is an encyclopedia of *Drosophila* mutations authored by Lindsley and Grell, and various stock cultures of wild type and mutant strains are maintained around the world.

absence, and quantity. Here are two interesting problems that seem appropriate to this topic.

(a) **Chirality of ipsdienol as a heritable trait of individual male *Ips pini*.** *Ips pini* occurs in two basic pheromone types (Birch and others 1980, Lanier and others 1972, Lanier and others 1980, Miller 1990, Teale 1990, Miller and others 1989). The eastern form produces and responds maximally to ipsdienol with an enantiomeric composition of 30 percent to 60 percent-(4R)-(-), whereas the western form produces and responds maximally to ipsdienol with an enantiomeric composition of 93 percent to 100 percent-(4R)-(-). The eastern form produces and responds strongly to lanierone (Teale and others 1991); the response of the western form is enhanced by lanierone, but males from this population do not appear to produce lanierone (Seybold and others 1992c). Populations from North America have been surveyed (Miller 1990, Seybold and others 1992b), and a zone of sympatry between the forms appears to occur in British Columbia. Teale (1990) has crossed eastern (New York) and western (Arizona) forms and demonstrated heritable patterns to the chirality of male-produced ipsdienol. He has also found a correlation between the response to enantiomeric blends by males and production in the eastern form of *I. pini*. We are pursuing similar studies with the western population.

(b) **Ipsenol as chemotypic marker for two populations of *Ips mexicanus*.** *Ips mexicanus* occurs as three distinct populations in western North America: coastal in *Pinus radiata*, *P. muricata*, and *P. contorta*; montane in *P. contorta murrayana* and *P. contorta latifolia*; and interior in other *Pinus* spp. The *I. plastographus* and *I. integer* complex can be broken down into three similar entities. In a survey of the enantiomeric composition of ipsenol and ipsdienol produced by male *Ips*, we have found that the coastal and montane populations of *I. mexicanus* differ in their ipsenol-ipsdienol phenotype. Coastal *I. mexicanus* produce ~90 percent-(4R)-(-)-ipsdienol, whereas montane *I. mexicanus* produce the same ipsdienol and >99 percent-(4S)-(-)-ipsenol. We have not studied an interior population of *I. mexicanus*. Thus, interbreeding studies of coastal and montane populations of *I. mexicanus* could be followed by traditional traits such as larval:egg niche ratios (Lanier 1967), as well as by ipsenol production. Coastal *I. mexicanus* could be treated as a

strain of *I. mexicanus* that is deficient in the ability to produce ipsenol.

2) **Characterization of biochemical pathways:** To accompany classical genetic analyses, we need to expand our knowledge of bark beetle biochemistry. Because of a series of pheromone biosynthesis studies with *I. pini* and *I. paraconfusus* using labelled precursors (Fish and others 1979, 1984, Hendry and others 1980, Vanderwel and Oelschläger 1987, Vanderwel 1991), these two species make particularly good candidates for initial studies on the enzymes involved in pheromone biosynthesis.

3) **Sex ratio condition:** One intriguing genetic problem that bears further study is the sex ratio condition discovered in *Ips latidens* and other species (Lanier and Oliver 1966). In this phenomenon individuals from certain populations carried a maternally transmitted factor that resulted in selective mortality of male embryos. A similar sex ratio condition also occurs in *Drosophila* spp. (Sakaguchi and others 1965, Ikeda 1965, Novitski and others 1965), and in recent studies the causative microorganisms have been isolated and cultured (Hackett and others 1986). Other sex ratio distortions in *Drosophila* spp. are caused by chromosomal and extrachromosomal factors. Molecular studies of a distortion in the latter group (hybrid dysgenesis) led to the discovery of the P-element transposon (Rubin and Spradling 1982). Application of modern biochemical and molecular biological techniques to the sex ratio condition in *Ips* may lead to similar discoveries. Lanier never published the fact that the condition also occurs in another species of *Ips* [*confusus* (LeConte)] and in the scolytid genera *Pityophthorus* and *Dendroctonus*.

4) **Construct gene libraries:** With the cooperation of Carol Alosi (Pacific Southwest Research Station, USDA Forest Service), we have begun to construct a c-DNA library of genes for *I. pini*. Large numbers of male and female western *I. pini* have been frozen for this purpose. Genomic libraries for the major scolytid species should be constructed and made centrally available to all researchers (the beginnings of a Scolytid Information Service?).