Letter to the Editor

Codon Usage and the Origin of P Elements
Jeffrey R. Powell and Jennifer M. Gleason
Department of Biology, Yale University

Codon usage in Drosophila is highly variable both from gene to gene within a species as well as within a gene between species (Shields et al. 1988; Staturi and Sullivan 1989; Sharp and Lloyd 1993). An extreme shift in codon usage for the same gene among species was documented for Alcohol dehydrogenase (Adh) between Drosophila melanogaster and Drosophila willistoni (Anderson, Carew, and Powell 1993). The major shift occurred for codons that are twofold redundant and can use C or U (T) in the third position. In D. melanogaster Adh, as well as generally in this species, the C-ending codons predominate, whereas in D. willistoni Adh, all such codon families shift to using predominantly U. Two more genes have now been sequenced in D. willistoni and at least based on these three genes, this shift seems to be characteristic of the species (table 1). While the transposable P element was first discovered in D. melanogaster, it has been strongly suggested that it may have originated in D. willistoni and have been acquired by D. melanogaster by horizontal transfer (Daniels et al. 1990; Kidwell 1993; Clark, Maddison, and Kidwell 1994). Here we ask the question as to whether the codon usage pattern of the one protein-coding gene in P elements (the transposase) is more similar to that characteristic of D. melanogaster or D. willistoni.

Table 1 summarizes the patterns. The P element has a codon usage pattern more similar to D. willistoni than to D. melanogaster. It is important to point out that the data for the P element shown in this table is for a copy isolated from D. melanogaster; P element sequences in D. willistoni are greater than 99% identical at the nucleotide level (Clark, Maddison, and Kidwell 1994), so codon usage for copies from this latter species is virtually identical. For the six amino acids with two codons that differ by ending in C or U the sample sizes are greater than 99% identical at the nucleotide level. In D. willistoni Adh, such codon families shift to using predominantly U. Two amino acids sup port the similarity between P elements and D. willistoni.

Table 1

<table>
<thead>
<tr>
<th>AMINO ACID</th>
<th>D. MELANOGASTER</th>
<th>D. WILLISTONI</th>
</tr>
</thead>
<tbody>
<tr>
<td>Gly</td>
<td>6 6 17 23%</td>
<td>9 8 46 8</td>
</tr>
<tr>
<td>GGC</td>
<td>8 14 71 43%</td>
<td>/ 12 41 7</td>
</tr>
<tr>
<td>GAA</td>
<td>5 4 41 28%</td>
<td>2 7 22 13</td>
</tr>
<tr>
<td>GGG</td>
<td>0 1 17 6%</td>
<td>0 0 6 4</td>
</tr>
</tbody>
</table>

Key words: codon usage bias, Drosophila willistoni, P elements, horizontal transfer.

Address for correspondence and reprints: Jeffrey R. Powell, Department of Biology, Yale University, New Haven, Connecticut 06520-8104; e-mail: jeffrey.powell@yale.edu.


Often significantly different from genes in D. melanogaster, especially the gene with the largest sample of codons (per), while it is in no case significantly different from the codon usage of the three D. willistoni genes. The “signature” of D. willistoni codon usage, the shift to U-ending codons at twofold degenerate sites, is evident in the P element.

This shift can also occur when C and U are redundant in the first position as for Leu (table 1). Again, both the D. willistoni genes and the P element use U-beginning Leu codons very frequently, whereas they are rarely used in D. melanogaster. Other amino acids support the similarity betwee P elements and D. willistoni.

Note.—Genus = Adh = alcohol dehydrogenase, Sod = superoxide dismutase, per = period. Numbers in the body of the table are the number of times each codon is used in that gene. “Overall” is for more than 250,000 codons available at the time of the review referenced. Sources of data: 1 Kristman (1983); 2 Kwiatowski et al. (1994); 3 Citri et al. (1987); 4 Sharp and Lloyd (1993); 5 Anderson, Carew, and Powell (1993); 6 J. M. Gleason (unpublished); 7 Rio, Laski, and Rubin (1986).
hybrid dysgenesis is induced by males from strains col-
lected from nature at different times, D. willistoni was more similar to its new "host." 

The most commonly used codon for glycine in D. willistoni is GGC, yet this codon is very common in the P element.

We can only conclude that codon usage in the P element is more similar to that in D. willistoni than in D. melanogaster. Assuming that transposable elements and the genomes in which they reside are subject to similar selection for codon usage and/or mutation bias, this observation supports the contention that the P element has a longer evolutionary history in D. willistoni than in D. melanogaster and, therefore, is added evidence supporting the hypothesis of horizontal transfer from D. willistoni to D. melanogaster. Based on whether hybrid dysgenesis is induced by males from strains collected from nature at different times, D. melanogaster probably acquired P elements about 45 years ago (Kidwell 1983). Assuming 10–20 generations per year, this implies that 450–900 generations have not been sufficient for the P element to evolve a codon usage pattern more similar to its new "host."

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LITERATURE CITED


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