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S Subramanian**Abstract**

Divergence of the sequences of reproductive genes has been accelerated by positive selection.

Significance and context

Secreted accessory gland proteins (Acp) have important roles in reproduction in *Drosophila* and also have interesting patterns of evolutionary change. They are involved in sperm storage, increasing the egg-laying rate of mated females, influencing egg hatchability, sperm competition and intersexual genomic conflict, and have thus drawn the attention of biologists. It has been shown by two-dimensional gel electrophoresis that Acps and other male reproductive proteins are twice as diverse as non-reproductive proteins. Until now the nucleotide sequences encoding the Acps were unknown and it was impossible to determine what factors had led to the apparent high divergence of this large class of proteins. Sequence conservation has been used as a criterion for identifying functionally important genes or gene regions, but functionally important regions can also be revealed in divergent genes if positive selection is involved in their adaptive divergence. A strong signature of positive selection for change is that the number of non-synonymous amino-acid substitutions per non-synonymous site significantly exceeds the number of synonymous substitutions per synonymous site. With the help of the recently completed genomic sequence of *Drosophila melanogaster*, Swanson *et al.* have now compared the gene sequences of *Acp* from *D. simulans* with *D. melanogaster*, and their results reveal that the rapid divergence of many reproductive genes between these species is due to positive Darwinian selection.

Key results

Swanson and colleagues compared the sequences of ESTs from the male accessory gland of *D. simulans* to those of orthologs from its relative *D. melanogaster* and showed rapid divergence in many of these reproductive genes. To identify the ESTs that are likely to be expressed specifically in accessory gland cells, the authors carried out a differential hybridization of a male-specific *D. simulans* accessory gland cDNA library against cDNA from female *D. simulans* males lacking Acps. A total of 212 independent genes was identified, 176 of which matched putative protein-coding regions in the annotated *D. melanogaster* genome; the remaining 36 matched 5' or 3' non-coding regions. Among the 176 independent genes, 19 sequences (that is, 11%) contained protein-coding regions with an excess of non-synonymous over synonymous changes. The interesting feature is that *Acp* genes had a significantly

greater level of non-synonymous substitution compared to genes not specifically expressed in accessory glands. Swanson *et al.* estimate that their EST screening has identified approximately 90% of the male accessory gland genes, including 57 novel genes. Their results suggest that the divergence of the reproductive gene sequences has been accelerated by positive selection.

Conclusions

The authors have called the above approach 'evolutionary EST analysis' and propose that it can be used to calculate the divergence of protein families.

Reporter's comments

The authors' objective was to identify potential candidate genes whose divergence was promoted by positive selection. To identify positive selection they used the synonymous to non-synonymous amino-acid substitution ratios. Using their 'evolutionary EST approach', in which EST sequences from a species are compared to a closely related one whose complete genomic sequence is known, they have shown that different evolutionary forces affect the *Acp* genes compared to non-*Acp* genes. This approach promises to be a powerful means of identifying potential targets of positive selection at a genomic scale and is readily applicable to any tissue or organism. Such studies could enable the demarcation of very closely related species using molecular data.

Table of links

Proceedings of the National Academy of Sciences of the United States of America

References

1. Swanson WJ, Clark AG, Waldrip-Dail HM, Wolfner MF, Aquadro CF: Evolutionary EST analysis identifies rapidly evolving male reproductive proteins in *Drosophila*. Proc Natl Acad Sci U S A. 2001, 98: 7375-7379. 0027-8424