EVOLUTIONARY BIOLOGY

Voyage of an ancient *mariner*

Margaret G. Kidwell

It is an ancient Mariner
And he stoppeth one of three.

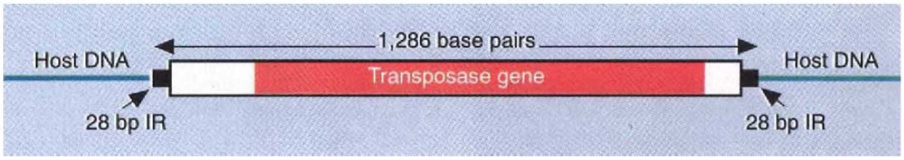
QUESTIONS about the origin and evolutionary age of mobile genetic elements have been around since Barbara McClintock first described 'controlling elements' in maize almost half a century ago. Now, with the help of the polymerase chain reaction (PCR), answers are beginning to emerge. The report by Hugh Robertson on page 241 of this issue[1] strongly suggests that the mobile *Drosophila* element, *mariner*, is of ancient origin. Robertson also describes a broad, but patchy, distribution of this element family, together with some unexpected relationships among *mariner* elements from the same and different species of host insect.

The *mariner* element was first identified in *Drosophila mauritiana*[2]. This species is restricted to the island of Mauritius and is a close relative of that genetic work-horse, the cosmopolitan species *Drosophila melanogaster*. At a little over one kilobase in length (see figure), members of the *mariner* family are relatively small[3]. They belong to a major class of transposable elements which have short inverted terminal repeats and differ from members of the other major class, the retrovirus-like elements, in using a DNA, rather than an RNA intermediate in transposition.

At the time of their discovery, only eight years ago, there seemed to be little reason to think that *mariner* elements would be any more widespread than the isolated species that carry them. More recent studies have indicated that these elements are broadly distributed in species of the melanogaster subgroup of *Drosophila*, although they are absent from *D. melanogaster* itself[4]. However, in more distantly related drosophilids, strongly hybridizing elements were detected only in a single species *Zaprionus tuberculatus*, which is estimated to have diverged from *D. mauritiana* at least 50 million years ago[4].

Now Robertson[1] has extended the search far beyond the Diptera. A previous serendipitous discovery of *mariner*-like sequences in the cecropid moth *Hyalophora cecropia*[5] allowed him to design degenerate PCR primers to the only two conserved regions of contiguous amino-acid similarity between the *mariner* elements of *D. mauritiana* and *H. cecropia*. He reports the presence of these elements in ten other species, representing six additional orders, including insects as diverse as bees, mosquitoes, silverfish, cat fleas and earwigs.

Four principal subfamilies of *mariner* elements have been identified so far, with the promise of more to follow. One new significant finding is the clear indication that *mariner* is very old; some of the subfamilies were apparently differentiated before the divergence of their arthropod host lineages 200–300 million years ago. In like fashion, similarities between predicted proteins of the *D. mauritiana mariner* element and the *Tc1* element from the nematode *Caenorhabditis elegans* have also been recently verified[6].



Structure of an active *D. mauritiana mariner* element inserted into host DNA. A single open reading frame constitutes the transposase gene. IR indicates inverted terminal repeats.

The presence of several subfamilies of *mariner* elements in several individual insect species is puzzling, as is the observation that some distantly related insects carry closely related *mariners*. Early divergence of the subfamilies with subsequent loss in some descendant species, together with occasional horizontal transfer across species boundaries, may provide the most likely explanation of the observed patterns. But other hypotheses to explain these results cannot yet be ruled out.

Among transposable elements, the *mariner* family seems not to be alone in its antiquity and broad, somewhat unorthodox, current distribution. For example, the *Ty1-copia* and *Ty3-gypsy* retrovirus-like transposable elements also appear to be very old and to be ubiquitous in plant genomes[7,8]. Like *mariner*, some incongruencies between the distribution patterns of these retrotransposons and their host phylogenies have implicated occasional horizontal transfer, sometimes between species in different kingdoms. The essential nature of 'jumping genes' may make them more prone than non-mobile genes to hop across species boundaries. This capability may also promote their long-term evolutionary survival.

These observations are not only of basic biological interest, but also have implications for potential applications. There is considerable interest in the development of generalized DNA vectors for the transformation of insects. However, the *Drosophila* P element that was used in pioneering experiments to develop this technology[9] unfortunately has a restricted host range; conversely, although the host range of some retrovirus-like elements is broad, other properties make their use for this purpose questionable.

Prospects for the application and development of *mariner* in genetic engineering are altogether more promising. In addition to its structural similarity to the P element, active *mariner* elements from *D. mauritiana* can integrate, in a stable fashion, into the germ line of another species from which they are naturally absent[10]. So the newly revealed broad host range of *mariner*-like sequences augers well for their possible use in tagging and cloning and for their development as effective transformation vectors over a wide range of arthropods.

Although some broad patterns in these new results seem to be emerging, caution in their interpretation is called for pending a better understanding of the evolution of multigene families. Transposable elements may evolve at faster rates than single copy genes, or may evolve differently in other ways. But can differential rates, or modes, of evolution explain the existence of unusually diverse elements in the same genome? How often does horizontal transfer of DNA sequences occur? What is the nature of the vectors involved? Is the host species merely a passive observer of the sometimes frenetic activity of parasitic DNA? Alternatively, do host and element genomes interact together for their mutual benefit? As usual, as old questions are settled a fresh and larger crop of them arises:

But tell me, tell me, speak again,
Thy soft response renewing —
What makes that ship drive on so fast?
What is the ocean doing?

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