

The value of a good fossil record

The timing of evolutionary events can be estimated from both fossil and molecular data, but what if these methods do not agree? *Dr Jan Pawlowski and Colomban de Vargas* argue that it may not always be the fossil record that is inadequate.

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The utility of the fossil record for determining the emergence of different groups of organisms has recently been questioned by molecular-clock based studies¹⁻⁴. Some researchers consider that differences in divergence times inferred from palaeontological and molecular data are due to gaps in the fossil record. Certainly, establishing the first appearance and range of a given species from the available fossils is problematic, and the accuracy of the fossil record depends both on the good preservation of specimens and on the proper identification of their morphological characters.

However, molecular-based phylogenies may also be subject to important biases. Although this debate has so far focused on the accuracy of the fossil record, in view of the growing use of independent data sets in phylogeny reconstruction, it is imperative to ask whether the molecular data used to test its reliability are themselves accurate.

Simple assumptions

The approach of using DNA sequence comparisons to infer taxonomic relationships has long since demonstrated its utility. However, its use as a "time machine" is much more controversial.

To infer origination times for species from molecular data requires the assumption that the rates of nucleotide substitution in a given gene remain constant or nearly constant with time. This is an astonishingly simplistic view given the complexity of biological processes. In spite of evidence that this hypothesis is incorrect, very little has been done to develop more accurate methods of molecular clock calibration. In comparison fossil dates have many advantages based as they are on the direct evidence of a given specimen being found in a given stratum.

Accurately dating the first appearance of a morphologically distinct species depends on the completeness of the fossil data. Ideally, a complete and continuous fossil record would provide reliable calibration points for all species. Although it is unlikely that such an ideal fossil record exists, we believe that some microfossils, and particularly the planktonic foraminifera, approach these optimal conditions. How then can we assess the fidelity of their fossil record?

A well-supported record

As Paul Pearson has discussed, there are several internal measures of accuracy, which make planktonic foraminifera one of the best stratigraphic tools for micropalaeontologists. Planktonic foraminifera are extremely abundant and widespread in marine sediment samples, and the preservation of their calcareous tests is usually excellent. In consequence they are widely used for calibration purposes by the oil industry and in marine geological research.

Large numbers of planktonic foraminiferal lineages have been extensively and independently examined based on hundreds of stratigraphic sequences. The ancestor-descendent relations within these lineages have been established using both morphological similarities and stratigraphic occurrences. Very often specimens with intermediate morphologies representing evolutionary links

between one species and another (intergrading morphotypes) are also available⁵. Moreover, the occurrences of planktonic foraminifera in marine strata have been precisely calibrated by radioactive dating and tested with independent biochronological data sets⁶.

The quality of the planktonic foraminiferal fossil record has also recently been tested using independent molecular criteria. Molecular phylogenies based on ribosomal DNA sequences confirm the majority of hypotheses based on stratigraphy and morphology alone⁷. This congruence lends confidence to the materials and methods used by micropalaeontologists, and supports the reliability of their phylogenetic reconstructions. Can we be similarly confident in the molecular phylogenetic approach?

Speeding and slowing clocks

By using multiple and accurate foraminiferal stratigraphic data to calibrate the molecular phylogenies, we were able to estimate the absolute rates of nucleotide substitution in their ribosomal genes⁷⁻⁹. These genes are the most commonly used for phylogenetic reconstructions and are generally assumed to be reliable chronometers of molecular evolution.

The absolute rates of substitution in ribosomal DNA have been estimated for only a few groups of organisms, including insects¹⁰, diatoms¹¹, echinoids¹² and vertebrates¹³. Between and within these groups, substitution rates vary from two- to five-fold. In foraminifera, even higher rates of variation are observed. For example, ribosomal genes in some planktonic foraminifera evolve fifty times faster than in some bottom living species⁸. Within the planktonic foraminifera, the rates are relatively constant in spinose globigerinids, but vary seven-fold in non-spinose globorotaliids⁹. These examples clearly indicate that the molecular clocks in foraminifera tick at very different rates.

Is it then justified to test the accuracy of the fossil record using the molecular clock hypothesis, when this requires extrapolation between groups with scarce fossil data? Can we even use the rates calculated within a group of organisms to infer the origin of this group? Can we exclude the possibility that rates of evolution change over time? Specifically, what if the emergence of a group of organisms coincides with an initial acceleration of substitution rates followed by a slowdown or period of molecular stasis?

The importance of time-checks

An accurate knowledge of a continuous fossil record is essential to detect such a phenomenon. Recently, in insect phylogeny, an example of episodic evolution in ribosomal genes has been detected in the earliest (or stem) branch leading to *diptera*, which was attributed to a change in directional mutation pressure¹⁰. Similar episodes have also been observed in the molecular phylogenies of foraminifera, suggesting that occasional accelerations of substitution rate have occurred at the time of emergence of some taxonomic groups.

Testing the hypothesis of an episodic character of molecular evolution seems particularly important in view of the recent controversy about the timing of metazoan radiation and origin of some groups of vertebrates¹⁻⁴. Perhaps we should consider the possibility that there have been significant changes in the rates of nucleotide substitution in taxa with remote origins before sending palaeontologists out to fill perceived gaps in the fossil record.

Before we can interpret the molecular origins of taxa a better understanding of molecular macroevolutionary processes is needed. This will only arise from more extensive use of combined stratigraphic and molecular data. In our opinion, the fossil record of planktonic foraminifera and other microfossils have a unique and unexplored potential for evaluating the dynamics of molecular evolutionary change.

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