Obituary

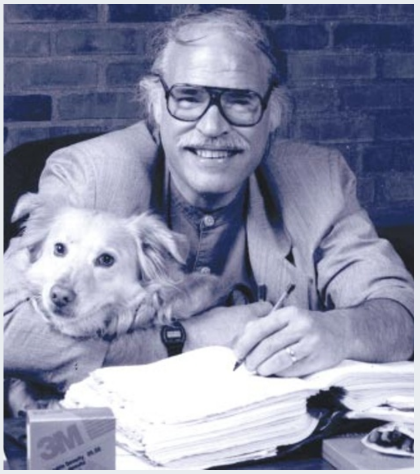
# J. John Sepkoski Jr (1948–99)

## Palaeontologist who analysed and modelled the history of life

Jack Sepkoski, who died suddenly of heart failure on 1 May, demonstrated more than anyone how the data collected by generations of palaeontologists provide a basis for investigating patterns in the history of life. He matched neither of the stereotyped images of a palaeontologist — the macho explorer and the student of dusty specimens in museum drawers. His field area was, unashamedly, the library.

Sepkoski's work on the history of diversity started in the 1970s at the University of Rochester, New York. He was strongly influenced by the equilibrium model formulated by Robert MacArthur and Edward O. Wilson in studies of island biogeography (that is, the number of species reaches a steady state when originations are balanced by extinctions). Sepkoski's kinetic model, extrapolated back into geological time and considered on a global scale, predicted an exponential rise in faunal diversity after the origin of multicellular animals, followed by a constant equilibrium. Sepkoski showed that the fossil record of marine taxonomic orders from the late Precambrian — around 600 million years (Myr) ago — to the present is remarkably consistent with his model. This provides a simple explanation for the radiation of animal life into major groups during the Cambrian in terms of exponential diversification. But Sepkoski recognized that orders are only a crude proxy for species (the taxonomic hierarchy ranges through phylum, class, order, family and genus, to species).

Sepkoski's analysis of family-level data showed that the history of diversity is more complex. An initial equilibrium, reached by the Late Cambrian (around 515 Myr ago), was followed by a more significant diversification that peaked in the Late Ordovician (about 450 Myr ago). Sepkoski's two-phase kinetic model involved separate evolutionary faunas — one characteristic of the Cambrian, the other of the rest of the Palaeozoic (510–245 Myr ago). The first was dominated by ecological generalists, and the second by more specialized taxonomic groups. This analysis confirmed that a plateau of diversity characterizes the Palaeozoic, and emphasized the profound effect of the extinctions at the end of the Permian (245 Myr ago). Sepkoski later confirmed that a third evolutionary fauna, the modern fauna, radiated mainly after this end-Permian extinction.




Sepkoski's plot of diversity through time has become the familiar image of the history of life. But as his research hit the limelight in the late 1970s he became something of a *bête noire* to a generation of older traditionalists, who complained that he did not have the rigorous taxonomic training required to ensure the reliability of his data. With characteristic irreverence, Jack caricatured this attitude at one meeting in the mid-1980s by wearing a badge bearing the initials TCCT — Taxon Counter: Casual Theorist! But Sepkoski was no casual theorist; he had the mathematical skills to model and interpret major patterns in the fossil record.

Moving to the University of Chicago in 1978, Sepkoski turned his attention to extinctions, largely in collaboration with David Raup. Major extinctions disrupt equilibria, although the rebound patterns fit kinetic models of diversification. Raup and Sepkoski first identified mass extinctions statistically as peaks that are different from normal or background levels. They also showed that extinction levels have fallen through geological time, implying increased optimization of fitness.

If Sepkoski's models of diversification generated controversy in some quarters, it was nothing compared with the effect of the bombshell that he and Raup dropped in 1984. They announced that there is a significant periodicity in mass extinctions over the last 250 Myr. Their preliminary time-series analysis revealed that the 12 major extinctions occurred at regular intervals of 26 Myr, a discovery that created waves well beyond the palaeontological community. Astronomers proposed Solar-System or Galactic mechanisms, including a hypothetical companion star to the Sun (Nemesis), which precipitated showers of comets on the Earth every 26 Myr. Other commentators suggested that the periodicity might be an artefact of the way in which fossil ranges are recorded, of the nature of higher taxonomic groups, or of the methods of statistical analysis. But Sepkoski robustly defended the periodicity hypothesis with a much larger database (of genera). He was careful to emphasize, though, that the demonstration of periodicity does not resolve the probable cause of extinctions, or even whether they were gradual or catastrophic events.

Sepkoski's analyses of the fossil record were by no means confined to marine invertebrates. He investigated the dispersal of mammals from the Tertiary period across the Panamanian land bridge (the Great American Interchange, which began around 3 Myr ago). With Conrad Labandeira he demonstrated that high insect diversity is the result of low extinction rather than high origination rates. The radiation of insects was not linked with the evolution of flowering plants, as commonly assumed, but began 100 Myr before their peak.

Sepkoski's main legacy is the patterns that he revealed in the history of life, and his analytical interpretations of diversity dynamics. He published a paper in 1993 entitled "Ten years in the library: new data confirm paleontological patterns" (*Paleobiology* 19, 43–51), which demonstrated that his conclusions on diversification and extinction remained robust despite considerable refinement of the data, including additions and corrections. The fact that these patterns are real is essentially due to the size of the database that Sepkoski painstakingly amassed. But confirmation was in no sense stagnation. Sepkoski continued to investigate issues in the history of life — most recently, rates of speciation, the dynamics of competitive interactions, and the relationship between diversity and ecological importance on a geological timescale.

Jack Sepkoski's research method — long hours holed up with palaeontological monograph and computer — belied his outgoing nature. He was equally at home addressing a major scientific meeting about his latest results. His generosity with both data and ideas, and his sense of fun and enjoyment of company, will be sadly missed. Palaeontology and evolutionary studies have been significantly set back by his untimely death.

**Derek E. G. Briggs**

*Derek E. G. Briggs is in the Department of Earth Sciences, University of Bristol, Wills Memorial Building, Queen's Road, Bristol BS8 1RJ, UK.*
*e-mail: D.E.G.Briggs@bristol.ac.uk*

UNIV. CHICAGO