BOOKS: PALEOBIOLOGY

Enough Remains to Work With

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The one thing that everyone seems to know about the fossil record is that it is incomplete. Darwin titled one chapter of *Origin of Species* "On the imperfection of the geological record" and noted that not only do most organisms not fossilize, most fossils are fragmentary, destroyed by metamorphism or erosion, or escape detection. The problems of partial data, however, are not unique to paleontology. As Stephen Donovan and Christopher Paul, the editors of *The Adequacy of the Fossil Record*, observe, no discipline has complete data at its disposal and, in most cases, potentially available data are only incompletely sampled. To be adequate, data need only be partially complete, but they must also be unbiased with respect to the parameters of interest. The central focus of this volume is whether the fossil record fulfills these criteria for adequacy.

The Adequacy of the Fossil Record
Stephen K. Donovan and Christopher R. C. Paul, Eds.
Wiley, Chichester, UK, 1998. 322 pp. $125, £50. ISBN 0-471-96988-5.

No simple answer can be given to this question. Data from fossils have been applied to a variety of evolutionary, ecological, and biological problems. Because different problems require data with different degrees of taxonomic, temporal, and geographic resolution, the fossil record's adequacy can be usefully addressed only in the context of specified questions. Most contributions to this volume assess the completeness of taxonomic and stratigraphic data at levels of resolution relevant to evolutionary problems; only a few explore the record's adequacy for studies of function or ecology.

Several chapters, employing a variety of independent methods, consider taxonomic completeness, the extent to which the fossil record samples biodiversity. These suggest that the record of species is surprisingly complete, preserving roughly 10% of species that have ever existed. Paul argues that this level of completeness compares favorably in magnitude to that accepted in other disciplines (for example, to our sampling of existing species).

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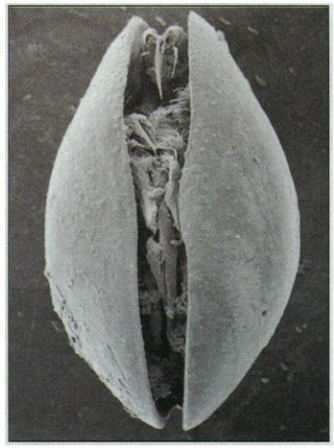
Completeness, however, provides only a partial measure of adequacy. What about bias? Paleontologists devote considerable attention to identifying factors that could produce a misleading fossil record. Inappropriate taxonomic practices, unequal sampling intensities, and effects of interactions between deposition and erosion are among the biases discussed in detail in this volume. By developing sampling techniques appropriate for particular biases and ensuring that errors are unbiased with regard to parameters of interest, researchers can reduce the chances that analyses of the fossil record will generate inaccurate signals.

Another topic dealt with extensively in *The Adequacy of the Fossil Record* is stratigraphic completeness, the relationship between a taxon's observed and actual ranges. The observed range is defined by a taxon's first and last appearances in the fossil record. Because of non-preservation and erosion, these range endpoints are unlikely to correspond to times of origination and extinction. It is knowledge of the latter, however, that is critical for studies of diversity, mass extinctions, evolutionary rates, evolutionary mechanisms, and biostratigraphy. The chapters on stratigraphic completeness demonstrate that this is an area where much methodological progress has been made. Charles Marshall discusses gap analysis, which uses the empirical distribution of stratigraphic gaps in a taxon's observed range to place confidence intervals on estimates of its actual stratigraphic range. (The method assumes that the distribution also applies to the record beyond the observed range, but the validity of this assumption can be tested with ancillary data.)



Complete remains. The vellum, appendages, and mouthparts of this 1.5 mm long ostracod, *Pattersoncypris*, from the Early Cretaceous Santana Formation of Brazil are among the details preserved by mineralization of the entire organism.

A second approach to assessing stratigraphic completeness relies on estimates of phylogeny. By identifying sister taxa from character-based cladograms and forcing them to arise simultaneously, this method interprets the stratigraphic gap between the first occurrences of sister taxa as evidence for an incomplete record. But, as chapters by Paul and by Peter Wagner note, through prohibiting ancestors and forcing the simultaneous origin of sister taxa, such character-based cladistic approaches may overestimate incompleteness. Moreover, Wagner argues that because hypotheses of relationship make predictions about the distribution of characters and the sequence of events, stratigraphic data should be used to test phylogenetic hypotheses rather than the other way around. He makes a compelling case that temporal information held by fossils should not be excluded from systematics.

Although taxonomic and stratigraphic completeness and biases are relevant when the fossil record is used in addressing evolutionary problems, other aspects of the record are important when it is applied to functional and ecological questions. Missing data on soft parts, behavior, or organismal interactions, and potentially misleading effects of spatial and temporal mixing characterize most of the fossil record. The available record is, however, highly variable. It contains many exceptional cases of preservation that provide virtual "snapshots" of past communities. Sometimes, as in the phosphatized fish from the Cretaceous of Brazil discussed by David Martill, morphological detail down to the subcellular level can be retained. Even when preservation is unexceptional, as for the Pleistocene reefs described by Benjamin Greenstein and colleagues, fidelity can be sufficiently high that direct comparisons with extant ecosystems can be made.

The editors of *The Adequacy of the Fossil Record* have managed to compile a comprehensive summary of many important topics related to the quality of the fossil record. The contributors demonstrate that the fossil record preserves data adequate for examining a wide range of evolutionary questions. Methods for handling incompleteness and biases are allowing researchers to apply data from fossils to an increasing variety of problems. Given the importance and breadth of issues covered, this volume should appeal not only to paleontologists but also to anyone interested in evolution and the history of life.

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