EVOLUTIONARY PALEONTOLOGY

Johannes S. Pignatti
Università di Roma La Sapienza, Italy

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Contents

Summary

Evolutionary paleontology dates from the late eighteenth century, but it has developed particularly in recent decades into the most dynamic subdiscipline of paleontology, changing fundamentally our understanding of the evolution of life on earth in geological time. The main aims of evolutionary paleontology are to reconstruct the history of life on earth and the patterns and causes of evolutionary change and extinction. The primary source of evidence for evolutionary paleontology is the fossil record, documenting the diversity of life through a uniquely long time span, but it is also strongly influenced by the advances of biology. This article outlines some important contributions of this subdiscipline of paleontology, such as the evolutionary behavior of taxa, evolutionary trends and generalizations, fluctuations in global diversity and extinction, and large-scale patterns and processes in space and time.

1. What is Evolutionary Paleontology?

Evolutionary paleontology (also called evolutionary paleobiology) is paleontology’s intersection with evolutionary biology. Its main aims are to reconstruct the history of life on earth (historical paleontology, phylogeny) and the patterns and causes of evolutionary change and extinction (biological and physical processes and unique historical events). On this definition, which is more restrictive than others, evolutionary paleontology and paleobiology are not synonymous: broader in scope, the latter also includes other research programs (for example, paleoecology, functional anatomy of fossil organisms, paleoichnology, taphonomy, and paleobiogeography), in which evolutionary goals may not feature prominently or be altogether absent.

The primary source of evidence for evolutionary paleontology is the fossil record, a vast and expanding observational database of fossils, assembled through the effort of systematic paleontologists and biostratigraphers over the past two centuries. Metaphorically speaking, the fossil record constitutes a kind of ledger, in which taxa (species or higher groups) are recorded as entries, documenting arrivals (immigration or speciation/origination) and departures (local or global extinction) for given paleoenvironments and communities over millions of years. Fossils, which occur in many sedimentary rocks, represent the dimension of time in the study of life.

In addition, the fossil record offers a temporal dimension on the distribution of systematic characters among fossil taxa. These characters, alone or in combination with stratigraphic data, provide evidence for evolutionary patterns such as divergence, parallelism, and convergence, and are necessary for reconstructing phylogenies.

During recent decades, evolutionary paleontology has developed into the most dynamic subdiscipline of paleontology, strongly influenced by the advances of biology. For this reason, it is also considered as a subdiscipline of evolutionary biology. The latter view is justified, since the basic aims of evolutionary paleontology largely coincide with those of other subdisciplines of evolutionary biology, among which are molecular biology, evolutionary genetics, evolutionary-developmental biology, and evolutionary ecology. It is therefore not surprising that the boundaries between evolutionary paleontology and other subdisciplines within paleontology and biology are not always clearly defined. The differences between evolutionary paleontology and biological systematics are also somewhat arbitrary: the main aim of systematics is reconstructing the phylogenetic relationships among taxa and their classification on the basis of these evolutionary relationships.

In any case, because of its subject matter and methods, four key paleontological issues distinguish evolutionary paleontology from evolutionary biology:

- First, the database of evolutionary paleontology is the fossil record. The intensity of fossil collecting and systematic study and the precision of stratigraphic resolution (age control) have witnessed an exponential growth in the past decades, greatly abetting our understanding of the history of life and evolutionary change in many marine and terrestrial environments. Roughly, the number of known fossil species exceeds a quarter of a million, belonging to over 40 000 genera and 4500 families. Although evolutionary paleontologists have always acknowledged the incompleteness and the biases of the fossil record, the Phanerozoic fossil record and possibly also that of the latest Precambrian are generally considered adequate to document major evolutionary patterns and to allow hypothesis and empirical testing. The data are particularly robust for Phanerozoic marine skeletonized animals and provide an exceptionally detailed window on the history of life on earth. These advances are mirrored for example in new additions and revisions to the *Treatise on Invertebrate Paleontology*, the most influential paleontological monograph series ever, and many other monographs on various fossil groups.

- Second, as indicated by many theoretical and analytical studies, different spatial and temporal scales are relevant in evolutionary paleontology; to some extent, different scales in space and time are linked.

  The spatial scales refer first to the size of the study area. For many purposes, a certain minimum scale of observation is necessary (for example, extinction at local, regional, or global scale). Moreover, fossils are contained in rock units, which are discrete and need to be correlated over distances. Also, the present location of any fossil-bearing rocks may be largely independent from their original position: a typical example is the migration of terranes, which causes the so-called "beached Viking funeral ship effect," when a terrane is accreted and unrelated fossiliferous rock units are juxtaposed. This in turn stresses the need for tectonic and paleogeographic control. Finally, post-mortem transport is frequent and also the reworking of fossils (exhumation and redeposition) must be taken into account.

  The temporal (that is, stratigraphic) scales of paleontology concern patterns and processes that occur over much longer time spans than those observable over human generations: this unique perspective on time is a most valuable asset in studies in evolution. Different kinds of time scales are recognized. Conventionally, the temporal continuum is divided into ecological time and evolutionary time. Ecological time encompasses the interactions of organisms with each other and with the environment, population changes, and distributional changes. Evolutionary time (also called macroevolutionary time) concerns species origination, extinction, and evolutionary trends.

  American paleobiologist Stephen Jay Gould suggested that three tiers of time are relevant for evolutionary processes: "ecological moments," geological time (millions of years; = Myr), and mass extinctions (generally, separated from each other by more than 20 Myr). Because evolution shapes ecological processes across all time intervals and species respond differently to disturbance over time, each of these tiers of time may correspond to distinct evolutionary phenomena. This threefold subdivision has been later supplemented by an intermediate tier, representing the Milankovitch cycles of climate forcing with periodicities of about 20–100 thousand years (= kyr). For the late Quaternary, even much shorter, centennial to millennial cycles have been recognized, called Dansgaard-Oeschger cycles; these cycles reflect rapidly alternating warm and cold climates, which affected biological communities, migration, extinction, and possibly speciation. Astronomical forcing is best recognized at higher latitudes from the onset of the first glacial climate (late Pliocene). Some kind of cyclicity has been found throughout the sedimentary record: recent work extends astronomically forced chronology up to the Oligocene and even earlier times, especially the Cretaceous.

- Third, evolutionary paleontology must take into account different confidence limits and biases on stratigraphic and other data: understanding the fossil record requires an awareness of its limitations. There is no doubt the fossil record represents an exceedingly small fraction of the organisms that lived in the past, and is strongly constrained by unequal representation through time and intrinsic biases. There remains the question of whether the data are of good enough quality.

The limitations of the fossil record are manifold: missing data, ambiguity of taxonomic characters and identifications, taphonomical biases, time-averaging, age-dating difficulties, differences in sampling or study effort, and availability of fossil-bearing sediments in space and time. Over the last decades, these and other limitations have been the object of careful analysis, and various theoretical and practical means have been proposed to minimize their effects. But among the questions studied in this field some remain highly controversial. Is the quality of the fossil record constant or declining with age? Is the marine fossil record (biased in favor of a mainly zoocentric perspective) better than the continental one? The classic view holds that its quality decreases with age and the marine fossil record is better than the continental one; both opinions have been recently challenged, and it has been argued that the marine record may not represent a good model for understanding the diversification history of life. Also, depending on the questions asked, in some cases the limiting factors cease to be such: for example, time averaging may actually become an advantage when it damps undesirable short-term noise.

A different but relevant question is the generalized assumption that paleontological species in the fossil record correspond to biospecies. As in biology, where controversies still rage in competing biospecies concepts, no consensus over species concepts exists in paleontology. Notwithstanding the very different approach to species concepts, in paleontology species are mainly recognized morphologically on the base of hard-parts (morphospecies) and possess a chronological dimension, which may lead to the establishment of chronospecies even in the absence of lineage splitting.

- Fourth, evolutionary paleontology is largely non-experimental, and includes parts that are descriptive, retrospective, and historical. This point may seem trivial or self-demoting, but clearly, because paleontology deals with the fossil record, it cannot directly experiment with the organisms it investigates. Nevertheless, some experimental approaches exist within paleontology (for instance, actuo-paleontology), and in biology some research programs involving large scales are predominantly non-experimental (for instance, macroecology).

2. Historical Perspective

The origins of evolutionary paleontology date back to the late eighteenth century, when the true nature of fossils was recognized. One cornerstone of evolutionary theory, the extinction of species, was first demonstrated in 1796 by the French scientist Georges Cuvier (1769–1832). Early in the nineteenth century, his compatriot Jean-Baptiste Lamarck (1744–1829) formulated a first theory of evolution. Cuvier and Alexandre Brongniart (1770–1847) recognized the catastrophic mass extinction at the Cretaceous-Tertiary boundary; and Alcide d'Orbigny (1802–1857) was the first to document numerically major and minor mass extinctions. Further cornerstones of evolutionary theory, the origin of species and natural selection, were introduced in 1859 by Charles Robert Darwin (1809–1882). Two chapters of his *Origin of Species* discuss the evolutionary relevance of the fossil record (documentation of life's history, evolution, and phylogeny; usefulness for prediction and testing of ecological and evolutionary hypotheses). Darwin predicted that the fossil record, in spite of its incompleteness, should reflect the phylogenetic connection of all life forms because they evolved by common descent. In 1860, the British geologist John Phillips (1800–1874) outlined a three-fold subdivision of Phanerozoic life and fossil diversity into Paleozoic, Mesozoic, and Cainozoic, the three geological eras still recognized today.

The late nineteenth century and the earlier part of the twentieth century witnessed a growing understanding of the fossil record. As mirrored in numerous monographs of unsurpassed value, at that time studies in systematics and biostratigraphy prevailed. Many of these works are attempts at inquiry into phylogeny, evolutionary functional morphology, and evolutionary paleoecology in various fossil groups, leading to further understanding of the evolution of life on the earth. Most importantly, the concept of the irreversibility of evolution, first formulated in 1893 by the French-born Belgian paleontologist Louis Dollo (1857–1931), became gradually accepted. Moreover, paleobiology started to assert itself as a distinct research program, thus determining a significant shift in paleontology from geology to the biological sciences. At that time however, the anti-Darwinian influence was still strong, including doctrines such as the inheritance of use and disuse, and orthogenesis and aristogenesis, championed by the leading American paleontologist Henry Fairfield Osborn (1857–1935).

In the 1940s evolutionary paleontology entered a new phase, when the neo-Darwinian or modern synthesis that resulted from the integration of evolutionary theory and Mendelian genetics began to take shape. Among others, the American paleontologist George Gaylord Simpson (1902–1984) helped to bring about radical change in the role of the fossil record within this synthesis. His most influential work, *Tempo and Mode in Evolution*, published in 1944, induced lasting changes in epistemology and methodology, leading to a more quantitative approach to the fossil record. Various concepts were introduced or redefined in this work, such as evolutionary rates, microevolution, macroevolution, phyletic evolution, patterns of survivorship, and large-scale patterns of evolution, although some of them (for example "quantum evolution") are now abandoned.

In the 1970s, profound changes in evolutionary paleontology emerged with the rise of phylogenetic systematics (also called cladistics) and new perspectives in speciation and the fossil record, especially under the influence of the punctuated equilibria model (see below).

The last decades have been characterized by rapid advances in fossil databases for the Phanerozoic, notable paleontological progress for the Proterozoic and Archean eons, and new analytical techniques and hypothesis testing afforded by computers. At the same time, the evolutionary role of abiotic factors and mass extinctions was assessed quantitatively. Factors such as extraterrestrial impacts, sea level variation, plate tectonics, climate forcing, and changes in the chemistry of the oceans and the atmosphere were welded together with other traditional and new (for example, molecular genetics) components of evolutionary biology and became part of macroevolutionary theory.

3. Main Research Topics of Evolutionary Paleontology

Evolutionary paleontology includes a range of perspectives, which often overlap. *Evolutionary functional morphology* studies the form and evolutionary function of phenotypic features (in particular, adaptation). *Evolutionary paleoecology* concerns the ecological features of fossil species (for example, ecological traits, life histories, and strategies) and how these features evolved and affected other species (for instance, predation, symbiosis, coevolution). *Evolutionary behavioral paleoecology* investigates evolutionary paleoethological features. *Molecular paleontology* represents the study of nucleotide sequences (DNA, RNA) from fossils. Few studies exist to date, because of the difficult preservation of these molecules and analytical problems, but some have produced spectacular results, as in cave bears and fossil humans. In the latter, strong differences in mitochondrial DNA (mtDNA) between Neanderthals and modern humans suggest that they did not contribute to the current human gene pool and thus most likely belonged to a distinct species. Finally, *evolutionary paleoanthropology* is the evolutionary paleobiology of fossil hominids.

A thorough inventory of the research topics of evolutionary paleontology might seem a daunting task. Four kinds of main research topics that have made important conceptual contributions are outlined in the remainder of Section 3, they are:

1. The evolutionary behavior of lineages, species, and higher taxa;
2. Evolutionary trends and generalizations (“rules”);
3. Long-term fluctuations in global diversity and extinction; and, more generally,
4. Large-scale patterns and processes in space and time.

Clearly, this list is not inclusive.

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Bibliography

Benton M.J. (1993). *The Fossil Record 2.* 845 pp. London: Chapman & Hall. [A detailed compendium on the stratigraphic distribution of fossil families.]

Benton M.J. (2001). Biodiversity on land and in the sea. *Geological Journal* **36**, 211–230. [An useful introduction for non-specialists to Phanerozoic biodiversity patterns.]

Benton M.J., Wills M., and Hitchin R. (2000). Quality of the fossil record through time. *Nature* **403**, 534–537. [An article for specialists suggesting an elegant solution to the problem of the completeness of the fossil record.]

Briggs D.E.G. and Crowther P.R. (2001). (eds). *Palaeobiology II*, 600 pp. Oxford: Blackwell Science. [A comprehensive collection of articles for students and researchers on various issues relevant to evolutionary paleontology.]

Conway Morris S. (1998). *The Crucible of Creation: The Burgess Shale and the Rise of Animals.* 242 pp. Oxford: Oxford University Press. [A stimulating overview on the "Cambrian explosion."]

Cracraft J. (1981). Pattern and process in paleobiology: the role of cladistic analysis in systematic paleontology. *Paleobiology* **7**(4): 456–468. [An introduction to the role of phylogenetic systematics in paleontology.]

Eldredge N. and Gould S.J. (1972). Punctuated equilibria: an alternative to phyletic gradualism. *Models in Paleobiology*, (ed. T.M. Schopf), pp. 82–115. San Francisco: Freeman, Cooper. [This widely-cited article introduces the evolutionary model of punctuated equilibria.]

Erwin D.H. (1993). *The Great Paleozoic Crisis.* 327 pp. New York: Columbia University Press. [A valuable discussion on the late Permian mass extinction, intended also for non-specialists.]

Gould S.J. (1989). *Wonderful Life: the Burgess Shale and the Nature of History*. 347 pp. New York: Norton. [A successful book providing an overview on the "Cambrian explosion" for the interested layperson.]

Jablonski D. (1999). The future of the fossil record. *Science* **284**, 2114–2116. [A concise summary on the state of the art in evolutionary paleontology]

Jablonski D., Erwin D.H. and Lipps J.H. (1996). (eds.). *Evolutionary Paleobiology*. 484 pp. Chicago: University of Chicago Press. [This collection of articles provides examples of relevant issues in evolutionary paleobiology directed toward readers who already have an understanding of the topic.]

McShea D.W. (1994). Mechanisms of large-scale evolutionary trends. *Evolution* **48**, 1747–1763. [This article offers a novel perspective on various mechanisms of evolutionary trends]

Meager T.R. and Futuyma D.J. (2001). (eds.). Evolution, science, and society. *The American Naturalist* **158**(Suppl.): 1–46. [An introduction to evolutionary biology understandable to the broader public, outlining the role of evolutionary paleontology and other biological subdisciplines.]

Sepkoski J.J. (1996). Patterns of Phanerozoic extinction: a perspective from global databases. *Global Events and Event Stratigraphy in the Phanerozoic*, (ed. O.H. Walliser), pp. 35–51. Berlin: Springer. [An article on Phanerozoic biodiversity patterns based on a global database.]

Stanley S.M. (1973). An explanation of Cope's rule. *Evolution* **27**, 1–26. [A classical article on evolutionary trends.]

Biographical Sketch

Johannes S. Pignatti was born in 1962 in Padova, Italy. His undergraduate studies began at the University of Trieste in 1980 and concluded in 1986 at La Sapienza University of Rome with a summa cum laude degree in Natural Sciences. In 1986 he enrolled in a doctoral program in Paleontology at the University of Modena on the Paleogene of the Maiella carbonate platform (central Italy), completing his Ph.D. in 1990. In 1990 he won an Accademia dei Lincei–Royal Society scholarship at the Natural History Museum (London). In 1991 he worked at the University of Basel, Switzerland as a postdoctoral fellow on the recent Foraminifera of Mauritius under the supervision of Professor L. Hottinger. In 1992 he obtained a two-year CNR fellowship at La Sapienza University of Rome. In 1994 he became a university researcher at the same university, where he has been an associate professor in Paleontology and Paleoecology since 2001.

His main scientific interests focus on the systematics, paleobiogeography, and paleoecology of Late Cretaceous–Miocene Neo-Tethyan larger foraminifera; biostratigraphy and paleoenvironmental analysis of Paleogene carbonate deposits; systematics and ecology of recent benthic foraminifera, with special reference to the Indo-Pacific and Mediterranean domains; and the systematics, biostratigraphy and structure of Mesozoic aulacocerid coleoid cephalopods.