INVERTEBRATE PALEONTOLOGY

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Summary

Mankind has been fascinated with interestingly shaped objects dug out of the ground or in rocks for millennia. In medieval times such fossils were prized for their supposed medicinal properties but, with the advance of science, they are now studied as the remains of organisms which lived millions of years ago in Earth history.The study of fossils (paleontology) requires knowledge of modern biology as well as aspects of geology. Invertebrate paleontology confines itself to research about animals without backbones but, since these form 97% of animal species, it is the largest branch of paleontology.

Invertebrates include microscopic plankton, sponges, corals, worms, shelled animals of various kinds, arthropods, and echinoderms. Paleontology aims to unravel the geological history of life on Earth, from its beginnings to the present day. Important aspects of the study include: how fossils are formed, fossil classification, evolution and extinction, ecology and ecosystems of the past and the uses of fossils for dating rocks and understanding ancient environments. Studies of ancient life are important not only to satisfy human curiosity but also because they offer unique insights into, for example, how climate change can affect ecosystems (including those which mankind inhabits), and the longevity and relationships of organisms.

1. Introduction

1.1. What is Invertebrate Paleontology?

Invertebrate paleontology is the study of fossil invertebrate animals: those animals which lack vertebrae, i.e., a backbone. Therefore, invertebrate paleontology excludes the study of fish, mammals, dinosaurs and other vertebrate animals, including Man, as well as plants and fungi. It comprises, however, the study of all other animals, which constitute some 97% of animal species alive today. There are two complementary aspects to the study of invertebrate paleontology: discovering, describing and classifying the variety of invertebrate fossil species; and more general studies (which apply all fossil organisms) such as how fossils are preserved in the rocks, how they might have lived, their distribution through geological time, and their uses in dating the geological record. In this review, the first part covers the various general themes, and then proceeds to descriptions of the different animal groups which are important in the fossil record.

1.2. The Nature and Origins of Paleontology

Fossils can be defined as any evidence of the former existence of life. This definition is rather broad and encompasses, for example, chemicals found in rocks which could only have been produced by the action of biological processes (chemicofossils), remains of the activities of animals (trace fossils) such as fossil footprints, trails, burrows and nests, as well as the more obvious body fossils which are the actual remains of the body of an organism or, more usually, the cast or mold made by the animal or plant within the rock.

Centuries ago, early humans discovering fossils might have had different interpretations regarding the origin of fossils than we do today. Many ancient myths and legends involving bizarre (often giant) beasts likely came about through attempts to interpret fossilized remains. One such example is the ancient Greek legend of the Cyclops; the physical evidence for this race of one-eyed monsters was very probably the discovery of extinct elephants (whose skulls bear a large hole in the front) on the island of Crete in the Mediterranean Sea. Other Greek and Roman writers, however, supposed that the presence of fossil sea shells high on mountains showed evidence for once higher sea levels.

From the later days of the Roman Empire onwards, Old Testament stories gained acceptance in the Western World as explanations for the origins of most things, and more fanciful ideas on the origin of fossils became prevalent. For example, St Hilda founded a monastery in the Town of Whitby in Yorkshire, England, in the 7th Century AD. On the coast next to the town ammonite fossils (Fig.) are abundant. Their resemblance to curled-up snakes led to the myth that they were, indeed, the remains of snakes turned to stone by the beneficial action of St Hilda. A veritable tourist industry grew up in Victorian times selling these artifacts, which commonly had heads carved onto them by local tourist dealers. Wearing these amulets would, of course, confer immunity from snake bite on the bearer. In Medieval times, the word fossil originated from the Latin *fossilis*, which means anything dug out of the ground, including not only true fossils but also gems and other interestingly shaped natural objects. The first

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descriptions of fossils (used in this broader sense) were mainly concerned with their possible beneficial uses, mainly medicinal. By the Renaissance, however, many scholars were beginning to realize that fossils represented the remains of once-living animals and plants. If they were not formed inorganically, or by God's whimsy (two early suggestions), then a number of questions arose, including how and when did they get into the rocks? Many fossils appeared to belong to species not known to be alive: were they living somewhere else on Earth (then largely unexplored) and, if not, were they really extinct? Noah's Flood became a handy explanation, in some people's minds, for both extinctions and the presence of fossil sea creatures on mountain tops. By the 18th Century, scientific thought had advanced to the point where fossils were recognized as the remains of once-living organisms and, in 1735, the great Swedish naturalist Carl Linnaeus included them in his classification scheme. By the mid-19th Century, when Charles Darwin wrote *On the Origin of Species*, few considered fossil to be anything other than organic remains, and the age of these objects, and how they got into rock strata, were beginning to become apparent.

2. Taphonomy

2.1. How Fossils are Preserved

Taphonomy is the study of how fossils are preserved. There are many different ways in which fossils can get preserved in rocks, but all organisms which become fossils follow the same general pathway from death to being discovered by a paleontologist. There are three stages in this process. The first, necrolysis, concerns the biochemical changes which happen to an organism during and immediately after death. These can include *rigor mortis*, decay of ingested food which can produce gases which rupture the carcass, and general breakdown and decay of soft tissues.

Biostratinomy is the second process, which involves breakup of the remains which are left after necrolytic activity has ended, and their incorporation into the rock, usually sedimentary rocks such as sandstone, mudstone, and limestone. Breakup can include disarticulation or trampling by scavengers, storms and currents transporting remains to another place than where the organism lived, boring and encrusting by other organisms, and various processes, chemical and physical, which might take place within the soft sediment. Further processes take place after entombment, and these fall under the category of diagenesis. This is a general term describing the processes that occur when sediments are converted into sedimentary rocks. For fossils, various physical chemical processes can occur which alter the original material or shape, including flattening, replacement by another substance, and heating up to remove volatile chemicals (producing oil and gas in the process). Sometimes, fossils already preserved in a rock can be eroded out and then reincorporated into another rock. This can cause erroneous dating of rocks unless the paleontologist realizes the process has occurred. Ultimately, the remains see the light of day again, usually after many millions of years, when the paleontologist breaks open the rock to reveal the beautifully preserved fossil. In most cases in nature, biological materials are lost during taphonomic processes, so it is only in rare cases that organisms get preserved at all. The preservation potential of an organism depends essentially on two factors: what the organism is made of and where it lives (or dies). Hard parts, such as teeth, shells, and bones, are much more likely to

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survive taphonomic processes than soft tissues such as blood, muscle and skin. Between these extremes lie tough organic materials like arthropod cuticle, wood, and cartilage. If an organism lives in an environment where sedimentation is taking place, such as sea-floor sediment, then it is more likely to be preserved than if it lives far from such places, for example on a mountain top. It should be clear, then, that the fossil record is dominated by marine shelled animals and that fossil birds, insects, and worms are rather rare.

2.2. Types of Preservation

2.2.1. Original Material

Rarely, and usually only in very young fossils, the original material may be preserved. Examples of this include extinct mammoths whose remains have been found almost unaltered, with flesh, skin and hair attached, in Siberian permafrost. Oils seeps, such as those at Rancho La Brea in Los Angeles, California, provide a trap for animals which then get preserved intact to some degree. The shells of most living bivalve mollusks have a nacreous layer (mother-of-pearl), which is composed of an unstable variety of calcite ($CaCO_3$) called aragonite. This layer naturally alters to the stable form of calcite over time, but in some, fairly young, fossils the nacreous layer remains intact. Relatively recalcitrant biological materials such as arthropod cuticle alter during fossilization by randomly repolymerizing to a substance called kerogen. Thus, fossils of such arthropods may appear the typical brown color of the original beetle, bug or spider, but the kerogen rarely contains any trace of the original chitin and other chemicals which made up the cuticle originally. Finally, a rather special case is that of amber. Amber is fossilized tree resin, which preserves insects and other organisms remarkably well. The carcass is dehydrated by the fossilization process, but the dehydrated remains can show original muscle structures, for example.

2.2.2. Permineralization

Many biological materials have a spongy texture: wood, bone and, indeed, sponges. Such materials allow the permeation of fluids containing minerals, resulting in a kind of petrifaction. Examples of this preservation are dinosaur bones and petrified wood. In the latter case, it is usually silica which is the permineralizing mineral, but calcite and other minerals can also occur.

2.2.3. Replacement

The original material of fossil can be replaced by another mineral, or by a different form of the same mineral. The latter is called re-crystallization, and it occurs when percolating ground water dissolves the original mineral, e.g., calcite, which is then re-crystallized in a different crystalline structure from the original. Another example, of this is when the unstable form of $CaCO_3$, aragonite, naturally alters to calcite over time. Complete replacement of original tissues with a different mineral can happen in a variety of ways. Volatile organic matter, when heated, will disperse as fluids, leaving behind a carbon film. Carbonization is the name commonly given to the preservation of fossil plants in this way; leaves commonly appear as a carbon film which faithfully

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reflects the leaf shape, veins, and any damage by leaf-feeding insects. Silicification is the replacement by silica (SiO_2). This can happen to shells which were originally made of calcium carbonate ($CaCO_3$), or soft parts. Replacement by iron pyrite (fool's gold, FeS_2) is called pyritization, and results in some rather beautiful gold-colored fossils. Generally, pyritization happens to fossils of animals which have been preserved in black shales lacking oxygen; in one example, Beecher's Trilobite Bed, the softer legs and antennae of the trilobites are preserved. Calcification is the replacement by calcite, but the original material need not have been made of calcium carbonate, and calcite sometimes replaces soft tissue. Phosphatization is replacement by calcium phosphate. Phosphatization can occur concomitant with decay of the carcass by bacteria. In the example of fossil fish from the Santana Formation, Brazil, exquisite details of the fish muscles and other soft tissues have been faithfully reproduced by phosphatic replacement of the bacteria which were decaying the tissues.

2.2.4. Molds and Casts

Many fossils are shells of some sort, which have an inside containing the soft parts of the animal, and the shell is on the exterior of the animal. When the soft parts decay during fossilization, the inside becomes empty and may become filled with sediment, or later with minerals derived from percolating ground water during diagenesis. Figure 1 shows the various results from different taphonomic processes on shells. Note that the cast is a replica of the shell, replaced by another mineral or by re-crystallization of original calcite. Molds are either internal or external, and reflect the morphology but in reverse (e.g., original exterior spines appear on an external mold as holes). Molds and casts are very common modes of preservation and can tell us great deal about the morphology of fossil organisms, despite their being merely impressions in the rock matrix.

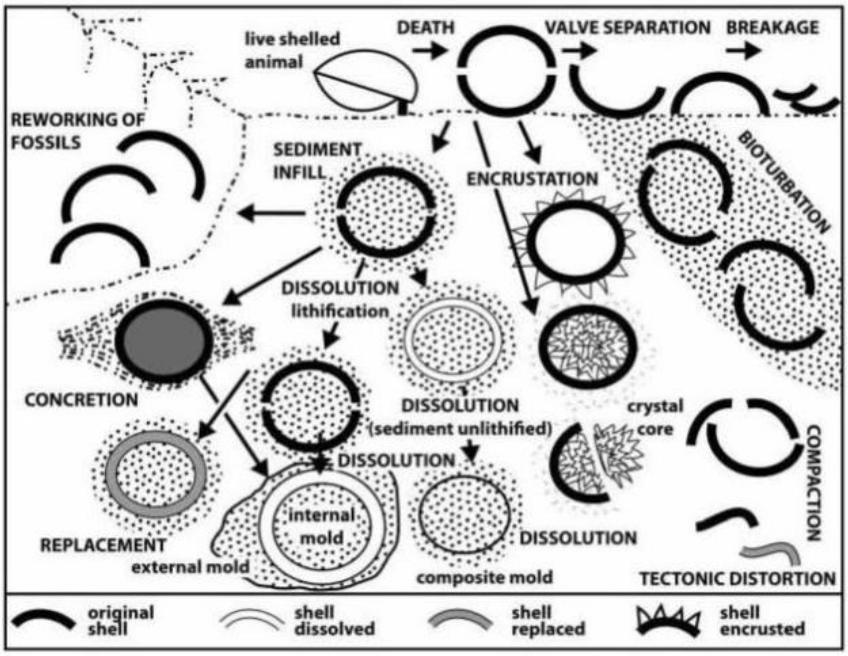

Figure 1. Modes of preservation of shelly fossils.

2.3. Fossil-Lagerstätten

Under certain taphonomic conditions, exceptional preservation of fossils results in a quite remarkable find, which the German paleontologist Adolf Seilacher and colleagues termed Fossil-Lagerstätten, after a similar term used by miners for a mother lode or bonanza. There are two types of Fossil-Lagerstätten. Concentration deposits, which preserve vast quantities of fossils which are unusual not for exceptional preservation but for the sheer numbers in one place, such as dinosaur bone beds and concentrated shell beds. Conservation deposits are remarkable not necessarily for great numbers of fossil but for exceptional preservation of soft parts, such as the amber deposits, tar pits, and Beecher's Trilobite Bed, already mentioned. Other examples of conservation deposits include the Cambrian Burgess Shale of British Columbia, Canada, the Pennsylvanian Mazon Creek nodules of Illinois, USA, and the Devonian Rhynie Chert of Scotland. Under normal fossilization, only organisms with hard parts would be preserved, but in these conservation deposits, even soft-bodied jellyfish and worms are found. Thus, Fossil-Lagerstätten give the paleontologist tremendously important glimpses into what whole ecosystems were like in the geological past.

3. Paleoecology

3.1. Introduction

Ecology is the study of the interrelationships of plants, animals and their environment. Paleoecology is ecology of fossils, and attempts to reconstruct the modes of life, interactions between organisms, and between organisms and their environment, in order to reconstruct past ecosystems. Paleoecologists need to make certain assumptions for their hypotheses to be testable. They need to assume that study of modern ecology provides reasonable analogs for the study of paleoecology. However, there are certainly ecosystems in the past that differed considerably from those we see at the present day. For example, the very early Earth had little oxygen in the atmosphere and life was not possible on land because of the dangerous UV radiation which bombarded our planet. Throughout much of Precambrian time, the highest life forms were primitive cyanobacteria, which formed mounds called stromatolites. It is possible that, in late Pennsylvanian times, there was even more oxygen in the Earth's atmosphere than the present day. Perhaps the biggest challenge to reconstructing ancient ecosystems is in the incomplete nature of the fossil record: the bias of hard-part preservation means that very little of the original biota is preserved in the fossil record. The paleoecologist tries to reconstruct a living community of organisms from an assemblage of fossils, and the two may be very different.

3.2. Physical Factors

Physical factors which affect organisms include (in the marine realm): water depth, temperature, light, nutrient supply, salinity, and substrate type. Many of these are correlated, water depth and light, for example. Moreover, working out the physical factors from the geological record can be difficult, and sometimes involves circular reasoning. For example, we do not know whether fossil corals had symbiotic algae (zooxanthellae) like many modern corals do, which helps their metabolism but forces

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them into the photic zone: the shallow water depths where light can penetrate for photosynthesis.

In the marine realm, organisms are concentrated in particular zones depending on their need for light, nutrients, substrate type, and other considerations. Animals and plants which inhabit the open ocean (the pelagic zone) consist of plankton (organisms which float), both plant (phytoplankton) and animal (zooplankton). Swimming animals are collectively called nekton. The ocean floor is divided into several zones which, from the coast out to deeper water are called: supralittoral (above the highest tides), littoral (between the tides), sublittoral (below the lowest tides on the continental shelf), bathyal (on the continental slope), abyssal (on the oceanic plain), and hadal (in the deep ocean trench). The depth at which organisms live depends largely on nutrient supply. Most organisms live in the littoral and sublittoral zones because many food chains rely on photosynthetic algae (seaweeds) to provide food for consumers. Also, while the upper layers of the pelagic zone teem with plankton and nekton, the benthos (organisms which live on the sea floor) are the most diverse. The greatest density of nutrients is on the sea floor itself (the benthos), where dead plankton accumulates, so that is where the highest diversity of organisms concentrates: the sediment-water interface. This interface varies itself: the sea floor can be very soupy, with a deep ooze formed from the remains of millions of tiny plankton; it can muddy, sandy, or rock hard. Some animals, such as oysters, need a hard substrate to attach to, while others are adapted to life in soft substrates or shifting sands.

Temperature, water supply, oxygen supply, support, and ionic concentration of body fluids matter little to fully marine organisms, but on land these vital components are highly variable. Land plants and animals need to compensate for variable water supply. Many terrestrial animals, such as arthropods, mammals and birds, cope with intermittent water by drinking and preventing water loss with a waterproof skin. Others cope by being able to dry up and rehydrate, examples being snails, and lungfish and certain arthropods adapted to living in seasonal pools. Many terrestrial animals live in damp places, such as soil, and migrate to deeper levels when the upper layers dry up. Still others simply live in water on land, including microscopic animals which thrive in interstitial water in soils. Of course, land animals need to get oxygen from air rather than water, so they have developed lungs in place of gills. Life was not possible on land for most of the earlier stages of the evolution of the Earth, so life developed in water, and all terrestrial animals and plants had their ancient origins in sea water.

3.3. Biotic Factors

Biotic factors which affect organisms include factors inherent in the organism, such as population structure (e.g., percentage of young *versus* adults; spatial distribution), and interactions with other biota (e.g., feeding, predation, symbiosis, parasitism). Different life-history strategies are employed by different species, even those living in the same environment. For example, in Man, there is a degree of infant mortality, but once the newborn has survived for a year or two, its life expectancy will be several tens of years. When plotted on a graph (*y* axis: log decreasing number of survivors; *x* axis: total life span), the curve for Man is strongly convex, only dropping in the last few decades. In the European Robin (*Erithacus rubecula*), while lives alongside Man in Europe, there is

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a very large infant mortality rate, and only a very few fledglings survive to adulthood. If they do, however, then the curve levels off before dropping sharply, like that of Man, in the last 20% of the life span. Such life curves can be deduced from the fossil record by measuring the sizes of animals, taking into account taphonomic effects such as winnowing (currents removing smaller shells) and how much time is represented in the sample: e.g., a catastrophic deposit will preserve the whole population, young to old, while a deposit representing gradual accumulation over a whole year might show seasonal spawning. Arthropods, which molt their skins, leave behind a series of different-sized fossils, each representing one molt. These fossil series can tell the paleontologist how many molts the arthropod went through in its lifetime.

The ecosystem is the totality of the biotic and environmental interactions in one place; for example, we can talk about a forest ecosystem, a pond ecosystem, and a littoral marine ecosystem. All organisms have an ecological niche; that is, the position the organism occupies within its ecosystem, taking account of the biotic and physical factors which it requires to exist, as well as the function the organism performs in the ecosystem.

Organisms in an ecosystem are commonly grouped according to their method of obtaining nutrients: their trophic level. Producers (autotrophs) are plants, algae, or microbes of various sorts, which build biomass using inorganic materials and energy, from sunlight (green plants and algae) or chemical energy (many microbes). Producers lie at the base of most (but not all) food chains.

Consumers (heterotrophs) occupy the next few links in most food chains; these animals rely either on producers or their food (herbivores), or on other consumers (predators/carnivores). Decomposers eat dead organisms, often converting them into usable food for other decomposers; e.g., fungi and bacteria break down dead organic materials in the soil, which might then be eaten by millipedes. Scavenger is the name given to larger animals which eat dead carcasses. Parasites get their nutrition by stealing it from a host organism without killing the host. All fossil organisms fall into one of these groups, but the nature of food chains in the past may be different from those we see today. For example, the early terrestrial food chain in the Silurian and Devonian periods was dominated by decomposers and predators, and had only a few, specialized animals which obtained their nutrition from green plants directly.

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Bibliography

Benton, M.J., Harper, D.A.T. (2009). *Introduction to Paleobiology and the Fossil Record*. xii + 592pp. Chichester, John Wiley & Sons Ltd. [Good, fairly recent student textbook on paleontology]

Boardman, R.S., Cheetham, A.H., Rowell, A.J. (eds.). (1987). *Fossil Invertebrates*. Cambridge, Mass., Blackwell Science. [Though old, this is a splendid compendium of invertebrate fossils]

Briggs, D.E.G., Crowther, P.R. (eds.). (2001). *Palaeobiology: a Synthesis II*. Oxford, Blackwell Scientific Publications. [More advanced topics in paleontology]

Clarkson, E.N.K. (1998). *Invertebrate Palaeontology and Evolution*, 4th ed. Oxford, Blackwell Scientific Publications. [Good student textbook on paleontology]

Moore, R.C. (ed.) (and other editors). 1953–. *Treatise on Invertebrate Paleontology*. 51 volumes published so far. Paleontological Institute, University of Kansas. [Ongoing encyclopedia on all aspects of invertebrate paleontology, with listings of genera; ideal for general information as well as fossil identification]

Nudds, J.R., Selden, P.A. (2008). *Fossil Ecosystems of North America*, 288pp. London, Manson. [This book describes several Fossil-Lagerstätten of North America for the student and general reader]

Selden, P.A., Nudds, J. R. (2012). *Evolution of Fossil Ecosystems, 2nd Ed.,* 288pp. London, Manson. [This book describes several Fossil-Lagerstätten around the world for the student and general reader]

Biographical Sketch

Paul Selden studied Geology and Zoology for his bachelor's degree at the University of Manchester, UK, and then went up to the University of Cambridge, Darwin College, for his PhD in fossil eurypterids. After teaching at the University of London, he spent most of his career at the University of Manchester teaching paleontology, before leaving in 2005 for the Natural History Museum, London. Since 2007, he has been Distinguished Professor of Invertebrate Paleontology, Department of Geology, and Director of the Paleontological Institute, University of Kansas. He has published widely in fossil arthropods, mainly on Chelicerata, especially in recent years on fossil spiders. He has served as President of the International Society of Arachnology and British Arachnological Society, Vice-president of the Palaeontological Association and Palaeontographical Society, and is editor of the *Treatise on Invertebrate Paleontology* and the *Bulletin of the British Arachnological Society*. He is a recipient of a Research Award from the Alexander von Humboldt Stiftung / Foundation.

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