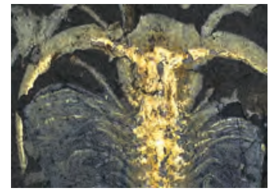
Fossils explained 56



Fossil–Lagerstätten

Possibly every palaeontologist, before and after Charles Darwin, has been well aware that the fossil record is very incomplete. Only a tiny percentage of the plants and animals alive at any one time in the past get preserved as fossils, both in terms of numbers of individuals and in terms of numbers of species. The palaeontologist attempting to reconstruct ancient ecosystems is therefore, in effect, trying to complete a jigsaw puzzle without the picture on the box lid and for which the majority of pieces are missing. Under normal preservational conditions probably only around 15 per cent of the species composing an ecosystem are preserved. Moreover, the fossil record is biased in favour of those animals and plants with hard, mineralized shells, skeletons or cuticles, and towards those living in marine environments. Thus, the preservational potential of a particular organism depends on two main factors: its constitution (better if it contains hard parts), and its habitat (better if it lives in an environment where sedimentary deposition occurs).

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Fossil-Lagerstätten

Occasionally, however, the fossil record presents us with surprises. Very rarely, exceptional circumstances of one sort or another have allowed an unusual preservation of the soft, unmineralized, parts of organisms, or have allowed preservation in environments where fossilization rarely happens. Rock strata within the geological record which contain a much more completely preserved record than is normally the case can be considered as windows on the history of life on Earth. Such strata were called Fossil-Lagerstätten by Dolf Seilacher in 1985, a name derived from German mining traditions, used there to denote a particularly rich seam of ore. In fact, there are two main types of Fossil-Lagerstätten: concentration and conservation.

Concentration Lagerstätten (*Konzentrat-Lagerstätten*), as the name suggests, are simply deposits in which vast numbers of fossils are preserved. Readers will be familiar with such deposits as coquinas (shell accumulations), bone beds, cave deposits and natural animal traps. The quality of individual preservation may not be exceptional, but the sheer numbers are informative, especially where they may contain complete growth series and thus enable accurate ontogenetic studies to be performed. Moreover, the great abundance of specimens also allows a more accurate statistical analysis of the composition of the ecosystem, which is especially useful in the reconstruction of food webs. True Concentration Lagerstätten should demonstrate some mechanism of concentration, for example, evidence of mass mortality, rather than simply sheer numbers of individuals.

Conservation Lagerstätten (*Konservat-Lagerstätten*), on the other hand, preserve quality rather than quantity, and this term is usually restricted to those rare instances where peculiar preservational conditions have allowed even the soft tissue of animals and plants to be preserved, often in incredible detail. Skin, hair, feathers, muscle tissue, cells with nuclei, ovaries with eggs, and even blood may be preserved. Proteins have been identified, even in some ancient (Palaeozoic) fossils, and DNA has been isolated, albeit only in much younger (Quaternary) examples. Readers should note, however, that the term Conservation Lagerstätten is also sometimes used for deposits that still yield articulated vertebrate skeletons without the preservation of soft tissue.

Conservation Lagerstätten

There are many different types of Conservation Lagerstätten, including those known as conservation traps. Well-known examples are those that include the entombment of insects and spiders in amber, the deep-freezing of ice-age mammals in permafrost, pickling in oil swamps and the mummification of tissue by desiccation.

On a larger scale are *obrution deposits*, where episodic smothering by fine-grained sediment ensures the rapid burial of mainly benthonic (sea-floor) communities, and *stagnation deposits*, where anoxic (low oxygen) conditions in stagnant or hypersaline (high salinity) bottom waters ensures reduced microbial decay, in predominantly pelagic (open-sea) communities. The well-known Middle Cambrian Burgess Shale of British Columbia, with its 'weird wonders' described by Stephen Jay Gould, is a perfect example of a benthic community preserved by obrution, while the equally renowned Jurassic Holzmaden Shale of southern Germany, with its pregnant ichthyosaurs and other pelagic marine reptiles, is a good example of preservation by stagnation. In fact, most Conservation Lagerstätten combine obrution and stagnation in the preservation of soft tissue, and the classic Bavarian locality of Solnhofen, which has yielded the ten known specimens of the world's oldest bird, *Archaeopteryx* (Fig. 1), is a perfect example of such a site.

Fig. 1. *Archaeopteryx* from Solnhofen, preserved by obrution and stagnation.

Taphonomy

Taphonomy is the name given to the process of preservation of a plant or animal as a fossil. It actually consists of three main processes: necrosis, biostratinomy and diagensis.

Necrosis refers to the death of an organism (or in plants to the shedding of parts), and may be induced physiologically (through old age, disease, or temporal/climatic shedding) or traumatically (by sudden catastrophic death or loss of parts in response to natural perturbations). Biostratinomy covers the course of events from death to burial in sediment (or entombment in amber, cave deposits, etc.). The time taken by this process can vary from a few minutes (as with insects trapped in amber, or mammals in tar) to many years for an accumulation of a bone bed or a coquina of shells. Ideally, for the exceptional preservation of soft tissues, the time between death and isolation from oxygen, decaying bacteria and scavengers should be short. Finally, following burial, the process of diagenesis begins: this is the conversion of soft sediment or other deposits to rock. Further destruction of organic molecules can occur during diagenesis; the action of heat can turn organic molecules into oil and gas, for example, and crushing in coarse sand can fragment plant and animal cuticles.

The preservation of soft tissue has three important implications. First, the study of soft part morphology, alongside the morphology of the shell or skeleton, allows a better comparison with related extant forms and provides additional phylogenetic information. For example, the classification of most modern molluscs depends on gill structure and other soft parts that are normally unavailable to the palaeontologist. Secondly, it enables the fossilization of animals and plants which are entirely soft-bodied and which would normally stand no chance of preservation. For example, it has been estimated that 85 per cent of the genera from the Burgess Shale were entirely soft-bodied and are therefore absent from Cambrian biota preserved under normal taphonomic conditions. The beautiful 'lace-crab' *Marrella* (Fig. 2), known from over 15 000 specimens in the Burgess Shale, and clearly a domi-

Fig. 2. The 'lace-crab' *Marrella*, common in the Cambrian biota of the Burgess Shale.

nant constituent of that ecosystem, is unknown in any other Cambrian locality anywhere in the world! The third implication follows—such Conservation Lagerstätten therefore preserve for the palaeontologist a complete (or much more nearly complete) ecosystem.

Snapshots of life

If all known Lagerstätten are arranged in chronological order, from the Archaean Gunflint Chert biota to the Pleistocene Rancho La Brea, for example, it is possible to follow the development of the Earth's ecosystems through a series of snapshots of life at a number of points in time. Whilst this can never give a complete picture of the evolving biosphere, it does allow the palaeontologist to see as completely as possible the ecological interactions of the organisms in that particular habitat.

Even among the earliest known Lagerstätten, the Gunflint Chert of Canada shows traces of a simple ecological system, with both benthonic microbial mats and planktonic forms. Whilst some of the organisms in this biota were photosynthetic, most used other chemicals such as iron for their metabolism. Thus, this ecosystem represents a very early phase in the development of life on Earth.

By late Precambrian times, multicellular organisms had developed, and a handful of localities around the world provide tantalizing glimpses into life in the oceans at that time. At Ediacara in South Australia, Charnwood Forest in Leicestershire, UK, and the Avalon Peninsula in Newfoundland (Mistaken Point), bedding planes preserve the so-called Ediacaran biota. These creatures were soft-bodied, three-dimensional, and many grew to large sizes. Whilst some can be classified as jellyfish and sea-pens (phylum Cnidaria), many cannot be identified with modern plants or animals. For example, the most common fossil in the Newfoundland biota, *Fructofusus*, is a frond-like, spindle-shaped form that occurs in great numbers on bedding planes, but its zoological (or, indeed, botanical) affinities are obscure.

Palaeozoic Lagerstätten

By the middle Cambrian, when the Burgess Shale of British Columbia was being deposited, relatively modern deep-sea ecosystems can be identified. This famous biota is dominated by arthropods. Crustaceans, chelicerates and trilobites are all known from the fauna, but a great many of the arthropods cannot be placed in modern arthropod subphyla. For example, the lace-crab *Marrella* (Fig. 2) has given its name to a group of extinct arthropods, the marrellomorphs, which are also known from the Silurian and Devonian, and which show similarities and differences to all the main arthropod groups alive today. The Burgess Shale deposits exhibit a wide variety of organisms, including Cnidaria, annelid and priapulid worms, primitive molluscs and chordates, as well as the arthropods. More than 80 per cent of these are soft bodied, and so this deposit is a true Conservation Lagerstätte, and the Burgess Shale provides a rare glimpse into sea life over 500 million years ago.

Fig. 3. Ordovician trilobite preserved in beautiful detail from Beecher's Trilobite Bed, New York State.

The Ordovician Period has few Fossil-Lagerstätten, but two sites are of exceptional interest. Beecher's Trilobite Bed in New York State, USA is best known for its wonderful preservation of trilobites by replacement of soft parts with iron pyrite; the fossils are, therefore, not only among the rarest in the world in showing the appendages of trilobites but also among the most beautiful of fossils (Fig. 3). Apart from trilobites, Beecher's Bed strata contain orthocone nautiloids, graptolites and brachiopods: a fairly typical assemblage for a deep-water Ordovician biota. The Soom Shale from South Africa contains an impoverished fauna but is famous for its preservation of fairly complete conodont animals. The conodont jaw apparatus had been known for many years and, indeed, conodont elements are widely used in biostratigraphy, but it was not until the 1980s that palaeontologists discovered that the jaws belonged to chordates. *Promissum pulchrum* from the Soom Shale was first described as a plant fossil! It is, in fact, a large conodont animal with bulging eyes.

The Silurian Period is similarly rather poor in Fossil-Lagerstätten, but more are coming to light; for example, the nodules containing beautiful, three-dimensionally preserved starfish, arthropods and worms from Herefordshire, UK, described by Derek Briggs and colleagues in 1996. The Bertie Waterlime biota from New York has, however, been known for many years for its beautifully preserved eurypterids and other fossils; indeed, *Eurypterus remipes* (Fig. 4) is the state fossil of New York! This Lagerstätte contains some of the earliest known scorpions, hinting at land life yet to come, yet also the peculiar trilobite *Naraoia*, which harks back to Burgess Shale times.

By the Devonian, life was possible on land and the localities of Rhynie, Aberdeenshire and Gilboa, New York, have yielded the most complete early terrestrial ecosystems of Europe and North America, respectively. Their taphonomic settings, however, could not be more different. The Rhynie biota, consisting of a great diversity of early vascular plants together with arthropods such as trigonotarbid arachnids, myriapods, mites, springtails and fairy shrimps, was deposited around hot springs whose sinters have preserved the fossils in three dimensions in translucent chert. At Gilboa, a similar fauna and flora is preserved in beautiful detail but completely flattened in shales. These early terrestrial ecosystems are quite basic in nature and very different from most places on Earth today. The simple plants, without leaves, had no true herbivores to attack them, but their remains were decomposed and recycled by millipedes, springtails and other detritus feeders that, in turn, were preyed upon by the arachnids and centipedes. Marine life in the Devonian is seen beautifully in the Hunsrück Slate of Germany, where fish, echinoderms and many kinds of arthropods are preserved in iron pyrite in black slates. X-rays have been successfully used to reveal the hidden morphology of these animals.

By Late Carboniferous times, land life was prolific although herbivory was still in its infancy, which could explain the immense build-up of forest litter and peat that formed the Coal Measures of Europe and North America. Many of these sediments contain ironstone nodules with exceptionally preserved fossils inside, and the best-known locality for these is Mazon Creek in Illinois. Decades of strip mining in the twentieth century left behind piles of overburden containing ironstone nodules which, when split, reveal exquisite plants and animals. Nodule formation must have been rapid because the failed escape trails of bivalves are preserved together with their maker in some nodules, and the laminated clay-silt matrix around the nodules shows a clear record of spring and neap tides–around 30 per lunar month in those days! There are two distinct biofacies at Mazon Creek: one is non-marine and includes terrestrial arthropods, such as giant millipedes, centipedes and spiders, plants, and freshwater sharks, crustaceans and clams; the other is marine, and includes non-marine forms washed into the sea as well as truly marine forms such as jellyfish, marine worms and molluscs, and the bizarre Tully Monster (a pelagic heteropodid gastropod).

Fig. 4. *Eurypterus remipes*, the state fossil of New York, from the Silurian Bertie Waterlime biota.

The Permian shows few Fossil-Lagerstätten—the magnificent reefs of Texas and the insect beds of Elmo, Kansas, may be mentioned—so we move swiftly to the Triassic. The Grès à Voltzia of Alsace, France, shows many similarities to Mazon Creek in terms of its biota—both are from deltaic environments after all—but most of the exceptionally preserved French fossils were trapped by microbial slime forming in drying-up pools rather than in ironstone nodules.

Mesozoic Lagerstätten

One of the most famous fossil localities in Triassic rocks is the Petrified Forest in Arizona. This National Park is just a small part of the much more extensive Chinle Group of rocks, famous not only for the abundant petrified logs of araucarian (Monkey Puzzle) trees but also for early dinosaurs such as *Coelophysis* and mammal-like reptiles such as *Placerias*.

Dinosaurs had really got going by Jurassic times, and nowhere is better known for their remains than the Morrison Formation which crops out widely across western USA. These are classic sites, worked by Othniel Marsh of Yale and Edward Cope of Philadelphia in the nineteenth century. Many of the famous dinosaurs were described by them, including *Apatosaurus*, *Diplodocus* and *Stegosaurus*. The Morrison Formation is a classic Concentration Lagerstätte because it is the huge accumulations of bones that are important, rather than the preservation of soft parts.

In Jurassic seas there were marine reptiles and ammonites, and the best place to see these is in the quarries and museums around Holzmaden, Germany. Holzmaden, with its iron pyrite preservation in black shales, and its lack of benthos for the most part, has been held up by Dolf Seilacher as an example of a stagnation deposit. Ichthyosaurs are a common component of the Holzmaden biota, and females are often found to have died whilst giving birth. Other marine reptiles are represented by plesiosaurs and crocodiles; there is a great diversity of fish, ammonites and spectacular driftwood logs covered with crinoids. A good example of soft-part preservation is that of the belemnoids with their tentacles and ink-sacs still intact. Perhaps the most famous of all the Jurassic sites is the Solnhofen lithographic limestone. Numerous quarries for building stone (and, at one time, lithography plates) along the pretty Altmühl Valley in Bavaria appear barren of fossils at first glance—this is no concentration deposit! But perseverance will yield coprolites, ammonites, pelagic crinoids, occasional crustaceans and fish. Extreme good luck will result in a horseshoe crab preserved at the end of its death trail, a dragonfly, a pterosaur, or possibly even *Archaeopteryx*—the earliest true bird (Fig. 1). It is thought that the Solnhofen fossils resulted from severe storms that swept marine animals into anoxic lagoons; the extreme winds also downed flying animals and plant debris from low-lying islands.

The Cretaceous Period has numerous Fossil-Lagerstätten. The Santana and Crato formations are two Lagerstätten which occur in close proximity to one another on the slopes of the Chapada do Araripe in north-east Brazil. They are quite different, however. The older, Crato Formation, is a thinly bedded limestone superficially resembling the Solnhofen, and which contains abundant land plants, insects, other arthropods, and mass mortalities of the fish *Dastilbe*. The younger Santana biota, on the other hand, occurs in phosphatic nodules and is dominated by a great diversity of fish. The nodules are commonly in the shape of the fish they contain. Fantastic pterosaurs such as *Anhanguera* and rare dinosaurs are known from these localities.

As is well known, at the end of the Cretaceous Period there was an extinction event that wiped out dinosaurs, ammonites and some other animal and plant groups, but close to the top of the Cretaceous strata in western USA is a sequence of rocks, the Hell Creek Formation, which preserves the remains of some of the last of the dinosaurs and their associated biota. Quarries in the Hell Creek Formation have yielded some of the most famous dinosaurs, in particular *Tyrannosaurus rex*, *Triceratops*, *Ankylosaurus* and *Pachycephalosaurus*. Early mammals, poised to take over from the dinosaurs as dominant terrestrial vertebrates very shortly, also occur in these beds. Hell Creek is both a concentration deposit, with some sites dominated by masses of bones of a single dinosaur species, and also a conservation deposit, for example a 'mummified' corpse of a hadrosaur has received much press coverage recently!

Cenozoic Lagerstätten

Cenozoic biotas differ much less from those of the present-day than do earlier ones. Three deposits of Eocene age provide a marvellous glimpse into land life during that epoch of Earth history. Near Darmstadt in Germany a pit dug for oil shale has yielded some of the most spectacular early Eocene fossils anywhere in the world. Destined to be filled with waste after the quarrying ceased, a successful campaign saved the pit, which is now a World Heritage Site. Grube Messel is best known for its fossil mammals, including the early horse *Propalaeotherium*, complete with its stomach contents, many species of bats, and the unusual *Leptictidium*, which apparently ran on its hind legs with its long tail used for balance. Messel birds have feathers preserved; there are exquisite snakes, turtles, crocodiles and frogs, and some of the beetles still show their iridescent coloration. The flora tells us that the Messel lake was in a subtropical forest.

The middle Eocene Green River Formation of Wyoming and surrounding states is famous for its fossil fish, which have been quarried around the little town of Kemmerer for sale to tourists, and can be found in nearly every fossil shop around the world. Literally millions of fossil fish have been found in the Green River lacustrine deposits, mostly the little freshwater herring *Knightia*, which commonly occurs as mass mortalities. Many other species of fish occur, including the holostean gar-pike and bowfin, the spiny *Priscacara* and the bizarre, cartilaginous paddlefish. Other organisms occur too, including an extensive land-plant flora, frogs, turtles, birds, bats, insects and spiders. In July 2007 only the second known snake (a neotropical wood snake) was recovered from Green River (the only other example has been lost since the 1930s!) The late Eocene Florissant Formation of Colorado represents lake deposits too, but the Florissant lake was dammed by volcanic mudflows. Between the volcanic ash layers diatom blooms preserved the finest fossil insects described from North America, as well an extensive flora of land plants. *Sequoia* tree stumps occur in one layer and are prominent landmarks on the trails in the National Monument erected to conserve this important deposit.

The exquisite preservation of insects and other biota in amber is hard to beat for beauty in the fossil record (Fig. 5). Historically, amber from the Baltic region of Europe has been collected for centuries. The

Fossil Ecosystems of North America, the new book by John Nudds and Paul Selden published by Manson Publishing, is reviewed in on page 160.

Fig. 5. Insects in amber are amongst the most beautifully preserved of all fossils.

Greeks called it elektron, and from the static charge that builds up when it is rubbed against wool, we get our word electricity. Amber is fossilized tree resin. Some trees produce resin profusely, and insects are attracted to it or get caught in it when it flows down tree trunks. Predators such as spiders and small lizards may get trapped when trying to capture the struggling insects, and plant parts get engulfed or blown by the wind into the sticky substance. There is no doubt that amber is a Conservation Lagerstätte—there is fine preservation of even internal organs by mummification—but amber is a very unusual sedimentary deposit. It samples biota from and around tree trunks, possibly far from the usual depositional environments such as seas and lakes. Amber has provided us with some unusual facts about biogeography. Some of the species found in Baltic amber, for example, are now found only in the southern hemisphere—the spider family Archaeidae is one example (Fig. 6) and is also remarkable because the first archaeid ever described was a fossil in Baltic amber. Amber from the Dominican Republic is now very common in gem shops. Being in a more tropical situation, Dominican amber is has many more ants than Baltic amber, which was in a more temperate climatic zone and is dominated by flies.

Fig. 6. A spider, relative of the Archaeidae, preserved in French Cretaceous amber.

Much of the Pleistocene of northern regions of the world was dominated by glacial climates, and even permafrost can act as a taphonomic trap: the frozen mammoths of Siberia for example. In southern California, well away from the ice sheets, another kind of sticky trap has preserved the local fauna in great detail: the tar pits of Rancho La Brea in downtown Los Angeles. Natural tar seeps can become covered in pools of water where animals go to drink. They become stuck in the sticky tar and then attract predators, which also get trapped. Rancho La Brea preserves the fauna of the Los Angeles region between 10 000 and 40 000 years ago. In it are found the remains of mammoths and mastodons, sabre-toothed cats, coyotes and dire wolves; also giant ground sloths, squirrels, rabbits, shrews, weasels, bats, and many more. More fossil birds are known from here than anywhere else, and include water birds, songbirds, raptors, and the giant, extinct teratorn with a wingspan of 3.5 m. Being such a young deposit, even human remains have been found, as well as the artefacts of man.

Many of the sites mentioned above (and described in more detail in our two recent books) have been known since the nineteenth century, but amazingly, new sites are still being discovered today, especially with the recent rapid development in the Third World and particularly in Asia. For example, the Jehol biota and Chengjiang faunas of China have only really become known in any great detail in the last decade. Research on all these sites is currently blossoming and the application of new techniques, such as CT scanning and 3-D printing etc., is revealing a wealth of incredible detail about the fossil record of which Darwin could never had dreamed.

Suggestions for further reading

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