1

General Points

1.1. Fossilization: a phenomenon that is always exceptional

In most ecosystems, dead organisms decompose and disappear in relatively little time. To begin with, the action of decomposers and necrophages breaks down the soft tissues of the bodies, and these organic remains are therefore not protected by being buried in the sediments. Secondly, the remains which are most mineralized – bones, teeth and shells, for example – are subject to bioerosion (by encrusting organisms, perforators, crushing carrion eaters, etc.) and physical fragmentation (due to transportation in water, temperature variations, etc.), and are gradually reduced to debris, eroded to a greater or lesser extent. The time needed for fossilization to take place is generally too long for the dead organisms to be preserved in mineral form, and therefore fossilization is a rare phenomenon as it is selective and complex. Only in a handful of special contexts – notably xeric or anoxic – is degradation slowed or stopped, allowing a few traces to remain in the sediments over long periods of time, and thus, by diagenesis (see Box 1.1), become fossils.

For a color version of all the figures in this chapter, see www.iste.co.uk/neraudeau/fossilization.zip.

Fossilization,
by Didier NÉRAUDEAU and Jean-David MOREAU. © ISTE Ltd 2025.

If we look at present-day ecosystems, it is estimated that two thirds of marine animals have little or no mineralized elements to their bodies (they have no "skeleton", in the broad sense of the word). Of the remaining third, which is more skeletonized, only a third has a significant likelihood of being fossilized. In other words, a third of a third of the original animal biodiversity – that is only around 10% of creatures that have lived – have the chance of being fossilized.

Diagenesis refers to the set of processes which occur, one after another, in the transformation of sediments into sedimentary rocks. This includes physico-chemical processes (compaction, desiccation, dissolution, precipitation, crystallization, temperature variations, etc.) and biochemical ones (reducing or mineralizing micro-organisms, etc.). Chronologically, a diagenetic sequence contains first the compaction of the sediment, then cementation, and finally (re)crystallization.

Box 1.1. *The concept of diagenesis*

Taphonomy is the discipline which consists of retracing all the processes – biological (putrefaction, carrion feeding, etc.), chemical (degradation, dissolution, mineralization, etc.), sedimentary (burial, filling, etc.), physical (UV exposure, temperature variations, etc.) and mechanical (transport, fragmentation, erosion, etc.) which have occurred between the death of an organism and its final fossilization. *Diagenesis* (see Box 1.1) has an important place in these various steps, combining sedimentary, chemical and physical processes. It should be noted that certain organisms may have been buried alive. In that instance, their taphonomic history began even before the moment of their death.

Box 1.2. *The concept of taphonomy*

Even within this small proportion of marine organisms which can be fossilized, most only give us incomplete fossil records (the skeleton without the soft tissues, an internal cast, a hollow mold), which are sometimes deformed (due to the pressure of sediment, tectonic motion, metamorphism), or indirect indications (tracks, burrows, coprolites, eggs, bite marks) of the species' anatomy. In the subaerial environment on land, where the burial of the organic remains in sediments is more random than in an aquatic environment (marine or lacustrine), the potential for fossilization is lower still.

1.2. The main processes of fossilization

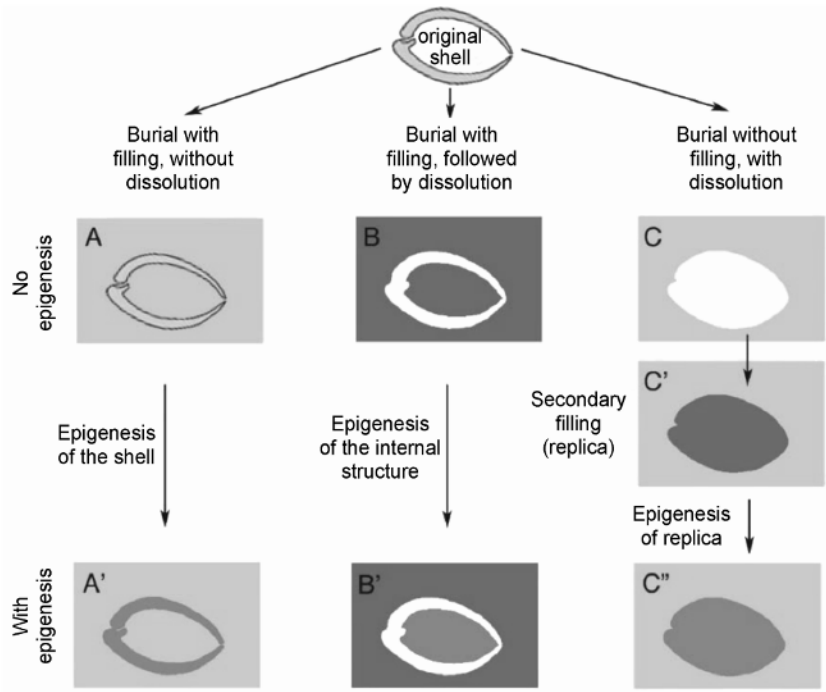

Figure 1.1. *Elementary types of fossilization*

NOTE ON FIGURE 1.1.– *The most common fossilization processes are based on the filling of the empty spaces in the organisms, notably after the decomposition of the soft parts, but also the preservation or dissolution of the mineralized parts. For example, for a bivalve animal (lamellibranch, brachiopod), if burial is accompanied by inter-valve filling, then the shell may be preserved identically (A), or in epigenetic form (A'). If the burial and the internal filling are followed by a dissolution of the valves, the final fossil will be an internal cast (B)* *made up of the initial intervalve sediment, which may sometimes be epigenetic (B'). In the event that the surrounding sediment does not penetrate the inter-valve space and the valves are dissolved, the final fossil can only be expressed on the walls of the cavity occupying the total volume of the organism (C); in a second step, if a new sediment fills that void, it will form a replica of the organism (C'), and in some cases, that replica may be epigenetic (C'').*

After burial of a skeletonized organism (shell, bone, test), the processes of fossilization depend on the taphonomic history (see Box 1.2) of the mineralized remains. The most commonly found processes can be summarized as three fundamental cases, ranging from the most complete to the most partial:

– preservation of the endo- or exoskeletal elements in a mineral form which has been modified to a greater (see Figure 1.1A') or lesser extent (see Figure 1.1A) after epigeny (see Box 1.3), thus preserving a true image of the organism's appearance, at least of its mineral envelope (shell of mollusks or test of sea urchins, for example);

– quasi-total filling with sediment (see Figure 1.1B) or a mineral (see Figure 1.1B') (epigenetic addition, see Box 1.2) of the organism's internal cavity, followed by the dissolution of its exoskeleton, producing an internal cast, which offers no indication of the organism's real volume and its external morphology, but merely reproduces, on the surface, the inverted relief of the internal surface of the shell or test;

– complete filling, either with sediment (see Figure 1.1C') or a mineral (see Figure 1.1C), of the void left in the rock by the organism's dissolution (see Figure 1.1C), producing a replica which shows the whole of the organism's volume and its external morphology.

On the basis of these three fundamental principles of fossilization, there are numerous combinations which can occur in the wake of the burial of a shell, with or without sedimentary filling, with or without dissolution of the shell, with or without secondary mineralization of the shell or filling of its internal cavities (see Figure 1.2).

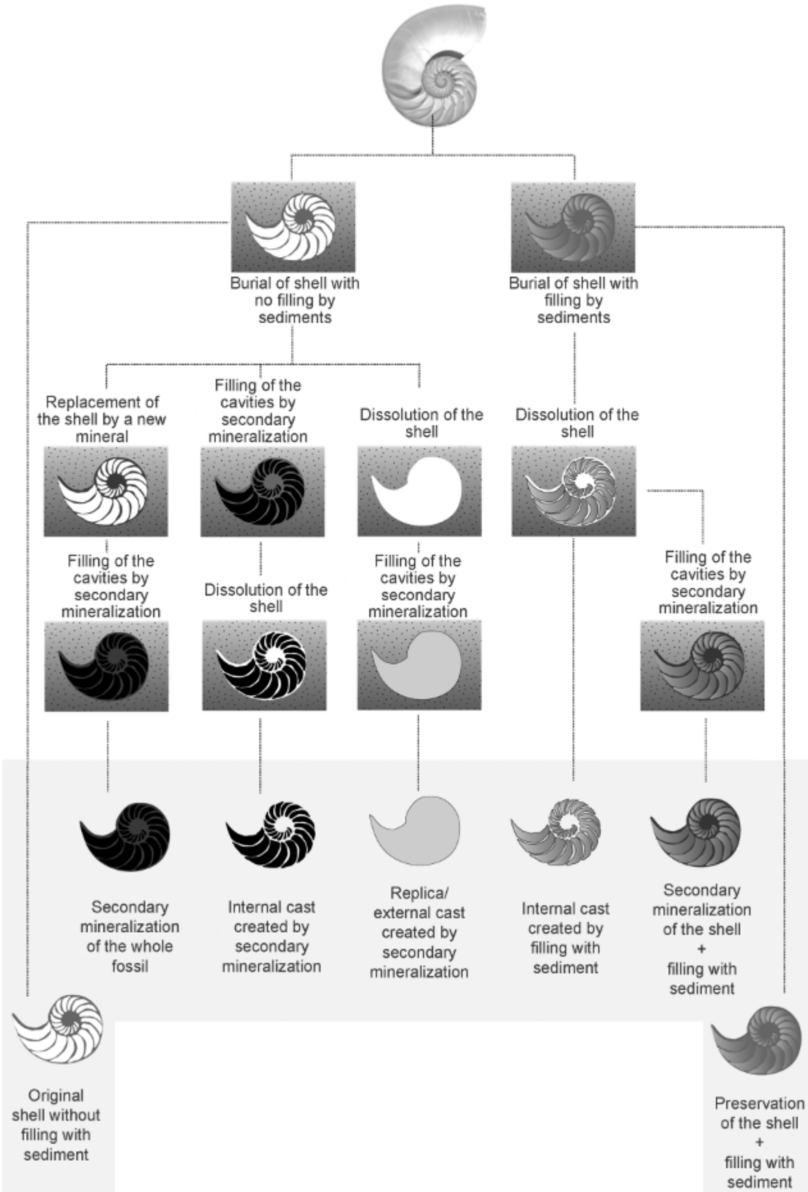

Figure 1.2. *The different variants of modes of fossilization*

NOTE ON FIGURE 1.2.– *Excluding the most elementary modes of fossilization (see Figure 1.1), there are numerous variants in the processes of fossilization. These depend on various combinations between filling or non-filling of the buried remains, whether or not they are dissolved, whether or not they undergo secondary mineralization, and whether a cast is created.*

The primary mineral constituting the skeletal elements of the original organism may be replaced by another mineral by means of isovolumetric substitution (perfect epigeny of the original skeletal elements).

However, this substitution may also occur in a secondary manner, at the level of an internal cast or replica which are formed, during an early stage of diagenesis, in a mineral form which differs from the final form.

Epigeny is a process whereby a mineral body changes its chemical nature without changing its shape. We also speak of epigenetics, or pseudomorphosis. When such a process affects a fossil, it does not alter either its volume or its shape. Epigeny generally occurs as the result of the circulation of a fluid (e.g. percolation of mineralized water, see Box 1.4), hydrothermalism, or atmospheric gas exchanges), which may or may not be combined with the action of micro-organisms (bacteria in the broadest sense).

Box 1.3. *The concept of epigeny*

Percolation is the gradual infiltration of a fluid into the pores of a material. In a geological context, for the most part, sediments are slowly traversed by a liquid (or possibly a gas). This process can be linked to the infiltration of surface water (due to gravity), to the "movements" of underground waters (the water table), but also to injections of fluid in the hydrothermal context, in particular temperature and/or pressure conditions.

Box 1.4. *The concept of percolation*

1.2.1. *Preservation of the endo- or exoskeletal elements*

There is practically no fossil record of vertebrates unless bones, teeth or both are preserved. The organisms' organic phase is typically lost, but their mineral part, composed of calcium phosphate (apatite), is preserved, with a greater or lesser degree of re-crystallization. Teeth are stronger than bones, and are often preserved in sedimentary contexts where the bones have been lost to dissolution. Hence, these are types of fossils which are not exceptional in terms of their nature, and can only be viewed as exceptional in terms of their representativity of such-and-such a species (for example, in view of the rarity of mammal teeth from the Jurassic (–201 to –145 million years ago, Ma), and the Cretaceous (–145 to –66 Ma)). Though bones can less easily be fossilized than teeth, they also represent fairly commonplace fossils, and are exceptional only in particular cases of mineralization or representativity of a taxon.

Fossils of invertebrates with shells (brachiopods, mollusks), carapaces (crustaceans) or test (foraminiferans, sea urchins) constitute as many cases of "ordinary" fossilization as there are taxonomic groups. All these organisms, which have exoskeletons, have good potential for fossilization of their mineral parts, and sometimes the soft tissues are lost during putrefaction. The test of sea urchins is probably the strongest component, with each skeletal element (the plate of the test or radioles) being composed of a very stable calcite from the life of the animal and the remnant during fossilization. However, it sometimes occurs that, during diagenesis, the recrystallization of the test fuses all the plates into a single calcite monocrystal. The aragonite of foraminiferans generally stabilizes as calcite during the course of fossilization, making them one of the most common microfossils, highly present in numerous ancient sediments. Similarly, the most common brachiopods, corresponding to articulate species, usually have a calcitic shell with an external cryptocrystalline layer and a fibrous internal layer, which remains stable during fossilization. Inarticulate brachiopods, whose shell combines calcium phosphate and chitin, are more fragile and less capable of withstanding diagenesis. In the carapace of crustaceans, calcium carbonate and chitin are combined. This latter ingredient, when it is abundant, renders the mineral envelope fragile, meaning it cannot easily be fossilized, and becomes fine and powdery, or even ghostly.

1.2.2. *Formation of replicas or countermolds*

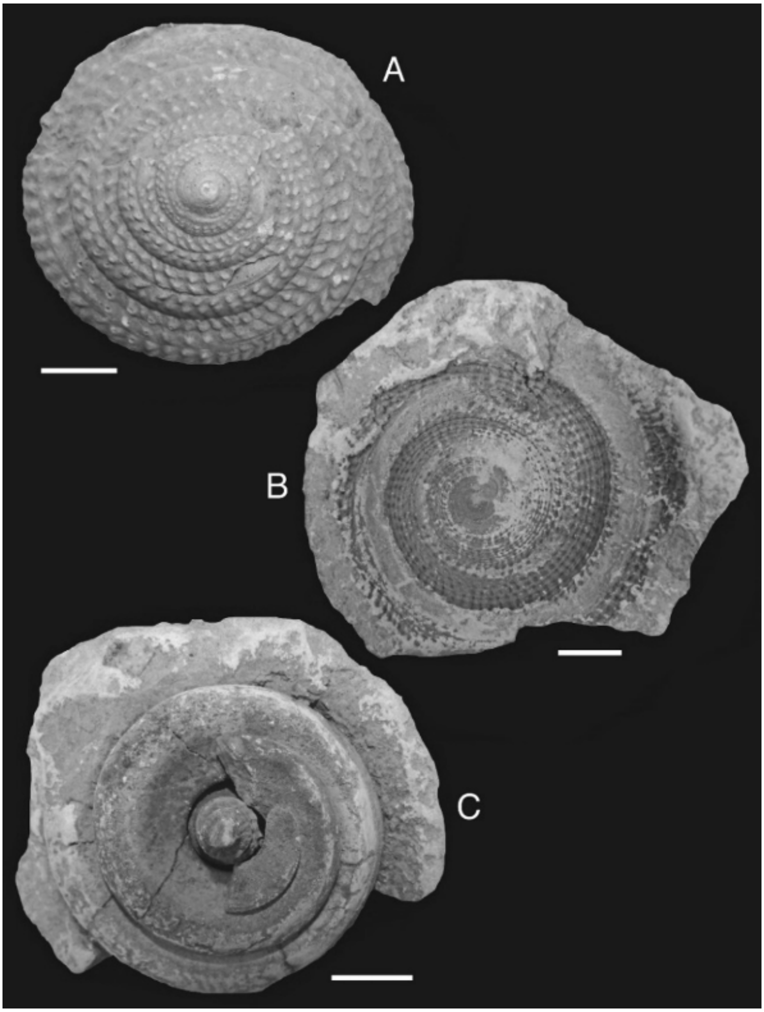

Plate 1.1. *The three types of fossil preservations obtained for the same gastropod mollusk (Pleurotomariidae)*

NOTE ON PLATE 1.1.– *A: limestone replica of the original shell with detailed preservation of the ornamentation of the shell's external surface; B: hollow imprint in surrounding limestone, showing the negative of the relief of the shell's ornamentation; C: internal cast of the shell, with filling of the spire towers in the form of a "rolled-up sausage" in a spiral shape (collection: IGR – Institut de géologie de Rennes; photos: D. Néraudeau). Scale bars: 1 cm*.

Often, organisms with a carbonate shell, especially mollusks, have their mineralized parts composed of aragonite, which is a type of calcium carbonate that is not very resistant to the dangers of diagenesis (thermal or acid "attack").

When that fragile shell is dissolved during diagenesis, its internal void (e.g. between the two valves of a bivalve or in the spire of a gastropod) sometimes remains free from early filling by sediments. The sediment containing the organism then contains a cavity in which the void left by the dissolved shell is found in addition to the void left by the animal's internal cavity. This total cavity has exactly the same volume as the original organism and the sediment which surrounds it, when it hardens, shows the negative of the *mold* of that volume (see Plate 1.1B).

If, subsequently, a new sediment infiltrates and fills that void, it forms a *countermold* of the original organism (see Plate 1.1A). This copy is generally called a *replica*, and usually forms in a carbonated context; it is chalky in nature. Examples of replicas formed in marl or sandstone are also known, but are rarer. The replica may have been created or altered by the percolation (see Box 1.3) of a mineralized fluid and be composed of a homogeneous mineral (for example calcite, opal or pyrite).

1.2.3. *Formation of internal molds*

When, during or shortly after its burial, a shell is filled with sediment, this sedimentary content will become lithified (see Box 1.5) and form a solid mold of the internal space between the valves (bivalves, brachiopods) (see Figure 1.1B) or inside a shell (ammonites, gastropods) or a test (sea urchins).

Following the hardening of that internal mold, the shell surrounding it may be dissolved (for example by acid attack by means of fluid percolation, see Box 1.3) and the internal mold then "floats" in the rock where it was formed, with the thickness of the dissolved shell creating a void between the internal mold and the surrounding rock (see Plate 1.1C). The surface of the internal molds reproduces the inverted relief of the internal surface of the original shell.

For example, in bivalve mollusks, casts of the surfaces where the adductor muscles attach, which are hollow on the internal faces of the shells, correspond to protuberances in the relief on the surface of the internal mold.

In sea urchins, the small holes corresponding to the ambulacral pores in the respiratory areas which pierce the test correspond to small "bumps" in the relief on the internal mold.

Lithification is the successive processes of compaction and cementing by which an initially mobile sediment is transformed into hardened sedimentary rock. Through compaction, the sediment loses the majority of its fluid content, notably liquid, and undergoes packing, losing volume to a greater or lesser extent. The cementing phases correspond to diagenetic crystallizations or recrystallizations (see Boxes 1.1 and 1.2), which can equally affect the particles of the sediment and the porosity between them.

Box 1.5. *The concept of lithification*

1.2.4. *Case study: geode formation*

Geode formation (see Box 1.6) is a special case, which corresponds to the crystallization of a highly mineralized fluid having percolated into certain cavities of the shells. Largely, this occurs when the organisms' internal cavities (total or partial) are not filled with sediment when they are buried (see Figure 1.3).

Unlike replicas or recrystallized internal molds, geodes do not fill all of the internal cavities of the shells. They merely coat the walls with crystals with centripetal growth, where the points generally converge towards a central space, which remains hollow (see Figure 1.3B'). The mineral nature of the crystals is determined by the chemical composition of the percolating fluid.

For example, in chalky terrain it is fairly common for the percolation of a carbonated fluid to cause calcite geodes to form in the cavities which it passes through. Similarly, in a context rich in silica (notably decalcification alterites), the percolation of a silicated fluid will form quartz geodes.

Besides these relatively frequent cases, numerous mineral species can form geodes in the original cavities or the dissolution cavities of fossil organisms.

It should be noted that independently of the geodes crystallizing in the internal cavities of fossils, crystalline outgrowths can sometimes develop on the outer surface of the shells or bones, when they are buried in a highly porous sediment or without direct contact with a portion of the fossilized remains (see Figure 1.3C').

A *geode* is a cavity lined with crystals within a rock (be it sedimentary, igneous or metamorphic). The cavity in question is sometimes that of a shell from a mollusk or brachiopod, a test from a sea urchin, or any other hollow part of a skeletonized organism. From germs (impurities, points of erosion or dissolution, etc.) on the internal surfaces of the cavities, crystals grow as a result of the percolation water or hydrothermal fluids which bring mineral compounds that make up the mineral species in the geode.

Box 1.6. *The concept of a geode*

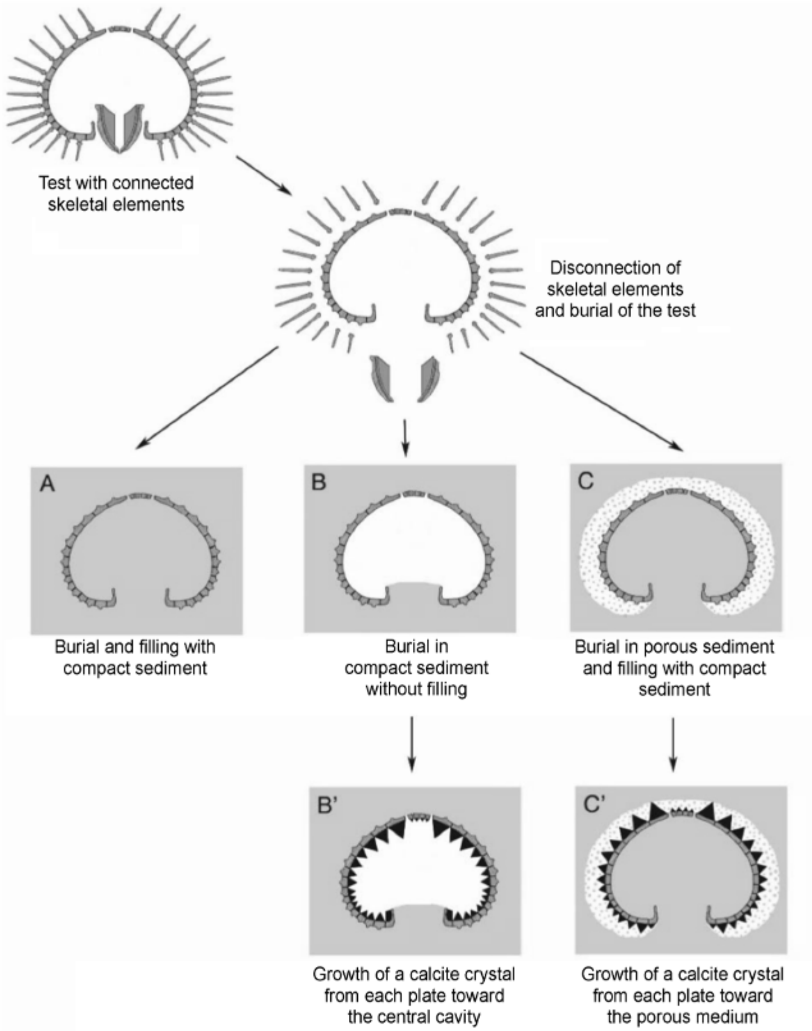

Figure 1.3. *Geodes and crystalline crusting*

NOTE ON FIGURE 1.3– *The burial of a shell or a test and its filling generally takes place in parallel with compaction of the sediment, which leaves no gaps either at the surface or inside the shelled remains (A). However, it sometimes happens that the internal cavity – for example, the inside of a sea urchin's test – is not filled with* *sediment (B). If a mineralized fluid (notably containing calcium carbonate or silica) percolates into the surrounding sediment, it can reach that internal cavity and crystallize there on the walls, forming a geode (calcite, quartz or other minerals) (B'). It may be that an organism's internal void is completely filled with compact sediment, but a substantial amount of porosity remains in the sediment that is in contact with the external surface of the shell, the test or even the bone (C). The percolation of a mineralized fluid into the surrounding sediment may lead to crystallization in that porous space, with crystals encrusting the outside of the organism (C').*

1.3. The concept of a Lagerstätten

In rare cases, certain processes of mineralization, with favorable contexts and facies, can lead to truly exceptional cases of preservation. These remarkable cases occur either sporadically, affecting only a few specimens at a local scale, or more generally across a fossiliferous site, a geological formation or a sedimentary layer.

In the occasional cases, it is a matter of exceptional preservation in the strict sense, yielding unexpected, spectacular, esthetically beautiful and particularly rare fossils. Above all, this relates to the phenomena of original mineralization/crystallization, fossilizations preserving the integrity and anatomical connections of the specimens, or the preservation of trophic situations involving two or more species (prey/predator, host/parasite associations, etc.).

In the more generalized cases, exceptional preservation relates to the vast majority of the groups and individuals associated in the same paleontological deposit. This type of deposit exhibiting exceptional preservation was dubbed a “Lagerstätte” (plural: Lagerstätten) by Adolf Seilacher in 1970. This term means a “storage place”, referring to the fossil content of a sedimentary deposit. There are two types which are differentiated by the exceptionality either of the quality of the fossils or of their quantity.

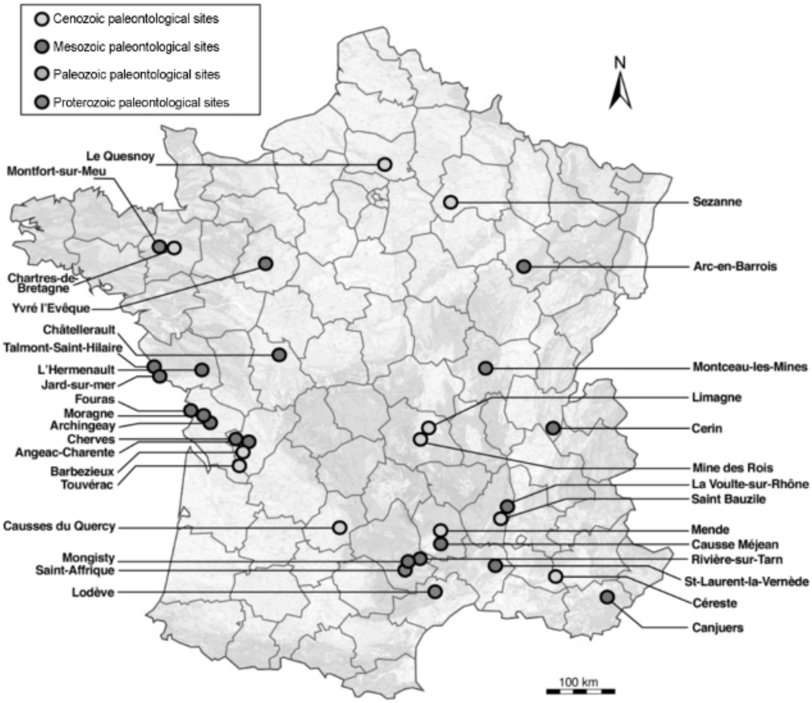

Figure 1.4. *Map of fossil deposits in France*

NOTE ON FIGURE 1.4.– *Map showing the location of paleontological deposits in France which are mentioned in this book, differentiated by the eon to which they belong: Proterozoic (pink), Paleozoic (green), Mesozoic (blue), or Cenozoic (yellow).*

The name “Konservat-Lagerstätten” is applied to facies which have an exceptional quality of preservation of the fossils, with almost complete preservation of anatomies, partial anatomic connections, 3D fossilizations, mineralization of soft tissues and variable combinations of these different remarkable cases.

The name “Konzentrat-Lagerstätten” applies to sites where an exceptional quantity of fossils are found, be they bones or tracks of vertebrates (the most usual cases), casts or cuticles of plants, or shells or tests of invertebrates. In such a context of remarkable accumulation, the fossilized organisms are not necessarily exceptional in terms of the quality of their fossilization, and they may well be less than complete or highly fragmented, with anatomical connections or dispersed elements.

This book gives an overview of France’s most remarkable mineralizations, facies and deposits in terms of original or exceptional fossilization, also touching on a number of fossils from outside of France to illustrate cases that are not found in the national territory (see Figure 1.4).