Events of Increased Biodiversity

Series Editor
Françoise Gaill

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Evolutionary Radiations in the Fossil Record

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Preface

This book is written for a broad audience who is interested in science in general and paleontology in particular. It is my hope that it will offer non-expert readers an effective introduction to the phenomena of diversification of life. The book is also intended for university students, for whose benefit it includes explanations and ruminations about this issue of diversification of the biological world, and of how that issue is approached in paleontology. Here, the question is dealt with from a standpoint based almost entirely on fossil data. Of course, here and there, examples are cited of the biodiversity in the world today, but nothing hugely detailed in comparison with the fossil examples given. The book is a personal treatise, guided by my own scientific specialty. It is also an accurate rundown of the situation as it stands, as paleontological data have, in the past, contributed to the recognition and later analysis of these phenomena of diversification.

I would like to express my sincere thanks to the many colleagues and friends who, in their different ways, have contributed to the writing of this book. Some of them looked over the manuscript with a critical eye in relation to the science; others the style; others walked me through the finer points of their particular areas of expertise, into which I (sometimes boldly) ventured. Still more, who are collection curators, opened their doors to me, allowing me to discover astonishing, exciting fossils, and also helping me to add some of my own to the collections. Of these various contributors, I am particularly grateful to: François Bretagnolle, Bruno David, Emmanuel Fara, Didier Merle, Thomas Saucède, Jérôme Thomas and Emmanuelle Vennin. In addition, I thank my students in general: from the first day of their first year of university to the day the most intrepid of them defended their PhD thesis. They often provide a fresh and pertinent view of the science of paleontology (sometimes certainly through their inexperience). In particular, in terms of the writing of this book, I would like to thank Igor Girault and Morgane Oudot who, in a manner of speaking, acted as (consenting) guinea pigs in compiling the relevant data and testing out the early pages of this book.

Finally, I am eternally grateful to Adeline, my wife, who patiently reviewed my spelling and the style of writing! My heartfelt thanks to her for that, and for everything else.

1

A Singular Work of Theater

1.1. A unique history

The history of biodiversity on the planet Earth could be compared to a work of theater. *Biodiversity* is a word which has been on the lips of many, often with a note of concern in the speaker's voice. Yet what is biodiversity? The word simply denotes the variety of biological organisms. When you walk through a forest, when you dive into the sea, when you roam through a wheat field, relax on the beach or trek through a desert, you can see this biodiversity all around you. Almost by definition, it is not identical everywhere: sometimes ubiquitous, sometimes more discrete, but always present on (or near) the surface of our planet and in the oceans. It has been this way for a long time. For an extremely long time. For hundreds of millions of years. For billions of years, even. Thus, biodiversity has a history – a very long one. In order to correctly and accurately analyze this biodiversity, it is necessary to look at its historical aspect, in context. With over 270,000 recorded species, flowering plants are, indubitably, a major part of the biodiversity present in the world today – all the more so when one considers that practically all vegetable material that we use in human foodstuffs comes from flowering plants. How come they are so diverse? When did this situation arise? Without understanding their diversification over the eons through geological records, we have no hope of accurately grasping the extent, nature and significance of their diversity today.

The idea I am attempting to put across in this book is a simple one: the story of biodiversity is, above all, a story of diversifications! Certainly, it is a story shot through with instances of extinction – sometimes by rather violent means. Yet the most striking feature of biodiversity is its incredible capacity for diversification. In scientific terminology, such diversification, when it is particularly significant, is called “evolutionary radiation”. This term will be used abundantly in this book. It is worth remembering: it denotes events of diversification of life on Earth. The study of evolutionary radiations is at the heart of this book.

Let us go back to the point made at the start of this chapter: the history of biodiversity on the planet Earth could, to a certain extent, be viewed as a work of theater. It has a beginning, a succession of “acts”, various actors – some at the head of the bill, and others with a more secondary role. Just like a play, the events take place against a changing backdrop. The position of the continents, the average sea temperature and the prevailing ocean currents are all elements of this “set” (among many others), which change over time. However, this resemblance with a work of theater is only superficial. Unlike a play, the story of biodiversity is not written in advance by a responsible individual. Indeed, it is not written in advance at all! It is, by its very nature, contingent. The events which occur on the evolutionary “stage” are primarily attributable to chance. A geological phenomenon, such as the opening of an oceanic rift, can give rise to changes in the environment which will play a role in the process of natural selection. Certain species encountering these new conditions will be able to adapt, whilst others will be driven to extinction. Those same species who do manage to adapt may then become extinct if the environmental conditions change again. The splitting of a geographic area into two – whatever the mechanism that causes it – may divide the population group of one species, and lead to the emergence of two new species. Random chance is a majorly important player in this work of theater. Thus, it renders the story entirely unique. Travel back in time, to the same exact conditions of the beginning of life on Earth, around 3.5 billion years ago, with the same actors and the same setting as before. Dim the house lights and raise the curtain, and let the action play out again. In all probability, you will see an entirely different story. This is the idea championed by Stephen Jay Gould (1941–2002), a renowned American paleontologist [GOU 89]. Although there are clearly demonstrated mechanisms which help to shape biological evolution – of which natural selection is one example – it is nonetheless true that evolution is, by nature, contingent.

Today, numerous academics are engaged in imagining the evolution of biodiversity in days to come. These projections are made over relatively short periods of time, and use the same actors (the species which are around today) and the same elements of set (the present-day environment), which they alter in accordance with various scenarios. In 2009, for example, Cheung and his colleagues [CHE 09] calculated the effects of the climate changes likely to occur by 2050 on the distribution of over 1,000 species of marine animals (primarily fish). One of the lessons from this study is the prediction of numerous local extinctions of species in certain geographical zones – mainly the subpolar and tropical regions. Studies such as this one are increasingly prevalent in academia today. They enable us to better understand the effects that the coming environmental changes are likely to have on biodiversity. However, it must be noted that these studies are very greatly focused on the near future: projections over a few dozen years at most. Making projections beyond that remains a risky business – very risky, even. Unpredictable events (those which are, by nature, linked to random chance) may considerably impact the performance of the projection models.

However, the future state of Earth's biodiversity is not the only issue worthy of interest. The biodiversity of the past is just as fascinating an object of study. The discoveries made by paleontologists looking at life in the past are far beyond what anyone could imagine. This exploration of the past helps answer the primary question of paleontology:

– what has been the history of life on our planet?

This central question invites other questions, some of which fit in entirely with the concerns of society today:

– what were the different actors that have played on that stage throughout the ages?

– how did some of those actors come to disappear?

– how does this past biodiversity illuminate what we know about biodiversity today?

– could the events of the past shed some light to help us better predict the future evolution of biodiversity on our planet?

Today, we can trace the outlines of the history of biodiversity thanks to fossils which bear witness to this past life. Fossils are the remains of ancient organisms or the traces of their activities: remnants in the form of bones, shells, teeth or traces of movement or predation, for example. Paleontologists discover and study fossils – not only to obtain a catalog of the most bizarre, most enormous or most ferocious forms of life, although this is an undeniably enjoyable activity! They study fossils in order to answer one of the greatest questions in modern science (posed a few lines earlier) what has been the history of life on our planet? Using their research, paleontologists reconstitute and order the different acts in that story, and the actors that have played out this singular piece of theater. It is by collecting fossils in the field that we are able to find out about the different actors. Yet this act of collection, however abundant, is not sufficient to precisely reconstruct the story. Paleontologists have only recently revealed their synthetic reconstructions of the history of life on Earth to the eyes of the public. By compiling the successive discoveries of fossils into gigantic databanks; by collating all pieces of paleontological information – the species found, their form, size, date of appearance and disappearance during geological eras, or indeed their habitat, paleontologists have collectively constructed a veritable civil register of the species which roamed our Earth throughout the ages: a sort of immense inventory which can be used to study the phenomena of biodiversity over the course of the different geological times.

The primary result already demonstrated seems astoundingly simple: the biodiversity on our planet has not always been the same over the course of the geological times. Indeed, at times, it has been singularly different. Today, we know that life appeared on Earth around 3.5 billion years ago, and then endured in mainly microbial form for a very long period of around 3 billion years, a period called the Precambrian Era (see Figure 1.1 and also Tables A.1-A.5 for all the references to geological times). A more complex form of life emerged around 540 million years ago, at the junction between the Precambrian and the Phanerozoic Eon. At that time, intriguing organisms appeared. Some of them would die out, leaving no descendants. *Anomalocaris*, the largest predator in the oceans at the start of the Cambrian (at the very beginning of the Phanerozoic, 541 million years ago), which could grow up to a meter in length, had a particularly original morphology which has never been copied since: an elongated body with bilateral symmetry, with an articulated outer cuticle, a rounded mouth with triangular teeth and a pair of articulated, segmented front appendages reminiscent of the morphology of a prawn’s tail. This line of predators (feeding on hard- and soft-bodied organisms) would live for tens of millions of years, before finally dying out with no descendants.

At that same boundary between the Precambrian and the Phanerozoic, anatomical elements never before seen appeared. Amongst other things, organisms invented the mineralized skeleton. They biomineralized! That is, they became capable of generating biominerals (e.g. to create a shell) – quite an invention! Shells, bones, carapaces, and indeed teeth, are examples of biomineralization which are entirely common today, but at the time, the emergence of biomineralization was a true revolution which would cause a seismic shift in the relations between organisms. This crucial period of the Precambrian/Phanerozoic shift, very rich in evolutionary events, also led to the establishment of most of the major body plans. These plans define the major categories of organisms by very particular anatomical traits, and characterize biodiversity as we know it today. Mollusks, arthropods, lophophorates, annelids, chordates and echinoderms are a number of kinds of organisms which emerged during this period. We shall come back to this point later on, in Chapter 4.

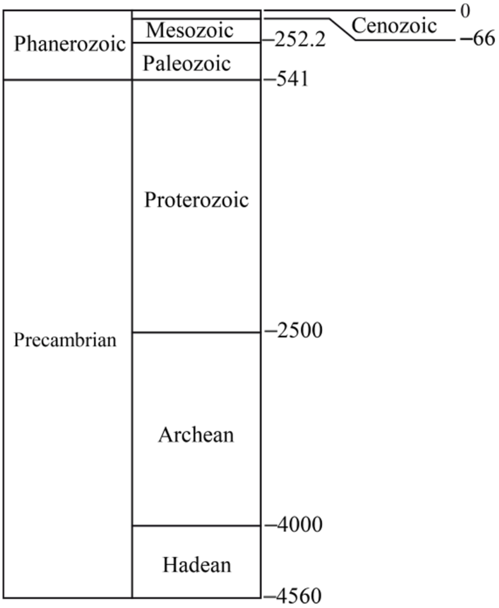


Figure 1.1. *Standard subdivision of the geological times. The ages are expressed in millions of years. Figure reproduced from [GRA 12]. Details on the Phanerozoic can be found in Tables A.1-A5*

1.2. A story filled with catastrophes and recoveries

By examining the inventory of past forms of life, we have discovered repeating patterns in the evolution of biodiversity. Sometimes, the number of species dwindles rapidly. For example, 252 million years ago (at the boundary between the Paleozoic and Mesozoic Eras), we see a sharp drop in biodiversity. Around 95% of species were exterminated. The Permian–Triassic mass extinction was the most catastrophic of the crises that have befallen the Earth during its history. In the Phanerozoic, we estimate that five such major mass extinction events took place, with species extinction rates estimated as between 76 and 95% [HAL 97], and over 20 second-order mass extinctions, which were slightly less intense than the primary events (Figure 1.2). In addition, we note a “background noise” of extinction events, of a few percent, which is constant throughout the geological record. The best known of the five mass extinctions took place 66 million years ago: the huge Cretaceous–Tertiary mass extinction event, on the boundary between the Mesozoic and Cenozoic Eras. It wiped out some of the major actors on the evolutionary stage. Amongst other organisms exterminated with no descendants, we lament the ammonites and the belemnites (cephalopods), the rudists (bivalve organisms with a highly developed shell), the marine reptiles, or indeed the flying reptiles. Contrary to the widely-held view, the dinosaurs that appeared during the course of the Triassic were not completely eliminated by this mass extinction. Certainly, a large number of them were exterminated, but others broke away and became differentiated long before this extinction, at the end of the Jurassic, from a group of carnivorous dinosaurs (the theropods). This differentiated branch formed the group of birds. This group survived through the mass extinction event at the end of the Cretaceous. Paleontologists have very largely demonstrated this historical link (a phylogenetic link) between these theropod dinosaurs and birds, by analysis of different shared anatomical features. Feathers, the shape of the furcula (the “wishbone”, formed by the fusion of the clavicles), or indeed the organization of the bones in the wrist, are features that demonstrate similarities between the two groups. Thus, observed through the lens of their ancestral links, birds are dinosaurs. We shall come back to this point at the end of Chapter 2.

In the collective imagination, mass extinctions occupy a central place. They are representative of the very catastrophes with which human history is so fraught. They terrify us. However, these mass extinctions, and the smaller-scale extinctions which go along with them, are not the only notable and recurring events in the history of biodiversity. The fossil inventory offers an even more surprising, and far less well known, image: that of evolutionary radiations. These events are characterized by intense diversifications of certain groups of organisms: an increase in the number of species and/or morphological diversification, sometimes coupled with the extinction or reduction of other groups of organisms. In terms of the history of life on our planet, evolutionary radiations are just as important, at least, as mass extinctions. They stand in testament to the organic world's ability to diversify rapidly; a sort of counter-point to extinction events. However, such radiations are less easy to account for. A mass extinction is an extremely sudden and rapid phenomenon which affects a large number of different groups of organisms. We can easily characterize each event by two numerical values: the geological age (e.g. 252 million years for the mass extinction at the Permian–Triassic boundary), and the extinction rate (95% of species for that same extinction) – two values to describe the event, and that is all! It is clear that the mechanisms leading to the extinction are varied and complex, but nonetheless, the situation can be summarized by these two values alone. On the other hand, two values are not enough to represent evolutionary radiations. Radiation events successively affect different groups of organisms, and are generally not concentrated at a precise moment in Earth's history. Although it may not seem obvious, past evolutionary radiations have been major contributing factors in the construction of biodiversity as we know it today.

Mammals, for example, are known to have been living since the Upper Triassic, around 220 million years ago. It is likely that the earliest mammals were small nocturnal insectivores. The evolutionary history of mammals over the past 220 million years demonstrates a paradox (see Figure 1.3). The extinction at the boundary between the Cretaceous and the Tertiary had a spectacular effect on this group. Spectacular, certainly, but not by a drop in biodiversity – quite the opposite, in fact! The effect on mammals was a phenomenal increase in their diversity from the beginning of the Cenozoic onward (from around 66 million years ago), just after the mass extinction. It was an evolutionary radiation which raised our numbers from only a handful of families to over a hundred. Let us be clear on what we mean here. A "family" is a level of the biological nomenclature which generally includes numerous species that are close relatives (see Chapter 2 and Table 2.1). In mammals, Felidae (cats), Equidae (horses), Elephantidae (elephants), Hominidae (humans) or Ursidae (bears) are examples of this. All these families include both currently present and past organisms. Others are known exclusively because of fossil organisms. Here, the number of families therefore represents the number of different main groups within mammals. Thus, by analyzing the inventory of fossil species, we can visualize a major evolutionary radiation (see Figure 1.3 for an illustration). However, the players involved in the initial radiation (the species or groups of species) just after the mass extinction event are not necessarily close relatives of the groups of mammals living today. Quite on the contrary, numerous groups involved in the initial radiation would later disappear, being replaced by new groups of mammals. The causes of diversification of mammals are difficult to accurately determine, for one simple reason: paleontologists use data which ultimately reveal what we call an "evolutionary pattern".

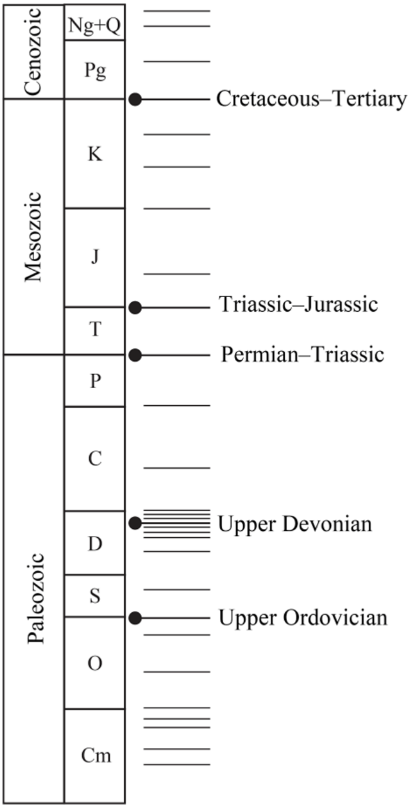


Figure 1.2. *Main mass extinctions that took place during the Phanerozoic. Each horizontal line represents a mass extinction event. Only the five greatest extinctions are labeled*

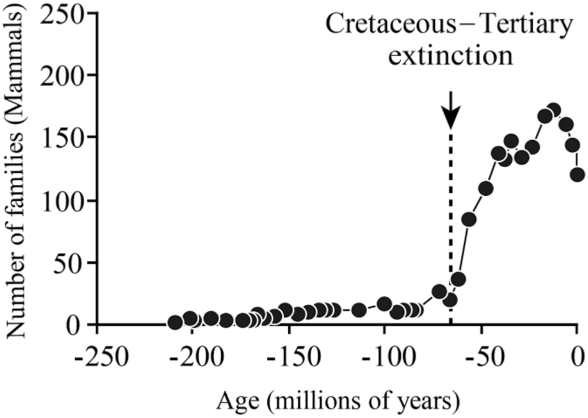


Figure 1.3. *Trend in the number of families of mammals over the geological times. The vertical dashed line marks the mass extinction event at the Cretaceous–Tertiary boundary. Note the spectacular increase in the number of families over the course of the Cenozoic (number of families according to [BEN 93], geological ages according to [GRA 12]). In this case, the mass extinction gave rise to an evolutionary radiation: a spectacular diversification of mammals*

Understanding the mechanisms (i.e. the causes) responsible for the evolutionary pattern is undeniably a scientific activity that is sometimes tricky, not to mention often speculative: indeed, it is not possible to construct an experiment to test the effect of a cause on organisms that no longer exist today and that have not been around for millions or even tens of millions of years! Nonetheless, we can allow ourselves a certain amount of speculation. Thus, in this book, I shall allow myself to speculate to a certain degree, although I shall attempt to merely relay the most fully confirmed hypotheses. In the case of mammals, upon which we are focusing here, it seems that two causes can be combined to account for the radiation of the group (see [ARC 11] for further details). To begin with, the extinction of the dinosaurs (nearly all of them – a point to which we shall come back in detail in Chapter 3) left vast swathes of ecological domains on Earth unoccupied: domains which were soon colonized by mammals. On the other hand, the rather warm climatic conditions a few million years after the start of the radiation would have been favorable for mammals. In reference to this warm climate, geologists call the corresponding geological interval the climatic optimum of the Eocene epoch (see Table A.1). This climatic event has been particularly widely studied because it constitutes a remarkable parallel to the current context of global warming.

Beyond looking for the possible causes of radiation, it must not be forgotten that the demonstration of the radiation event is also a complex exercise in its own right. In the next chapter, we shall examine the scientific methods used to achieve these results, in detail.

1.3. Evolutionary radiations: major phenomena in the history of biodiversity

Evolutionary radiations warrant detailed study for at least two reasons. One relates to the history of biodiversity (we have just illustrated this point using the example of mammals). Evolutionary radiations have been at least as important as extinction events in shaping the different periods of life throughout the history of the Earth. This is the crucial point in this book. The biodiversity that we observe around us today is the present step – a transitory step – in these successions of extinctions and radiations. The other reason touches on a more theoretical area. The study of evolutionary radiations helps us to construct a clearer picture of the modes of biological evolution, and particularly its rhythms. Studying them enriches our knowledge of the way in which biological evolution works.

These events of rapid expansion of biodiversity, these evolutionary radiations, are the heart of this book. As readers must understand, an evolutionary radiation is not a geological object (such as a mountain), nor is it a paleontological object (such as a dinosaur skeleton) or an ecological object (such as the tropical rainforest). In fact, it is, at first glance, an abstract phenomenon – abstract because it is perceived not by the observation of an object, but by the observation of data that have been accumulated, dissected, compiled, digested and analyzed. Abstract it may be, but it is of prime importance: it fashions biodiversity. We shall focus on this phenomenon as paleontologists observe it in the fossil record. We shall study its modes and define its consequences. However, before going to the heart of the subject, with a view to properly equipping the reader for this foray into the world of fossils which are sometimes hundreds of millions of years old and examining the radiations and their effects, it is first necessary to touch on a number of questions (Chapter 2):

– what are the data which enable us to observe the events of the story of biodiversity?

– do these data reveal pertinent information?

We can then delimit this phenomenon of evolutionary radiation and place it back into a more general context (Chapter 3):

– how can we detect evolutionary radiations in the fossil record?

– are there several different types of evolutionary radiations?

In order to lend this book a more demonstrative quality, and to support my argument, I will then go on to dissect (in the same way as does a paleontologist when describing a new fossil) a few concrete examples of evolutionary radiations (in Chapter 4). Flowering plants, ammonites, sea urchins and indeed the animals of the ancient oceans of the Cambrian will all be used as illustrative and demonstrative examples of this major phenomenon (though one which is largely unknown to scientific amateurs).

Finally, the epilog to this story enables us to look once again at the phenomenon in the broader context of biodiversity and its dynamics (see Chapter 5). Without wishing to completely reveal the end of the book, attentive readers will already have realized that evolutionary radiations have emerged as natural events which are synonymous with optimism for biodiversity.

2

The Fossil Record

2.1. A treasure trove of fossils

Amellago, Morocco, January 2001. After 3 days trekking through the mountains of the Moroccan high atlas, a French/Moroccan team of paleontologists and geologists, of which I was a member, reached a rich outcrop of fossils. Amongst the fossils we found seven specimens of ammonites. These marine cephalopod mollusks are easily identifiable by their spiral, chambered shell. They date from the lower Jurassic – a period of Earth's history ranging between 201 and 145 million years ago (see Table A.2). The ammonite shells collected are recognizable by the morphological features. In the present case, some of them were particularly striking: the lack of a keel, the presence of significant constrictions and thin ribs, a very round-shaped cross-section, or a particularly sinuous suture line (the line at the meeting point of the shell and the internal walls). Although the individuals were not all absolutely identical (exhibiting a few minor morphological variations), I considered them all to belong to the same fossil species: a species of the genus *Alocolytoceras* (the genus is the level in the biological nomenclature just below the species; thus a genus covers several species – see section 2.4.1.2), known at the end of the lower Jurassic and the start of the mid Jurassic. In scientific language, this species is known as *Alocolytoceras coarctatum* (Figure 2.1).

The discovery of new fossils is not always an exceptional thing. On each field mission, we find a multitude of new specimens that enrich our knowledge of the fossil flora and fauna of the region under study. In the case in point, however, the discoveries were sufficiently interesting for us to publish the main results [BOU 08]. Whether or not results from the field are published, they almost always represent crucial discoveries to add to the inventory of fossil species. The sort of "civil registry" of species enables us to view, and therefore accurately explore, the variations in biodiversity through the history of the Earth (see Chapter 1). The seven specimens from the species *Alocolytoceras coarctatum* found in Amellago thus supplemented the information that was already known about that species. Other paleontologists have found it and described in geological layers from the same age in Italy, France and Portugal. Ultimately, this species is now known to have lived precisely at the end of the lower Jurassic period – more specifically during the Toarcian Stage (see Table A.2). This stage itself is subdivided into eight successive slices of time (which we call chronozones), representing a total of 8.5 million years. The FAD of this species (*First Appearance Datum*, i.e. the oldest recorded instance of a species' presence) is precisely the fifth chronozone of the Toarcian; its LAD (*Last Appearance Datum*) is the seventh. These two parameters (FAD and LAD) can thus be used to precisely define the geological interval in which a fossil species lived.

Figure 2.1. *Ammonite shell uncovered in the region of Amellago (Central High-Atlas, Morocco), belonging to the species* Alocolytoceras coarctatum *(UBGD 276073). P. Neige's collection (photos by P. Neige)*

Go further with this approach and compile different sources of data for all fossil groups – the specimens already discovered and described in the existing body of literature, unknown ones from your own discoveries in the field, or indeed fossils which the world has forgotten, buried at the bottom of collection drawers at museums and universities the world over – and you will obtain an enormous inventory contained in a database, which can be used to explore biodiversity through the geological ages. You are quite right: we have not yet unearthed all of the fossils all over the world. Consequently, the FAD and LAD of the species already discovered may well change as new specimens are discovered. Worse still, certain individuals that have lived through the geological ages were not fossilized – all paleontologists know this:

– the fossils contained in sedimentary rocks represent only a fraction of those creatures which have actually lived on Earth: those which have not been fossilized are lost forever;

– paleontologists study an extract (a sample) of what is contained in sedimentary rocks: that extract is known about thanks to the type of field work described at the start of this chapter. Evidently, a great many fossils still remain to be found in sedimentary rocks.

As is noted by Benton and Harper [BEN 09], the same term is sometimes used to denote these two different samples of past biodiversity (the part preserved in the rocks, on the one hand, and the known portion of that preserved sample, on the other). That term is given as the title of this chapter: the “fossil record”. In the eyes of some, the fossil record is not only what we already know of a fossil group, but also everything that remains to be discovered in sedimentary rocks all over the world. For others, meanwhile, the fossil record is only that which we already know about a fossil group (i.e. the fossils already extracted from the sedimentary rocks). For the purposes of this book, we shall employ the first definition: the fossil record of a group is all of the fossils of that group which exist, whether they are in collections or are still in the sedimentary rocks.

Thus, by its very nature, that fossil record is incomplete: the organisms which have lived on Earth are not all fossilized in rocks.

Furthermore, what we study (in this book, for example) is a sample only of that fossil record: the sum of the information gleaned from the scientific literature and from the specimens kept in the collections. This sample takes the form of a paleontological database which we can actually study (see section 2.4). Hence, the crucial question is not whether or not the paleontological database is incomplete [JAB 09] – it is, beyond a doubt! The question is whether it is possible to extract from it any relevant information regarding the history of biodiversity, and particularly the evolutionary radiation events, in spite of this incompleteness. This chapter discusses how and why the major fossil inventories constitute an invaluable, pertinent tool in reconstructing the story of biodiversity in general, and analyzing evolutionary radiations in particular.

2.2. From organisms to fossils, and from biocenoses to taphocenoses

The systematic description of fossils found in the field by generations of paleontologists all over the world has given rise to a wealth of knowledge about the story of life on planet Earth. Nonetheless, not all organisms have been fossilized to the same extent. Therefore, we do not have the same degree of precise knowledge about all zoological and botanical groups. Those which have mineralized parts (e.g. a shell, a test, bones, teeth, etc.) will become fossilized more easily. On the other hand, it is evident that the fossil record of jellyfish – animals whose bodies are composed essentially of water – is particularly scant! However, unlike what we may be led to expect, it is not entirely non-existent either: certain jellyfish have been found in a fossilized state. Even within species that do have mineralized parts, certain groups are much more fully documented than others. Such is the case, for example, with the ammonites which were very prevalent in the ancient seas during the second half of the Paleozoic and the whole of the Mesozoic. The shells of these ammonites are easily and frequently fossilized. Paleontologists soon identified them as very good time-telling fossils (i.e. good biostratigraphic fossils): species evolved quickly and are widely distributed in geographical terms. Thus, they offer an effective temporal division of the geological ages during which they lived. Hence, our knowledge of them has been being constantly improved by paleontologists anxious to find temporal markers. All these discoveries provide a fairly detailed and very well documented view of the history of the ammonites. Therefore, it is unsurprising that, today, these organisms offer an excellent group for study in the field of evolutionary sciences – particularly for analyzing the pace of evolution.

The science of studying the mechanisms of fossilization is known as taphonomy. The term was coined by the Russian paleontologist Ivan Efremov (1908–1972) in 1940 [EFR 40]:

> "I propose for this part of paleontology the name of 'taphonomy,' the science of the laws of embedding".

The discipline owes its name to the Greek roots "*taphos*" (meaning tomb, crypt or burial), and "*nomos*" (meaning law). This branch of paleontology examines the mechanisms that affect an organism between the moment of its death and the moment of its discovery as a fossil in the field by a paleontologist. In reference to the term "taphonomy", we call these "taphonomic mechanisms". For a long time, little was known about these mechanisms. The fossils were there, in the field, and their taphonomic history mattered little. Today, many paleontologists are interested in this discipline, and we are gaining an increasingly full understanding of how organisms become fossilized. In the case of the ammonite *Alocolytoceras coarctatum* mentioned above, the taphonomic mechanisms did not preserve the soft parts of the cephalopod (e.g. the tentacles, the eyes, the gills, the digestive tract or the nervous system). Only the shell is preserved, but its origin mineralogy has changed. Initially made of aragonite (a mineral belonging to the calcium carbonate family), it is now calcite (another mineral from the same family). This mineralogical transformation is simply due to the natural instability of aragonite, which gradually and naturally transforms into calcite over the years.

The taphonomic processes also affect the preservation of the biocenosis (all of the living beings that coexist in a defined space). They transform it into taphocenosis (the set of organisms that are fossilized together). This taphocenosis is rarely a perfect image of its biocenosis. Certain organisms that were originally present may be missing (not fossilized, displaced and fossilized elsewhere, fossilized but later destroyed, or indeed fossilized but never unearthed); others may be added (by mixing between successive sedimentary layers, or indeed by mixing between organisms that originally lived in different places). In other words, when a paleontologist analyzes a paleontological find, most of the time, s/he perceives only part of the reality when the organisms lived. However, there have been exceptional paleontological sites found where the organisms that lived together in a biocenosis have all been preserved together in the taphocenosis. These sites, obviously, offer a more accurate view of the original biocenosis. Some such sites are characterized by the exceptional quality of the fossilization of the organisms, with all of the anatomical details being preserved (see Figure 2.2), sometimes even including the soft parts of the organisms in mineralized form. These sites are known as *Lagerstätten* – a term borrowed from German, meaning "deposit". They have yielded innumerable fossils that have become symbolic of paleontology, such as the *Archaeopteryx* (see section 2.4.1.2).

2.3. Can the fossil record reveal relevant information?

In this section, we shall answer this question firstly with a historical approach, from Darwin up to recent works of research, and then we shall look at some examples of techniques that can be used to compensate for the incomplete nature of the fossil record.

2.3.1. *A question highlighted by Darwin*

Chapter IX of Charles Darwin (1809–1882)'s opus "*On the Origin of Species*" (1859) is entitled "On the Imperfection of the Geological Record" [DAR 59]. It closes with a clear and unapologetic statement from its celebrated author:

> "For my part, following out Lyell's metaphor, I look at the natural geological record, as a history of the world imperfectly kept, and written in a changing dialect; of this history we possess the last volume alone, relating only to two or three countries. Of this volume, only here and there a short chapter has been preserved; and of each page, only here and there a few lines. Each word of the slowly-changing language, in which the history is supposed to be written, being more or less different in the interrupted succession of chapters, may represent the apparently abruptly changed forms of life, entombed in our consecutive, but widely separated, formations".

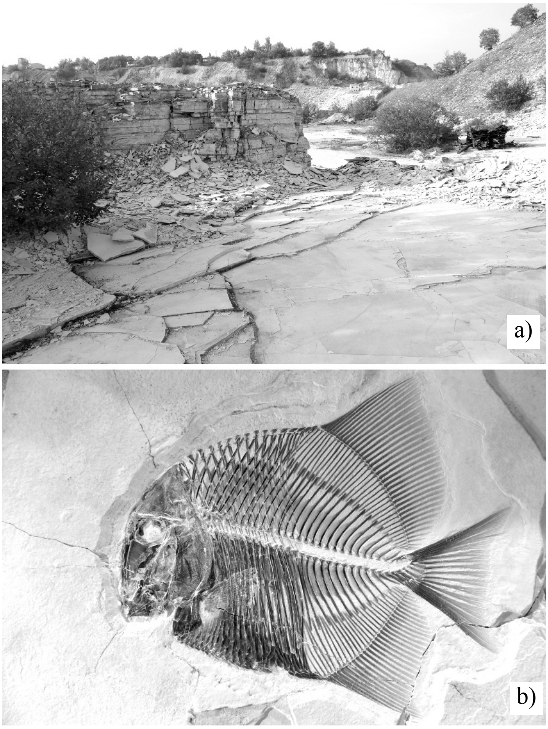


Figure 2.2. *a) Photo of the quarry in Solnhofen (Germany) – one of the best-known Lagerstätten, dating from the upper Jurassic. b) Example of a remarkable fossil collected from these exceptional paleontological deposits: a teleostean fish from the upper Jurassic (size: around 180 mm). Note the fineness of the fossilized structures. Specimen held at the Jura-Museum Eichstätt (Germany) (photos by P. Neige)*

Thus, in Darwin's view, the geological archives, which contain the paleontological data and constitute the fossil record, represent merely a small fragment (and in incomplete one, at that), of what has truly happened on our planet. In his opinion, we cannot depend upon that record to illustrate or demonstrate the rhythms or ways of biological evolution. "Lyell's metaphor" cited by Darwin (Charles Lyell, 1797–1875, was a renowned British geologist) is simple enough to understand. Take this book about evolutionary radiations, randomly tear out half of the chapters, and then from those that remain, half of the pages. Do the same for the lines in those pages that have not been eliminated: blot out half of them, and then do the same for the words in the lines which are still present. Finally, attempt to read whatever remains to you. In all likelihood, you will understand absolutely nothing.

Darwin's "relationship" with paleontological data has been commented upon on many occasions [GOU 02, SEP 12]. Today, it seems clear that Darwin's entrenched opinion about the imperfection of the geological (and therefore also paleontological) record was heavily influenced by his need to defend other parts of his own theory: by criticizing paleontological data, he protects his model of gradualism, which stipulates that evolution occurs by way of slow and gradual changes, for which there is very little evidence from paleontological data. In other words, by downplaying the completeness of paleontological data *a priori*, he is able to defend, *a posteriori*, against trenchant criticism of his gradualist model. On a more general level, Darwin's position of specifically criticizing paleontological data, which he deems *a priori* to be overly biased, seems untenable. Let us examine it by analogy with the data on the biodiversity existing today. Scientists have identified around 1.5 million species which currently populate our planet. By methods of extrapolation [MOR 11], we estimate that there must be around 11 million in existence in total. Hence, there are no less than 9.5 million remaining to be described (86%). Put differently, our view of the current biodiversity – i.e. the biodiversity around today – looks rather moth-eaten! In Darwin's time, the situation was even worse. Does that mean that we should not use the data available to us in attempting to understand the rules of organization of biodiversity along the lines of altitude or latitude? Certainly not. However, these data are just as skewed as are paleontological data. Nonetheless, we can make use of them, because in certain cases, sufficient data are available to us to carry out very detailed scientific studies (e.g. regarding the distribution of bird species around Great Britain). The same is true of paleontological data.

With that said, it must be recognized that although Darwin adopts a rather extreme position in relation to the insufficiency of geological archives, in doing so he raises a crucial point regarding the very nature of paleontological data.

2.3.2. *One year later: John Phillips*

The paleontologist John Phillips (1800–1874) was a pioneer in fossil-record analysis. In 1860 [PHI 60] (one year after Darwin's treatise was published), he published a book entitled "*Life on the Earth: its Origin and Succession*", which includes a graph showing the diversity of marine life through the geological ages. Note, however, that the Germany geologist Heinrich Georg Bronn (1800–1862), in the first half of the 19th Century, had already published a compilation of paleontological data that was far more complete than Phillips', but did not include a diversity curve [BRO 41, BRO 51]. To construct his diagram, Phillips counted the fossil species discovered in Great Britain, published in 1854 in the "Catalogue of British Fossils, 2nd Edition" by John Morris (1810–1886) [MOR 54]. The time division that he used for the count was not very accurate. He counted the species belonging to three major periods: the Paleozoic, the Mesozoic and the Cenozoic (and gave the values in tables in his book). He then corrected these values, relative to the thicknesses of the geological strata for those three eras, as known in Britain. By more closely examining the variations in those three geological eras, he deduced the relative variation in diversity of life over the course of the geological ages (see Figure 2.3). This curve shows a life less rich in species for the Paleozoic, a significant drop in the number of species between the Mesozoic and Cenozoic and, to a lesser extent, between the Paleozoic and Mesozoic, and two very significant periods of increase of the number of species: at the start of the Mesozoic and of the Cenozoic.

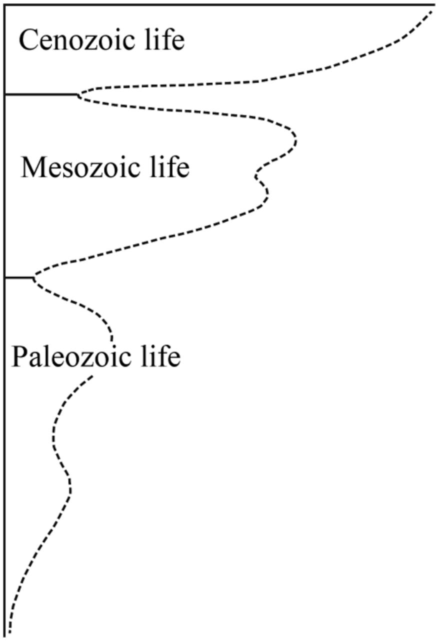


Figure 2.3. *Variation in diversity of life over the course of the geological ages (modified from [PHI 60]). The axes (not graduated in the original book) represent the geological age (vertical axis) and the number of species relative to the thickness of the geological strata (horizontal axis)*

It is particularly noteworthy that Phillips himself made the effort to check his results using another data source. In order to do so, he used the same method (number of species corrected in relation to the thicknesses of the strata) to recalculate the relative diversity of live over the geological ages, but this time using data gained by the French paleontologist Alcide d'Orbigny (1802–1857) and found values comparable to those he had already obtained.

Today, we know that this curve is an approximation which is sometimes relevant (the breaks between the major geological eras have, since, been largely confirmed) and sometimes erroneous (the slight diversity during the Paleozoic is largely called into question), for the story of biodiversity on our planet. In spite of the few faults in his analysis, Phillips demonstrated a significant degree of modernity in his scientific approach, both by the compilation of data and also by checking against another source of data. It was only towards the end of the 20th Century that this approach would be developed fully.

2.3.3. *A few examples of bias in the fossil record*

As previously explained, it is evident that the paleontological data are incomplete and that they may be tainted with bias:

– they are incomplete: even if we were able to extract all of the fossils for a given group from all the sedimentary rocks in all the world (i.e. if we were able to have a complete fossil record for that group), even then, it would not represent the exact history of a given group of organisms because the fossil record itself is incomplete (certain individuals have not been fossilized);

– they may be subject to bias: the sample of the fossil record that we know may, for example, be directly linked to the sampling effort made by paleontologists. Western Europe is the birthplace of paleontology. The number of fossil species known there is considerable, partly because of the tradition of studying fossils, which has thus given rise to numerous collecting expeditions and publications over the past 200+ years. On the other hand, though, certain geographical areas have been very little explored up until now, and the record of specimens there will, consequently, be less rich, partly because of this lack of effort in sampling. This type of sampling bias also exists with regard to the estimations of the number of species in a present-day biocenosis: the marine biodiversity of today, for example, is far better known in the vicinity of oceanographic stations than right in the middle of the oceans.

On the other hand, there are numerous cases where the uncertainties are almost eliminated. For example, as we have seen, ammonites have an excellent fossil record. One reason for this is that their shells are easily fossilized. However, another (equally important) reason is that paleontologists have studied them widely because they are useful in biostratigraphy. The sample of the fossil record is very good, because we have a very large number of publications describing ammonites, and even more ample resources in collections all over the world. Hence, the sampling bias is probably fairly minimal.

In order to adequately illustrate this effect of bias in the fossil record, below we discuss three additional examples: the first relates to the overall history of biodiversity during the Phanerozoic; the second to the belemnites (fossilized cephalopods with an internal shell); and finally, the third to the dinosaurs.

One of the major issues that paleontologists tend to have to deal with is particularly closely linked to the bias caused by the way in which the fossil record is sampled. What has the evolution of the number of species been over the course of the geological ages? Some elements of a response were provided by a study on marine invertebrates published in 1972 by the American paleontologist David M. Raup [RAU 72]. In his view, the fluctuations in the number of species found by simple tabulation of the data gleaned from the fossil record partly reflect the surface area and volume of sediment available in each deposit. Hence, Raup qualified the graph of the evolution of species during the Phanerozoic as the "*change in apparent species diversity*", explicitly noting the "apparent" nature of the data, and therefore the fact that they should not be read as a direct reflection of the fluctuations in past biodiversity [RAU 72; RAU 76]. The subtitle of his article in 1972 [RAU 72], published in the journal *Science*, is explicit in this regard:

> "The increase in the number of marine species since the Paleozoic may be more apparent than real".

One of the conclusions of Raup's study and those which came in its wake is that the image that we have from the fossil record of the evolution of the number of species on this enormous scale of temporal investigation (the Phanerozoic: over 540 million years) is essentially guided by the geological history of planet Earth. This does not mean that the evolution of the number of species over the geological ages can never be traced. However, we learn here that the sample of the fossil record that we have cannot be used, in its current form, to trace that history: it needs to be corrected first. This also means that if we pose the question on another timescale – e.g. an analysis over a few million years – in a more homogeneous geological context (with slight variations in the surface areas of outcrops available for the geological ages under study), it will probably not be necessary to take account of this problem. In such a case, the existing fossil record of species can be a helpful tool in tracing the true evolution of the number of species during the period in question. It is up to us – the paleontologists – to produce a representative sample of that fossil record in our research.

Let us examine another example. Of the numerous fossil organisms studied by paleontologists, belemnites occupy a paradoxical place. The remains of these fossil cephalopod mollusks are particularly common in sedimentary rocks from the Jurassic and the Cretaceous, for one simple reason: belemnites have an extremely solid mineralized structure, made of calcite, called the rostrum, and is therefore easily fossilized (hence, we consider that belemnites have an excellent fossil record). The rostrum is a structure internal to the animal, more or less conical in form, usually pointed at the back end and hollow at the front (to accommodate a chambered structure called the phragmocone, which acted as a ballast). The function of that shell (the rostrum and the phragmocone) was probably to help balance the animal, by providing weight at the back end where it is lodged, so the belemnite lived in a horizontal position, much like a squid today (belemnites and squid have close phylogenetic links). These belemnites also have other mineralized structures, which are far more fragile and therefore fairly uncommon in sedimentary rocks. It is astonishingly easy to find belemnite rostra in marine sedimentary rocks from the Jurassic and the Cretaceous, although it is a much more painstaking task to precisely collect them, prepare them in the laboratory and catalog them. The remarkable Museum in Semur-en-Auxois in France holds a multitude of such rostra exhibited in glass cases, carefully aligned alongside one another, stuck to small cardboard sample holders (see Figure 2.4). Elsewhere, in other museums and at certain universities, the same is true. The belemnites are there, precisely aligned!

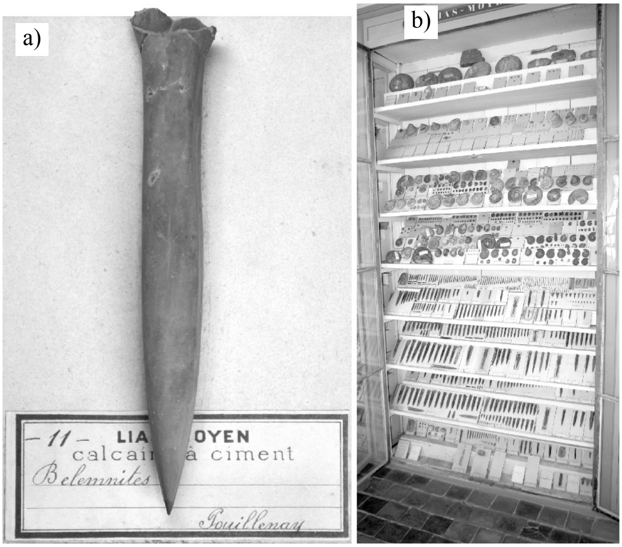


Figure 2.4. *Belemnite rostra from the Jurassic on exhibition at the Semur-en-Auxois Museum (France); a) close-up of a specimen presented on a cardboard mount; b) view of a glass exhibition case – fossil ammonites and nautilus at the top, and belemnites at the bottom (photos by P. Neige)*

Thus, one might reasonably expect belemnites to be very well known and widely studied by paleontologists. This is absolutely not the case! There are precious few scientists who focus on these organisms. Amongst the handful of belemnite specialists, Robert Weis from the National Museum of Natural History in Luxembourg is an expert particularly in Jurassic species. In a study in which I am currently engaged, in collaboration with Weis, we are seeking to discover the mechanisms of evolution of this group which, according to our initial estimations, could be characterized by an evolutionary radiation at the start of the Jurassic. To begin with, we constructed a database of belemnites (on the basis of their fossil record) for a period of thirty million years at the start of the Jurassic. This base contains the most accurate data published in the specialist literature, unpublished data from our own work in the field, and data unearthed in the collections of various museums. The study relates solely to the species in an extensive marine paleogeographic domain called the Western Tethys Ocean, which today corresponds to outcrops of sedimentary rocks stretching across the whole of Western Europe, Eastern Europe and the Maghreb. By compiling the different geological maps of this immense geographical region, we gain access to the distribution of the outcrops which could potentially contain belemnites from the age under study. We need only pinpoint the outcrops of marine sedimentary rocks from the Jurassic (see the shaded areas in Figure 2.5). A simple glance at the geographical distribution of the data included in our inventory, in comparison to that of the outcrops which could potentially contain these organisms, shows that our sample of the fossil record of belemnites from the early Jurassic is correct for certain geographical zones, but particularly poor for others (the black dots in Figure 2.5). Whilst the northern part of Europe is relatively well known, we know much less about the southern and eastern parts, and the Maghreb. In these areas, therefore, the data are incomplete. This type of sampling bias invites two conclusions: (1) a study on Northern Europe would be worthwhile (we can study the means of evolution of the group in that geographical region), and (2) it is necessary to go back into the field to acquire data in Southern and Eastern Europe and in the Maghreb before we can understand the evolution of the group in that area.

Figure 2.5. *Comparison of the distribution of outcrops (shaded areas) and known data on the belemnites (black dots) from the lower Jurassic (map background and Jurassic outcrops modified from [DOM 09])*

The instances of bias in the fossil record are sometimes even embedded in the details. Everyone knows about dinosaurs! These extraordinary animals fascinate children and adults alike. We know that the majority of these animals died in the mass extinction event marking the boundary between the Cretaceous and Tertiary (see Chapter 1). However, what exactly do we know from their fossil record as that extinction approached? This was the question asked by a team of American paleontologists [FAS 04]. By compiling the data known about the dinosaurs at genus level, the authors of this study reached two conclusions. Firstly, the data show that dinosaurs diversified anew in the upper Cretaceous, just before their almost-complete extinction. Secondly, the exact means of their near-extinction are difficult to observe on the basis of the fossil record available to us. Indeed, by restricting the database to a very limited and precise timescale, the authors are forced to exclude the majority of the data on dinosaurs discovered in Asia. The reason for this is very simple: the geological age of the dinosaurs found in Asia is particularly unclear. In other words, we know with certainty that dinosaurs lived in Asia during the upper Cretaceous in Asia, but we do not know precisely *when* during the upper Cretaceous they lived (the period spans around 34 million years). This being the case, our sample of the fossil record is apt for a study at the scale of the whole of the Mesozoic Era, but inapt for a specific study at the scale of the upper Cretaceous alone. At this finer scale, the portion of the fossil record which we know today mainly reveals the history of the dinosaurs in North America (where the dinosaur specimens discovered have been more accurately dated) rather than the history of the dinosaurs all over the world. Hence, the authors of this study recommend not only going back into the field (as was the case with the example of the belemnites given earlier), but to find solutions to specify the exact geological ages of the Asian dinosaurs from the upper Cretaceous already recorded in their database.

2.3.4. *Tools for controlling the fossil record and its sampling*

The question which arises for paleontologists, therefore, is how to deal with the incomplete nature of the fossil record and the potential bias that could affect its sampling, either prior to the analysis (by using effective sampling methods), or afterwards (by using methods to assess and possibly correct any bias). In the specialist literature in paleontology, there are dozens of studies which analyze, classify or correct the biases that can affect the fossil record. Here, we shall take a look at some simple and illustrative examples.

Imagine we want to determine the number of fossil species present in a given deposit. It is easy to understand that the more specimens we observe, the greater will be the probability of finding species, and therefore the higher the number of species in the deposit is likely to be judged. If we observe 10 specimens, we will obtain at most 10 species (and even that is unlikely, because usually, there are certain species that dominate collections in terms of the number of individuals: the number of species is always lower than the number of specimens observed). If we observe 200 specimens, we might find 20 species. How about if we observe 2,000? How about 20,000? How, then, can we estimate the number of species in the taphocenosis without that number being directly determined by the effort invested in sampling? This is the question that I have, for several years, been asking my students on the MA program in Paleontology and Geology at the University of Burgundy (France). They need to determine the number of species of microfossils in a paleontological deposit from the Lutetian in the Paris Basin (the Lutetian is a stage defined in reference to the city of Lutetia – the ancient name for the city of Paris – which falls during the Cenozoic in temporal terms – see Table A.1). For reasons of standardization, the example here is given for organisms whose size is between 250 and 500 μm. This bracket includes many species of foraminifera (unicellular organisms with a mineral skeleton), ostracoda (small crustaceans) and algae. In this exercise, we have no problem with access to observations: the microfossils are particularly abundant, very well preserved, accumulated in loose rock, and can therefore be isolated from one another easily. With a stereo-microscope, we can observe them, sort them, arrange them by species or genus, and therefore count them to our hearts' content.

There are various approaches that can be used to determine the number of species in that deposit. In our case, we use a simple method derived from the practices of naturalists who wish to know the number of species in a biocenosis today – e.g. the number of species of birds living in a forest. All we need to do is to compile a graph (see Figure 2.6) showing the relationship between the number of successive observations and the cumulative number of species obtained during the count. The resulting curve is called the species accumulation curve, or sampling effort curve. In theory, its overall form should be logarithmic: it initially shows a region of increase (the more observations we make, the more species we find), followed by a plateau (we can stop counting because the plateau indicates that we are close to attaining the number of species in the taphocenosis or the biocenosis under examination). The results obtained by the MA students at the University of Burgundy conform to that theory. It is necessary to observe a large number of specimens before we reach the second phase of the curve (Figure 2.6 left). With over 200 specimens counted, the student who has made most observations has still not reached the plateau phase. In other words, there are still numerous species to be discovered. The difference between the curves constructed by different students (Figure 2.6 right) demonstrates the random nature of the sampling: not all the students will observe the specimens (and therefore the species) in the same order. This difference is also attributable to whether or not the students manage to discover the rarer species: they will not be sampled by all of the students. Put differently, through random chance, certain students will be able to discover the species making up the taphocenosis more quickly than others, and not all the students will end up with the same inventory of species. Beyond a large number of observations (each student would need far more than 200), all the curves would tend to converge toward a value which offers an estimation of the number of species contained in that taphocenosis (marked as “S” in Figure 2.6, left).

This simple technique (and there are other, more complex methods) can thus be used to determine the requisite sampling effort (here the number of fossils to be observed) to obtain a good indicator of the number of species contained in a taphocenosis. In addition, we now have statistical tools that can extrapolate from these curves and calculate what the number of species would be, in theory, if we were to pursue the counting process to completion [GOT 11].

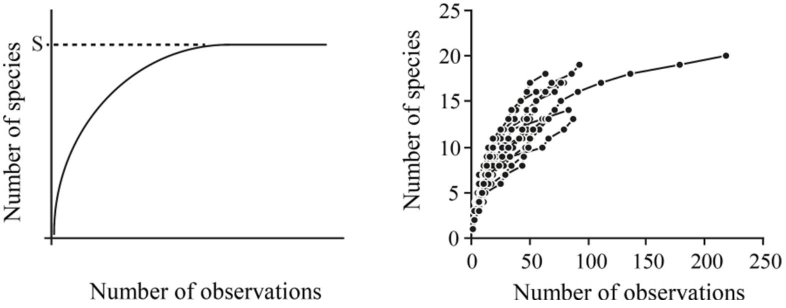


Figure 2.6. *How to determine the number of species present in a paleontological deposit. Left: theoretical curve for the relation between the number of fossils collected and the le number of species obtained during the collection. Right: actual case for a deposit from the Lutetian in the Paris Basin. Each curve represents the result obtained by a student on the Geobiosphere MA at the University of Burgundy (2012–2013)*

This reasoning can also be applied in other contexts – e.g. to compare the number of species between two paleogeographical provinces. When we examine a biodiversity phenomenon (such as a radiation event) using a large quantity of data harvested from the scientific literature, we can, *a posteriori*, test the degree to which our sampling in each of the two provinces is representative, and whether or not the two are comparable. In order to correct such bias (or at least visualize it), paleontologists use methods known as re-sampling. In the example of the comparison of the paleogeographical provinces, similarly to the reasoning employed earlier with regard to the microfossil deposit, we can bet that the province with more deposits (and/or that which is more fully studied by paleontologists) will have more species. Does this higher number of species reflect a true dominance in that province in terms of number of species, or is it simply the effect of a sampling bias (fewer deposits studied in the second province may mean fewer species discovered)? In light of this problem, re-sampling methods may be used to calculate the likely number of species in the two geographical provinces if we had access to the same number of deposits in both of them. We can cite a concrete example of this type of study, conducted in 2009, by the study of ammonites from the lower Jurassic in the Western Tethys Ocean by Jean-Louis Dommergues and his collaborators [DOM 09]. In the lower Jurassic, the Western Tethys is typically divided into two paleogeographical provinces (one in the north and one in the south), accommodating sometimes different species.

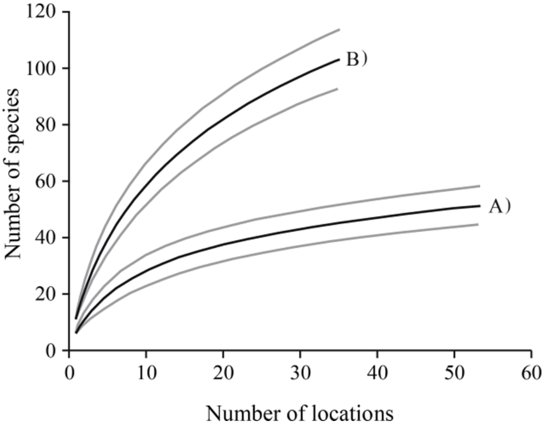


Figure 2.7. *Analysis of the fossil record of ammonites from the lower Jurassic (example covering the Jamesoni chronozone, the start of the Pliensbachian stage). Curve A represents the ammonites found in the northern part of the Western Tethys, and curve B the same statistic for the southern part. The gray curves illustrate the 95% confidence interval for curves A and B (modified from [DOM 09])*

The results of the study on ammonites (illustrated in Figure 2.7) are surprising. The province about which most is known (the northern one) exhibits a curve which is not yet saturated (it has not yet reached the plateau phase, shown in Figure 2.6), but we can imagine that with a few extra deposits to examine, it will be (Figure 2.7, curve A). Hence, we can estimate that between 50 and 60 species of ammonites existed in that province during the time-period studied (the start of the Pliensbachian stage – see Table A.2). The lesser-known province (in the south) exhibits a paradoxical result. The species accumulation curve is far from saturated (it is continuing to rise – Figure 2.7, curve B), which is unsurprising because relatively few deposits there have been examined. We need to explorer many more sites for the species accumulation curve to level off. However, this lower number of deposits has already revealed a higher number of species than in the northern province (curve B is always above curve A in Figure 2.7). This is where the paradox arises! In spite of our lesser knowledge of the southern province (because we have studied fewer sites), we can state without ambiguity that it is much more diversified than is the northern province. We can make this affirmation because for an equivalent number of deposits (say, 30) the southern province is far more diversified (it contains around 100 species) than the northern one (which contains only 40 species).

Used one after another, all these methods for studying the fossil record, or our sample of it, ultimately enable us to properly calibrate our paleontological analyses. The main lesson to be drawn from this is simple. A paleontological database contains information that may be relevant and informative in certain conditions of temporal and/or geographical analysis. As we have seen, there can be no question of studying the biodiversity of the belemnites from the lower Jurassic in Southern Europe with our database in its current state: it is much too fragmentary. However, the history of the biodiversity of the belemnites in Northern Europe can be explored.

2.4. Construction and examples of paleontological databases

The development of computer tools has been of enormous benefit for paleontology. Now, everyone has the means to construct a computerized database containing a large amount of information. Today, such databases are numerous, and some of them are available for public consultation. In this section, we shall detail the prerequisites for the construction of a database, before going on to examine a few examples of openly-accessible databases.

2.4.1. *Constructing a paleontological database to quantify biodiversity*

Numerous simple software programs (spreadsheets) or more complex ones (relational database programs) can be used to compile data, sort them, order them, and consult them in regard to one or more criteria. Thus, we could use a database to record the temporal distribution of a series of fossil species. To that, we could add a variety of information depending on the aim of our study, e.g. the paleogeographical distribution, the type of sedimentary rock containing the fossils (which would give us indications about the environments in which they were buried), the species found together, etc.

In practice, though, constructing a database may prove to be a complex task [FOR 04]. In the data published before the 20th Century, you will find no mention of irregular sea urchins in the first part of the middle Jurassic (called the Aalenian – see Table A.2). Irregular sea urchins are sea urchins whose typical five-part radial symmetry is disturbed by the addition of bilateral symmetry (see section 4.4). You will find mention of them before the Aalenian, at the end of the lower Jurassic, and you will find them after the Aalenian, right up to the present day. What is the reason for this absence? Is it that they vanished and then reappeared several million years later? Of course not. They are absent simply because the Aalenian is a temporal unit that was proposed in 1864, which was not immediately accepted and adopted by all scientists. For many years, this slice of time was included in the immediately more recent slice, called the Bajocian. Hence, paleontologists at the time classified these sea urchins and other fossilized organisms they found in the Bajocian (at the very start of the Bajocian, granted) rather than in the Aalenian. Yet we are speaking of exactly the same period of time. The problem raised here, therefore, is of the standardization of paleontological data. How can we compile data with the same frame of reference for species that we know about from works published over the course of the past 200+ years, by paleontologists all over the world? This issue goes far beyond the strict context of paleontology, but in the specific case of this science, the answer lies in a double standardization. Firstly, we have the standardization which pertains to the stratigraphic framework – how can we unambiguously express the dates of apparition and disappearance of fossilized specimens (FAD and LAD)? Secondly, we have the standardization relating to the recognition of the fossil groups: the species or any other taxon for classification of the organisms (a taxon is a level of biological nomenclature: a genus, a family, an order, etc. – see section 2.4.1.2 below). How can we ensure that we use the same name for all of the individuals in a group, whether they are found in North America, Europe or Africa?

2.4.1.1. *The geological timescale*

The geological timescale (see Figure 1.1 and Tables A.1-A.5) is a universally-shared frame of reference that can be used to pinpoint a fossil organism, or any other object or geological event, in the geological ages. This frame of reference is used by all geologists and paleontologists. For example, ammonites are known to have existed from the Devonian (see Table A.4) to the end of the Cretaceous (see Table A.2). For everyone, the Devonian corresponds to a specific chronostratigraphic unit (a slice of geological time) situated between the Silurian (which is older) and the Carboniferous (more recent). These three units of time are contained in the Paleozoic (see Tables A.4 and A.5). For everyone, the Cretaceous corresponds to the chronostratigraphic unit at the end of the Mesozoic. There may be a certain amount of divergence as to the exact ages (expressed in millions of years) marking the beginning and end of the various units. These divergences stem primarily from the methods used to calculate the ages. In spite of these few divergences, we can categorically state that today, there is a broad consensus as to the temporal division of the geological ages – at least as regards the Phanerozoic period, which ranges from -541 million years to today.

In this book, by convention, we shall use the division of the geological ages standardized by the International Commission on Stratigraphy (ICS). The detail is given up to the "Stage" level in Tables A.1-A.5 (also see Figure 1.1 for an overview). The corresponding chart can be downloaded from the ICS Website (http://www.stratigraphy.org). The geological ages, expressed in millions of years, used throughout this book are those published in the treatise by Gradstein *et al.* in 2012 [GRA 12]. It is a complex task to perceive the immensity of the geological ages. Geology and paleontology students can attest to that. It takes time and experience to correctly understand the values stated and handled in our branches of science (e.g. -66 million years, -541 million years, etc.), which are far beyond our usual, human perception of the passing time. Suffice it to say that the elementary block that we use in paleontology is a million years, in just the same way as a year is a typical marker used to situate an event in a human life.

2.4.1.2. *Organism classification*

Biological nomenclature is the common frame of reference used by scientists (paleontologists, zoologists and botanists), invented by Carl Linnaeus (1708–1778) in the mid-18th Century, which can be used to catalog and classify species into hierarchical groups [LIN 58]. Thus, it is a standardized lexicon of the names of species and other hierarchical groups. For example, species belong to different genera, those genera belong to families, and families belong to orders (all these categories are listed in, and two examples are given). The system is sometimes called "binominal nomenclature", because a species is denoted by two words. For instance, *Archaeopteryx lithographica* is the scientific name denoting a fossil organism that combines certain characteristics of birds (feathers, wings and a beak) and certain features of dinosaurs (teeth, claws and a bony tail). This organism, which lived at the end of the Jurassic, has another name – its common name: the archeopteryx (this is the so-called "vernacular" language). Here, the two denominations are similar (*Archaeopteryx lithographica* for the archaeopteryx), but sometimes they can be very far removed from one another (e.g. *Panthera leo* for the lion). By convention, since the adoption of the Linnaean system, these two words (e.g. *Archaeopteryx lithographica*) correspond to the name of a species, and are printed in italics in publications. The taxonomic levels above that of the species (we speak of supra-species taxonomic ranks) are denoted by a single word. "Mammalia" is the scientific term found by Linnaeus himself in 1758 [LIN 58] to speak of mammals. Readers keen to learn more about the rules of biological nomenclature (or zoological/botanical) are more than welcome to do so! The internationally-standardized rules can be found on a variety of Websites. The International Commission of Zoological Nomenclature has a Website (http://iczn.org) that contains a great deal of information, including a detailed explanation of the zoological nomenclatural code (http://iczn.org/iczn/index.jsp). In addition, the International Association for Plant Taxonomy runs a Website (http://www.iapt-taxon.org) which also contains the nomenclatural code, but this time as it applies to algae, fungi and plants (http://www.iapt-taxon.org/nomen). These two codes (zoological and botanical) exhibit a few slight divergences [WIN 88], but in general their philosophies are very similar. There are no rules specific to fossil species (or at most a few minor adjustments). Their scientific names obey the same strict rules as do the zoological and botanical nomenclatures.

The classification of species is sometimes controversial, as indeed is the very notion of what a species is. The vast majority of scientists use the definition of a species offered by biologist Ernst Mayr (1904–2005) in 1942 [MAY 42]:

> "Species are groups of actually or potentially interbreeding natural populations, which are reproductively isolated from other such groups".

Whilst zoologists and botanists use all sorts of arguments to define species, paleontologists for their part focus on the morphological features preserved in fossils. With this technique, they group together individuals that have one or more traits in common, although these traits may exhibit variations between individuals. Thus, in the strictest sense, the species determined by paleontologists are primarily morpho-species.

2.4.1.3. *Quantifying biodiversity*

The number of taxonomic units (usually the number of species, but also, for example, the number of genera or families) is the most common biodiversity indicator used by paleontologists and biologists: it is the taxonomic richness. Note, however, that whilst this taxonomic approach is the most usual method, it is nonetheless very restrictive (it does not take account of all aspects of biodiversity), as is observed by biologist Kevin J. Gaston [GAS 96]:

> "A large number of papers open with the recognition that species richness is only one measure of biodiversity but proceed to treat it as if it were the measure of biodiversity".

The same observation has been made by paleontologists [ROY 04]:

> "Taxonomic patterns are only one aspect of biodiversity and may often mask interesting spatial patterns of morphological, functional, or phylogenetic diversity".

Counting the species, genera or families is therefore a typical and informative activity used by numerous paleontologists. Over the years, paleontologists have constructed a very particular iconography to observe the evolution of the number of taxa (species, genera, families, etc.) through the geological ages. We construct "spindle diagrams" representing the number of taxa as a function of the geological age. They are very useful, because the representation they offer is easy to understand. The wider the spindle, the more diverse the group of organisms is. Figure 2.8 presents an example of this iconography. At a glance, we note a spectacular radiation in the number of birds (Figure 2.8(b)) during the Cenozoic (note the scale, here in number of families, on the right of the graph).

We shall also describe biodiversity by a means other than the number of taxa, by directly quantifying the variability of the morphologies of fossil organisms, regardless of their belonging to one species or another. Note that there are many other solutions for quantifying biodiversity, besides those mentioned here – taxonomical or morphological – e.g. to quantify the functional, ecological, behavioral or indeed phylogenetic aspects. Although they are all worthy of interest, they fall beyond the bounds of this book, and therefore will not be discussed here.

Traditional biological nomenclature is not always appropriate for the quantification of biodiversity. One of the major issues is that the named groups do not necessarily represent what might be termed "natural" groups. In other words, that nomenclature does not always correctly reflect the biological evolution of the organisms. Imagine that we wish to study the evolutionary history of dinosaurs (we very briefly touched on this group in Chapter 1). Today, we are able to define dinosaurs by the presence of certain morphological features that are characteristic of them: amongst other things, they share a complete perforation of the acetabulum (the cavity which accommodates the head of the femur in the pelvic basin), at least three fused vertebrae and an asymmetrical hand with the two external digits being shortest. In theory, our study should include all the species of organisms that derive from the first population or species bearing the distinguishing characteristics. In practice, we cannot be certain of knowing this first population or species (indeed, it is unlikely that individuals from that population have been fossilized). This is not a major problem, because we know of an ancient species of dinosaur, dating from the Triassic (see Table A.3), to which it bears a resemblance. Therefore, in our analysis, we must include this species and all of its descendants. It is there that the problems begin to arise! In Linnaeus' classification, there is a group of organisms called "Dinosauria", first named by Sir Richard Owen (1804–1892) as being an "Order" within the "Class" of reptiles (see Table 2.1). Alongside them, this classification also includes the group "Aves" (birds) – a term invented, once again by Linnaeus, in 1758 [LIN 58], which is recognized to be at "Class" level, i.e. the same level as "reptiles". The term "dinosaur" evokes organisms from the Mesozoic, with reptilian appearance, which died out at the end of the Cretaceous. In the normal sense, and in the view of Owen, it does not include birds. However, this is only a partial view of the group of dinosaurs. Today, we know that, from a phylogenetic point of view (it is the phylogenetic perspective which offers the most faithful depiction of biological evolution), dinosaurs and birds form one big collective. All species of dinosaurs and birds have a common ancestor, and thus all descendants of that ancestor are either dinosaurs or birds, and no other group of organisms. This type of coherent group is called a clade – a term which will be used frequently in the pages of this book. The taxonomic group "Dinosauria" thus incorrectly omits an enormous set of organisms called birds, which are placed in the class of "Aves". In summary, there are two taxonomic groups (Figure 2.8(a) and (b)) which, in fact, describe a single clade (Figure 2.8(c)). Let us look again at our study of the evolutionary history of the dinosaurs. If we wish to effectively depict that history, we need to include all the descendants of the first population or species of dinosaurs (which is, for now, dated in the Triassic – see before), in other words, not only dinosaurs in the conventional sense of the word, but birds as well. Thus, the biological nomenclature does not always accurately reflect evolutionary reality. For the little history, paleontologists have had to adapt their lexicon to take account of the discovery of the phylogenetic link between dinosaurs and birds. In order to circumvent the ambiguity of the term "dinosaur", we now speak of "avian dinosaurs" for those which are closer relatives of birds, and "non-avian dinosaurs" for those of other lineage, which did, indeed, become extinct at the end of the Cretaceous.

	Example 1	Example 2
Kingdom	Animalia	Animalia
Sub-kingdom		
Super-phylum		
Phylum	Chordata	Mollusca
Sub-phylum	Vertebrata	
Super-class		
Class	Mammalia	Cephalopoda
Sub-class	Theria	Coleoidea
Super-order		Decapodiformes
Order	Primates	Sepiida
Sub-order		
Super-family		
Family	Hominidae	Sepiidae
Sub-family	Homininae	Sepiinae
Genus	*Homo*	*Sepia*
Sub-genus		
Species	*Homo sapiens*	*Sepia officinalis*
Sub-species	*Homo sapiens sapiens*	
Vernacular name	Human	Cuttlefish

Table 2.1. *Main taxonomic subdivisions (case of zoological nomenclature). Example 1: classification of the human species. Example 2: classification of a cephalopod (a cuttlefish). Classifications drawn from various sources. The vernacular name is the name in everyday language*

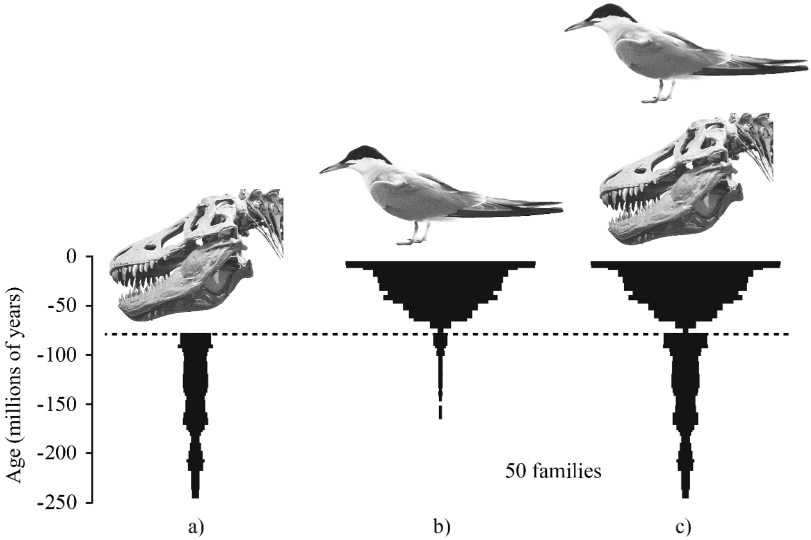


Figure 2.8. *Two points of view for analyzing biodiversity using spindle diagrams (number of families according to [BEN 93], geological ages according to [GRA 12]) (photos: P. Neige)*

COMMENTS ON FIGURE 2.8.– a) and b) In biological nomenclature, dinosaurs and birds are classified separately. Therefore, the story of the dinosaurs finishes at the end of the Cretaceous (the dashed line indicates the Cretaceous/Tertiary mass extinction event). c) However, phylogeny tells us that in fact, dinosaurs and birds belong to one and the same phylogenetic group (a clade). The story of the dinosaurs therefore continues even today through the group "birds", which experienced a spectacular radiation during the Cenozoic. Specimens illustrated: skull of a theropod dinosaur exhibited at the American Museum of Natural History in New York; a tern photographed on the banks of the Hudson River in New York.

There are a multitude of other taxonomic errors similar to that described above. These errors are the result of the criteria employed to classify organisms since the 18th Century. The organism classification system that we still use today (the Linnaean system) is extremely practical, but it too has its limits. The groups identified in that system sometimes have part of their line of descendants cut off (for instance, the group "dinosaur" does not include the group "bird"). We call this type of false extinction a pseudo-extinction. Some scientists have recently proposed a different classification system for ranks beyond that of the species, which more closely reflects the evolutionary histories of the organisms. However, the vast majority of scientists still continue to use this system, invented by Carl Linnaeus, because of its practical aspects, although it may give rise to a certain amount of bias when we are attempting to detect the history of groups over the course of the geological ages. Let us not be overly pessimistic. In most cases, today, we are already able to recognize and avoid these taxonomic pitfalls in our studies of past biodiversity, and particularly for the study of evolutionary radiations.

2.4.2. *Examples of databases*

There are a multitude of paleontological databases – perhaps as many as there are paleontologists. Some of these databases are entirely or partially open for consultation, and therefore anyone can try his/her hand at detecting evolutionary radiations by looking through them. We shall cite five examples here: two historical and three more recent.

2.4.2.1. *Two historical standards*

When digging through the available paleontological databases, two stand out. They represent historical standards and have been abundantly used, giving rise to numerous scientific discoveries.

In 1978, the American paleontologist John Sepkoski, Jr. (1948–1999) published one seminal article in which he analyzed the evolution of the taxonomic diversity of marine animals (marine metazoa) at "Order" level, for the whole of the Phanerozoic [SEP 78]. His approach consisted, in part, of compiling the data gleaned from specialist paleontological literature – the work of a true archivist. Several additional articles would follow. In 1982 he published the first version of his database at "Family" level [SEP 82]. In 1993, he published a famous article with the evocative title “Ten years in the library: new data confirm paleontological patterns” [SEP 93]. Ultimately, over the course of nearly 20 years, Sepkoski was constantly updating his database and using it to analyze the fossil record. His most detailed database – cataloging specimens at genus level and including all marine animals – was finally published a few years after his death [SEP 02]. Some of Sepkoski’s results gained huge success far beyond the bounds of paleontology. His famous marine diversity curve, constructed at “Family” level (see Figure 2.9) or “Genus” level, and sometimes called the “Sepkoski curve”, is very frequently used as an initial reasonable approximation for the history of biodiversity of marine animals. Today we know that this model is not entirely free of bias, but it remains (and will always remain) a paleontological standard-bearer. The data (in terms of genus and geological stage) are freely available at http://strata.geology.wisc.edu/jack/.

With no less than 845 pages, “*The Fossil Record 2*” edited by Michael J. Benton in 1993 [BEN 93] is a goldmine of information. It is the continuation to an initial overview published in 1967 by Harland *et al.* [HAR 67]. It catalogs all the families of organisms known to have been present during the Phanerozoic (see Figure 1.1). The data on each group – e.g. the gastropods or bryophytes – were compiled by one or more paleontologists specializing in that group, so the book has 90 contributors in total. The paper version exists in the form of a catalog. More recently, the data contained in that work have been made available (http://www.fossilrecord.net/ fossilrecord/index.html). On the basis of these data, it is possible to trace a multitude of the evolutionary history of groups of organisms, including in the continental domain. For example, Figure 1.3 in this book is based on data compiled from that overview. While the data may have become a little outdated (they were correct at time of compilation, and new discoveries have since led to modifications of the knowledge), this database is, nonetheless, extremely useful to quickly and summarily analyze the history of the organisms that have lived on Earth.

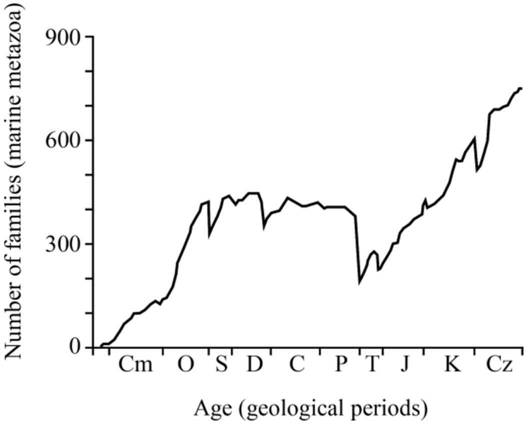


Figure 2.9. *"Sepkoski curve": this curve represents the evolution of the number of families of marine metazoa during the Phanerozoic (modified, based on [SEP 81]). The ages are expressed in geological periods (Cm: Cambrian, O: Ordovician, S: Silurian, D: Devonian, C: Carboniferous, P: Permian, T: Triassic, J: Jurassic, K: Cretaceous), except for the Cenozoic (Cz)*

2.4.2.2. *The quest for a complete database: PBDB*

The PaleoBiology DataBase is a paleontological database that was set up in 1998. It is based on a model of online collaboration between over 350 specialists in particular groups of organisms. Today, it contains over a million occurrences (an occurrence is a taxon found in a given place for a given age). The almost-Utopian aim of PBDB is to compile all of the paleontological data available in the scientific literature. Its Web interface, which is open to all, offers numerous analytical and exploratory possibilities. From its home page (http://paleobiodb.org) you can view data on geographical or paleogeographical maps ("Launch Navigator") and refine searches using taxonomic and/or temporal filters – a true immersion in fossil biodiversity. Another Internet resource (http://fossilworks.org) can be used to explore that database in greater detail.

2.4.2.3. *Trans'Tyfipal®*

The model developed by the database Trans'Tyfipal® is very different. The aim of this database is to catalog all the typical specimens (those used as a reference when first studying a fossil species) and figurative specimens (those used to enhance our knowledge of a fossil species) kept in France. Its Web interface (http://transtyfipal.u-bourgogne.fr) allows users to view the fossil specimen, locate the institution (e.g. a museum, a university) which holds it, obtain exact references for the original publication, or read its diagnosis (anatomical description) of the typical specimens. If you try your luck with the specimen of the species *Alocolytoceras coarctatum*, illustrated at the start of this chapter, you will see that it is located at the University of Bourgogne (France) with inventory number UBGD 276073 (see Figure 2.1). You can also see three other specimens of the same species (two from Morocco and one from Portugal), figuring in the same publication alongside the first [BOU 08]. Thus, in this database, which contains tens of thousands of photographs of typical or figurative specimens, the fossils are scientific objects which can be used to study the biodiversity of the past. However, they are also heritage objects, standing testimony to the activity of publication of the paleontologists, which will serve eternally as a reference and international standard for the definition of fossil taxa.

2.4.2.4. *ReColNat*

The *Réseau des Collections Naturalistes* (ReColNat) is a recently-founded consortium that brings together numerous establishments in France that keep natural-science collections (natural history museums, universities, research laboratories and museums, etc.). The aim of this program is to facilitate access to all of the natural history specimens – including paleontological artifacts – conserved in France. Via its Internet portal (http://recolnat.org), it is possible to consult objects, set up one’s own virtual laboratory, add comments or indeed suggest new determinations. An important point of that Website is the use of a participative science system to improve knowledge of the collections.

2.5. Yes, the fossil record can be used to study the history of biodiversity

Ultimately, the paleontological databases, the techniques used to sample the fossil record and the tools employed to examine the resulting samples mean we can be reasonably optimistic about the use of that fossil record, with a view to exploring the history of biodiversity. As we have seen, the transition from collecting fossils in the field to constructing a graph illustrating biodiversity through the geological ages is a lengthy task. It is lengthy, but doable, with the conditions required to produce robust results (reproducibility, potential bias testing, etc.). It is not possible to find an answer to every scientific question we can come up with: the fossil record is, by nature, incomplete, and its sampling is sometimes not sufficient to furnish an answer to a given question. However, some questions certainly can be resolved. In the following pages (particularly in Chapter 4), we shall explore some of these questions – specifically targeted at analysis of the events of extension of biodiversity.

3

The Phenomenon of Evolutionary Radiation

3.1. What is an evolutionary radiation?

An evolutionary radiation is a rapid increase in the diversity of a clade. The diversity of the clade is generally measured by a taxonomic value (the number of species, genera, etc. – see section 2.4.1.3). This diversification indicates a very positive balance between the number of apparitions and the number of extinctions of taxa within the clade. At a time $t + 1$, there will be more taxa than at time t. During the course of an evolutionary radiation, this balance very rapidly becomes highly positive, in comparison to the evolutionary patterns that we usually observe.

The question of the variation in evolutionary pace between or within different groups of organisms is by no means new. The American paleontologist George Gaylord Simpson (1902–1984) laid very fertile groundwork for a discussion in 1944 in his book "*Tempo and Mode of Evolution*" [SIM 44]. Chapter 4 therein ("Low-Rate and High-Rate Lines") opens with the following:

> "The most casual student of animal history is struck by the fact that while most phyletic lines evolve regularly at rates more or less comparable to those of their allies,

> here and there appear some lines that seem to have evolved with altogether exceptional rapidity and others that change with such extraordinary slowness that they hardly seem to be evolving at all."

Thus, in Simpson's view, we can define a normal pace for the evolution of clades. Remember, here, that we are talking about evolution viewed through a taxonomic prism, which, in the case of fossil organisms, thus corresponds to fundamentally anatomic and morphological evolution. Besides the so-called "normal" rates, certain clades sometimes exhibit particularly slow rates of evolution, whilst others evolve particularly rapidly. In this book, we shall not go into detail about slower rates of evolution, which could fill an entirely separate book. Evolutionary radiations, for their part, obviously belong to the latter category: they are instances of particularly rapid rates of evolution.

A crucial point in the analysis of radiations pertains to the phylogenetic relations between the organisms we are studying. This point, which was mentioned in the previous chapter, reveals a pitfall inherent in biological nomenclature: the system does not take account of all of the descendants of a common ancestor – e.g. studying dinosaurs without taking birds into account. The important point, though, is to understand clearly that recognition of a radiation needs to be undertaken on a set of species or taxa that constitute a natural group (a clade – see section 2.4.1.2). This is self-evident. If we are to make pronouncements about the pace of evolution of a group, it is crucial that the group in question make cohesive sense! In our case, making sense means two things: that the species or taxa share a common ancestor, and that they include all the descendants of that ancestor.

3.1.1. *Two examples of radiations, taken from organisms living in the world today*

The most symbolic example of adaptive radiation (a particular case of evolutionary radiations which we shall define and examine later on) is that of the finches living today on the Galapagos Islands (Figure 3.1). The birds in that archipelago, located over 900 kilometers off the coast of Ecuador in the Pacific Ocean, are interesting for two reasons. Firstly, they offer an excellent case study of radiations in an insular context. Secondly, it was these finches that Darwin used as a model when constructing his theory of evolution by natural selection. During his voyage aboard the *HMS Beagle* (a former British Royal Navy sloop given a second lease of life for the purpose of scientific exploration), between 1831 and 1836, Charles Darwin, during a stop-off at the Galapagos Islands, observed the birds. Since Darwin's work, these birds have impassioned numerous researchers. Today we know that there are 14 or 15 species [GRA 08]. All of them share a common ancestor – an ancestor that is not shared by any other species besides these Galapagos finches (hence, this group of species is a clade). The ancestral species probably arrived on the Galapagos Islands 2-3 million years ago, and the start of the radiation is dated at two million years ago [GRA 08]. In summary, this radiation produced 14 or 15 species of birds in the space of only two million years.

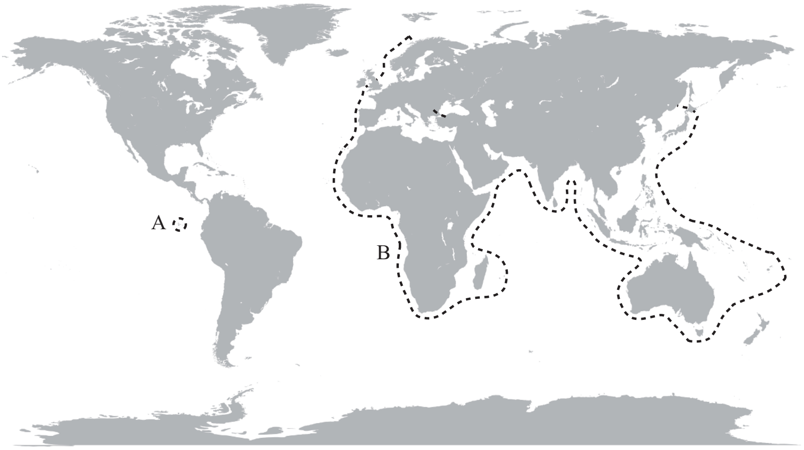


Figure 3.1. *Geographical distribution (outlined by the dashed line) of Galapagos finches a) and cuttlefish b). The radiation of the finches took place over the course of around two million years; that of the cuttlefish over around 30 million years*

Insularity is not the only context in which radiations can take place. The radiation of cuttlefish (cephalopod mollusks) was accompanied by a phenomenal geographic colonization. Cuttlefish are fascinating animals: so fascinating, in fact, that we shall take the time to describe them in detail here – a digression which is motivated by simple naturalistic curiosity.

Cuttlefish are fascinating creatures. They are cephalopods, just like squid and octopuses, of which they are close relatives. They have a highly-developed cephalic part (the head), with a brachial crown including arms and tentacles. This area contains a very high-functioning central nervous system. The posterior part of the animal, called the palliovisceral complex, is greatly developed and tubular or flat in shape. Adult cuttlefish can measure from a few centimeters up to a meter for the largest specimens. At a brief glance, we can identify them as members of the group of cephalopods, because of two external anatomical features:

– they observe their prey and their environment with W-shaped pupils. Their sophisticated visual system enables them to assess the distance between them and their prey;

– they develop a wide lateral fin that covers the whole of the palliovisceral complex, and is interrupted at the rear of the body.

In contrast, squid have rounded eyes and lateral fins located only on the rear part of the palliovisceral complex. Nearly all squid, that is; there is one, called *Sepioteuthis* (literally the "cuttlefish squid"), which has a fin similar in shape to that of the cuttlefish. Octopuses, for their part, have a rounded palliovisceral part with no fin. Cuttlefish have other very unique anatomical features. Just like squid, cuttlefish have ten appendages around the mouth (octopuses have only eight). Two are larger than the others: these are the tentacles. The other eight are the arms. In cuttlefish, these tentacles are retractable, and indeed are usually kept retracted in pouches inside the body (unlike squid, whose tentacles are always external). The anterior end of the tentacles has a widened area with a cluster of suckers. Anatomists have given an evocative name to these extremities: they are "tentacular clubs". Cuttlefish violently throw the tentacles out of their cavities to attack their prey, and grip using their suckers. Add to this the fact that they have an excellent visual system, and it is easy to see that their prey – e.g. crabs walking along the sea bed – have next to no chance of escaping such an attack. The most surprising thing is yet to come, though. Cuttlefish possess an internal shell, called the bone (or cuttlebone) or the sepion (see Figure 3.2(a)) on the animal's dorsal side, above the pallial cavity (this cavity contains many of the animal's organs, such as its heart, digestive system and respiratory system). In spite of its name (cuttlebone), this structure has nothing in common with the bone of a vertebrate – it is simply a question of mirroring vocabulary. Cuttlebone is a very "crumbly" substance made of aragonite – a mineral similar to calcite. If we look more closely at the sepion, we see one face that is generally rough and another with a smooth part on one side and a striated part on the other. The latter face (smooth at one end and striated at the other) is the ventral side of the sepion. Each striation corresponds to a layer of aragonite. The layers accumulate, stacking up on top of one another, with a slight change as the animal grows. The parallel striae visible in the ventral face thus show the posterior parts of the different layers. They are held to one another by small pillars, also made of aragonite, so that there is a space between two successive layers (see Figure 3.2(b)). This cuttlebone plays a very specific role: it helps alter the animal's weight, and therefore adjust the cuttlefish's overall density, by an ingenious system of filling and purging of the internal cavities, which play the same role as ballast tanks in a submarine. That is to say, submarines mimic a stratagem developed a very long time ago by cuttlefish or other cephalopods. This way of working enables them to maintain a density close to that of seawater, and therefore exist even within the water column.

In terms of their living environment, cuttlefish are found in shallow seas, from the coastline to up to 600 meters depth. They always stay near to the sea bed: to feed, to reproduce or indeed to lay their eggs. This way of life considerably limits their ability for colonization, both because of the depth (no deeper than around 600 meters) and because of the presence of a sea bed (they cannot live in open water, far from the bottom). In other words, and this is a paradox, it is impossible for a cuttlefish – which is, nonetheless, an organism that is perfectly adapted for marine life – to cross the Atlantic Ocean! Let us look again at the evolutionary radiation of this unusual animal. Today, we can see a little over 100 species of cuttlefish. Their sepion is a very special feature which proves the common origin of all these species – the proof is confirmed by molecular data (thus, they constitute a clade). The fossil record indicates that the clade originates from around -30 million years, very likely in a paleographical zone equivalent to the marine domain currently to the east of India [NEI 03]. From this temporal and geographic origin, cuttlefish demonstrate an unusual radiation, because it includes very widespread geographical expansion: they are now present along coastlines from Norway to Japan, also including Africa, India and Australia (see Figure 3.1).

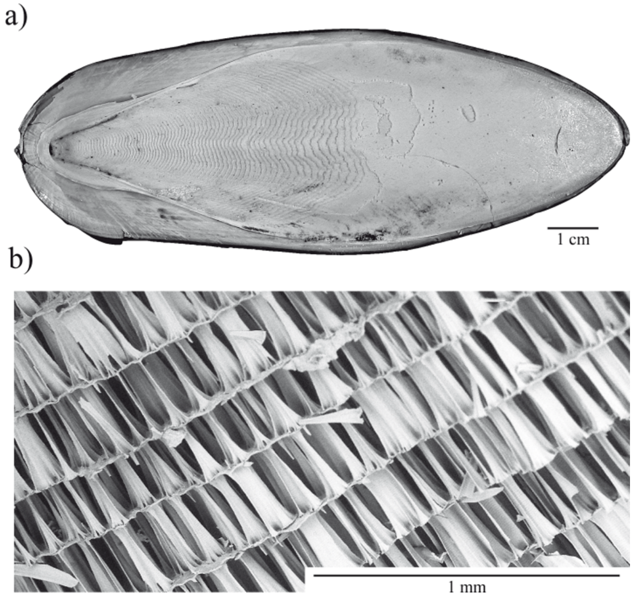


Figure 3.2. *a) Ventral view of a cuttlebone from the genus* Sepia *(UBGD 278895) – anterior part of the animal shown on the right. The striated area to the left of the sepion corresponds to an accumulation of layers, added one on top of the other (see the text). The smooth area on the right is the final layer; P. Neige's collection. b) Cross-section of the striated area of a cuttlebone from the genus* Sepia *(photo taken with a scanning electron microscope). The accumulated layers are clearly visible in the photo, and are connected to one another by a multitude of small perpendicular pillars (photos by P. Neige)*

In summary, the portrait that we can paint of this radiation shows the emergence of around 100 species in the space of 30 million years. This example allows us to touch on another important element in the study of radiations which we have, up until now, overlooked. When we study the radiations of groups of organisms living today, it is not possible to take account of those species which have already become extinct. In the case of cuttlefish presented here, we have only a very incomplete knowledge of their fossil history (since the beginning of the radiation 30 million years ago). It is highly probable that other species also existed, but have not left a fossil trace (or that their fossils have simply not been discovered yet). Hence, these fossil species simply cannot be included in our count!

There are many other examples available today which illustrate spectacular paces of diversification. They also bear witness to the phenomenon of evolutionary radiation (cichlid fish, lizards, plants, etc.). To detail these examples would exceed the remit of this book, which focuses on the specific case of radiations in the fossil record. The two examples detailed here have enabled us to lay down some simple foundations as to exactly what these radiations are, using organisms with which we are familiar.

3.1.2. *Taxonomic diversification*

Figure 1.3 in this book illustrates a radiation event. It is visible through the rapid increase in the number of families of mammals since around 66 million years ago. In terms of the overall balance, therefore, there are more new families appearing than families becoming extinct. This evolutionary pattern is fairly commonplace in the fossil record. When we examine the history of the teleosteans (a clade which includes the majority of the organisms that we call fish), we observe a pattern that is fairly similar to that of mammals. The number of families was low over a lengthy period from their first appearance, around 220 million years ago, to around -60 million years (see Figure 3.3). Then, there was a spectacular increase in diversity up until around -45 million years, and the upward trend continues today, but at a slightly more modest pace. This means that the number of different groups of teleosteans (and thus probably also the number of species) increased significantly over the space of a short period of time. Represented with the iconography of the spindle diagram (remember our discussion in Chapter 2), the radiation of the teleosteans is perfectly visible, as is the spectacular increase in the number of families 60 million years ago (see Figure 3.4).

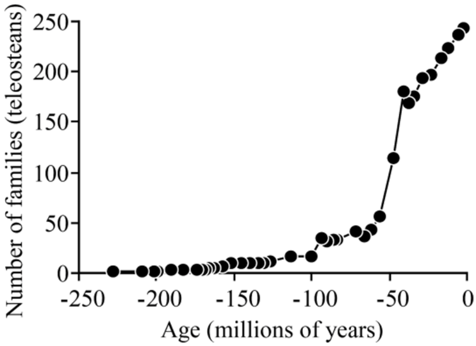


Figure 3.3. *Evolution of the number of families of teleosteans over the geological ages (number of families based on [BEN 93] data; geological ages based on [GRA 12])*

This diversification, or that of mammals, which we saw above, is observed at a supra-species scale: i.e. beyond that of the species. We then speak of the observation of a macroevolutionary phenomenon. By definition, macroevolution is evolution that takes place at the scale of a species and beyond, unlike microevolution, which occurs at the scale of populations. The study of macroevolutionary patterns and processes is dominated by paleontologists, who have always been interested in such things (for examples, see section 2.3.2). More recently, this broad scale of evolution has also been explored by specialists in the ecology of present-day organisms, giving rise to a scientific discipline called macroecology. The objective of that discipline [PRI 03] is to establish the relations which exist between the organisms and their environment, which involves analyzing their abundance, their distribution or their diversity (usually by employing fairly sophisticated statistical techniques). Once again, the phenomenon of radiation can be demonstrated and explored in detail. This macroevolutionary (or macroecological) approach is largely accepted today by specialists in biological evolution, whether they work on organisms in the world today or fossil organisms (see [REZ 09] for examples).

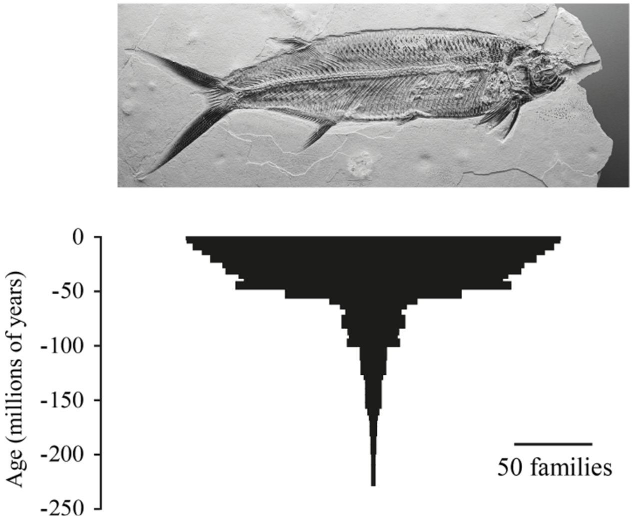


Figure 3.4. *Evolution of the number of families of teleosteans over the course of the geological ages, presented in the form of a spindle diagram (same data as were used for Figure 3.3). Illustrated specimen: teleostean fish from the Jurassic (specimen housed at the Jura-Museum Eichstätt, Germany) (photo by P. Neige)*

3.1.3. *Morphological diversification*

In parallel to tracking the evolution of the number of taxa over time (see Figures 1.3 or 3.3), paleontologists are increasingly frequently looking at the evolution of organisms' morphologies. Going back to a few lines ago, we have seen that the number of families of teleosteans increased greatly between -60 and -45 million years. However, this observation actually tells us nothing, or precious little, about the morphological diversification of these fish. Are the organisms from the start of the radiation, 60 million years ago, morphologically similar to one another? Do they, on the contrary, exhibit widely varied morphology? The number of families cannot provide an answer to this question – simply because the recognition of taxonomic groups (species, genera, families, etc.) focuses greatly on a few anatomical features, omitting many other morphological traits. Hence, examining the diversity of the shapes is not a redundant activity in taxonomic studies. Let us look at another example. We observe two collections of shells found in various paleontological deposits. In our example, we find eight specimens of fossilized gastropods from the Lutetian (see section 2.3.4 and Table A.1): four specimens for each of the collections, all from a different species and a different genus – i.e. eight genera and therefore eight species in total.

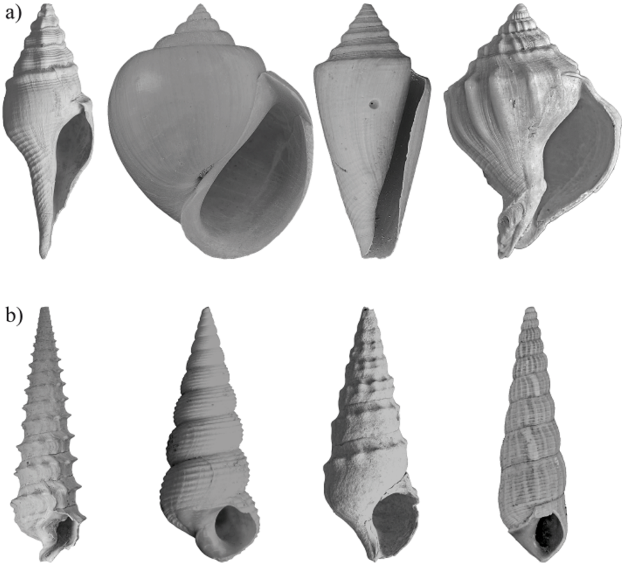


Figure 3.5. *Two sets of fossil gastropods found in paleontological deposits dating from the Lutetian (specimens are depicted as the same size so as to better be able to appreciate the similarities and differences in morphology) (photos by P. Neige)*

COMMENTS ON FIGURE 3.5.– Each series consists of four different genera, so four different species. Series a) exhibits greater morphological diversity in terms of the shell than series b). Top to bottom, left to right: *Clavilithes* (UBGD 278896), *Crommium* (UBGD 278897), *Eoconus* (UBGD 278898), *Strepsidura* (UBGD 278899), *Serratocerithium* (UBGD 278900), *Sigmesalia* (UBGD 278901), *Batillaria* (UBGD 278902), *Diastoma* (UBGD 278903). Collection of P. Neige.

At first glance, the two collections exhibit the same degree of diversity – at least in terms of the number of species: there are four species per collection. The same is true in terms of the number of genera: there are four per collection. How about in terms of morphological diversity, though? Figure 3.5 illustrates the specimens from the two collections. It seems obvious that collection *a* has greater morphological diversity than *b*. Yet, in both of the series (*a* & *b*), there are the same number of taxa (four species and four genera). Here, the morphological diversity represents a very particular feature of biodiversity, which is different to that characterized by taxonomic diversity.

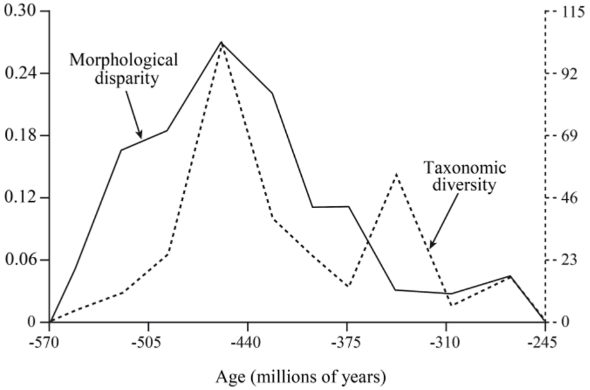


Figure 3.6. *Evolution of the biodiversity of blastozoans (echinoderms) during the Paleozoic. Two measures of biodiversity are calculated: the morphological disparity (left-hand axis), and taxonomic diversity (number of genera, right-hand axis). For comparative purposes, the two curves in the graph are standardized to the same highest level. Data modified from [FOO 92]*

Since the early 1990s, paleontologists have been particularly interested in this morphological diversity, and attempting to quantify it. Because it directly expresses the morphological variation without considering the number of species or taxa, it offers an additional perspective on the taxonomic diversity of biodiversity. To prevent any ambiguity in terms of vocabulary, we call this measure of biodiversity "morphological disparity". That which applies to taxa is called "taxonomic diversity". To quantify this morphological disparity, we must first describe the morphology of the organisms and then quantify the morphological differences. Thus, we can measure the degree of variation in the form of the organisms in a clade over the geological ages. Mike Foote, of the University of Chicago, is one of the paleontologists who has most fully studied morphological disparity. In a study published in 1992 [FOO 92], he explored the history of the blastozoans (Paleozoic echinoderms) from their origins and their early radiation at the start of the Cambrian (see Table A.5) to their eventual extinction in the Permian (see Table A.3). He counted the number of genera over the geological ages, on the one hand, and the morphological disparity, on the other (see Figure 3.6). The results indicate that the radiation phase is characterized by morphological disparity which is relatively greater than the taxonomic diversity: the disparity curve in Figure 3.6 rises faster over geological time than does the diversity curve. Put simply, this means that early in their history, the few genera of blastozoans that existed were very diverse, morphologically speaking. Then, the radiation event is characterized by the arrival of new genera whose morphologies were simply intermediaries between the original genera. The maximum radiation was reached about 450 million years ago, with a peak in both the number of genera (taxonomic diversity) and morphological variation (morphological diversity). This method of study is particularly relevant in the study of radiation that interests us here, but also in the study of extinction events [ROY 97]. The most common result is that the clades reach their maximum morphological diversification earlier than their maximum number of taxa (species or other ranks) during their history [HUG 13].

3.2. The different categories of evolutionary radiations, and their causes

Categorizing evolutionary radiation is a complex but necessary exercise: complex because we are dealing with the thorny issue of changing rhythms of phenomena that take place over millions of years; but necessary because this categorization should enable us to better understand the causes of these radiations.

3.2.1. *Adaptive radiation*

Adaptive radiation is a rapid increase in the number of species with a common ancestor, characterized by great ecological and morphological diversity. The driving force behind it is the adaptation of organisms to new ecological contexts. For Simpson [SIM 44], adaptive radiation may not necessarily apply at the scale of the species, but may just as well apply at a higher taxonomic level (major groups of organisms may also appear by adaptive radiation). The diversity of Galapagos finches, discussed above, results from adaptive radiation. It can even be said that theirs is the most typical, most famous case of adaptive radiation studied by scientists. During the course of evolution, their beaks have changed in size and morphology so that they are now adapted to different diets: some species eat mostly animals (e.g. insects), others seeds or plants; some feed in the trees, and others on the ground. Ultimately, it is the variety of environments and food resources that led to the rapid differentiation of these species of finches. All these species share a common ancestor and are now characterized by broad ecological (their diets are different) and morphological (the size and shape of their beaks are different) diversity.

The expression “adaptive radiation” is extremely popular in the scientific community. Nevertheless, there are those who feel it is not appropriate, both for practical and semantic reasons. Olson and Arroyo-Santos identified the use contexts of this term in specialized literature [OLS 09]. The results of their study are striking. This expression is, indeed, very widely used, but in very variable contexts or situations of study. Some people speak of adaptive radiation within a single species; others of radiation amongst all life on Earth – i.e. amongst several million species (or even tens of millions, according to estimations). Between these two extremes, Olson and Arroyo-Santos found intermediary situations. In their view, the term is used in so many different contexts that in practice, today, it no longer means anything specific. Along with this practical observation, we can make a semantic criticism. The term “adaptive radiation” includes two words. Unfortunately, these two words are related to two different scientific approaches, although they are very complementary. The word “adaptation” is linked specifically to an evolutionary process. The beaks of Galapagos finches have adapted to different types of food supply through an evolutionary process. The word “radiation” expresses taxonomic diversity. When we look at a radiation event, we describe an increase in biodiversity. This is an evolutionary pattern (see section 1.2): 14 or 15 species of Galapagos finches have emerged in the space of two million years (see section 3.1). An evolutionary pattern is the result of an evolutionary process. The 14 or 15 species are an observable result of an evolutionary adaptation. By combining patterns and processes of evolution, the expression “adaptive radiation” creates ambiguity. This is not without consequences, and may have given rise to misunderstandings between scientists from different cultures. When specialists in present-day ecology look at an adaptive radiation event, they will tend to focus on demonstrating the link between a supposedly adaptive feature and the organisms’ environment. When paleontologists look at those same adaptive radiations, they are more likely to explore the number of species over time in detail. Thus, these two scientific communities have quite different approaches to the same phenomenon, in terms of whether it is discussed from the perspective of the evolutionary process or the pattern. However, today, there is a set of approaches which allows us to address these two aspects in tandem. As indicated by Brooks and McLennan [BRO 02], it is at the intersection of the two approaches (one side the study of adaption, the other that of the taxonomic diversification) that the most robust and most interesting studies of adaptive radiation take place.

Despite criticism and comments on the term “evolutionary radiation”, it is entirely understandable that this type of radiation is predominantly studied by scientists. The evolutionary biologist Dolph Schluter devoted an entire book to this subject, exploring this phenomenon in great detail [SCH 00]. Simpson saw it as the explanation of the diversity of the entire living world [SIM 53]. In this book (Chapter 4), we discuss some examples of adaptive radiation in the fossil record.

3.2.2. *Non-adaptive radiation*

In some cases, the phenotypic variability (the variation in the appearance of organisms) of a set of similar species does not appear to be structured by any environmental factor. Whilst these species share a common ancestor and appeared quickly, nevertheless, it is certainly a case of evolutionary radiation. It is, therefore, a non-adaptive radiation. The mechanism that explains this type of radiation is relatively simple. It occurs if speciation (the emergence of different species from a common ancestor) precedes ecological divergence. This speciation can arise from the geographical isolation of populations of the same species, in favor of a geological phenomenon – e.g. the division of a territory into zones containing the same type of environment. The species will then diversify genetically but exhibit little phenotypic divergence.

3.2.3. *Post-extinction radiation*

This is the very specific case of evolutionary radiation which takes place after a mass extinction (they are, therefore, known only in the fossil record). In Chapter 1, we touched on this concept of mass extinction. Over the past 540 million years, we see five major and 20 second-order mass extinction events (see Figure 1.2). Many paleontologists have looked for possible periodicity of the major extinctions in geological time. After much debate, the current consensus is that there is a lack of periodicity: overall, major extinctions are distributed randomly during the Phanerozoic. These events are characterized, above all, by the intensity of the extinctions affecting species. The point that most interests us in our present study is not that characteristic of extinction but the next stage in the story. Indeed, mass extinctions offer extraordinary opportunities for the subsequent recovery of biodiversity. Undoubtedly, the most striking point is the fact that the major actors in the "play" before and after the extinction are not necessarily the same. The sequence of mass extinction and post-extinction radiation allows the structure of biodiversity to change fundamentally. Mammals, which have been present since the Triassic, diversified widely at the time of the radiation in the wake of the Cretaceous/Tertiary extinction, after the extinction of the non-avian dinosaurs. Thus, in the space of a few million years, the biodiversity of land-dwelling vertebrates was profoundly changed. There are many similar examples which punctuate the history of biodiversity.

There is nothing to suggest that a post-extinction event should not be an example of adaptive radiation. However, neither is there anything to suggest that it must be. In fact, it is actually probable that post-extinction radiation is not linked to any adaptive nature. Indeed, these radiation events take place in a highly turbulent environment where there are few competing species, because most have died out in the extinction event. Radiation can thus be simply related to chance: the chance of a species not being exterminated by extinction and the chance to diversify in an environment without many competing species.

Post-extinction radiations are part of a clearly-identified sequence of events [HAL 97, BRO 10]:

– step 1: mass extinction event. Environmental pressure is sufficiently strong and abrupt for a large number of species to be unable to adapt and, therefore, be doomed to extinction;

– step 2: post-extinction recovery. Usually, some particular lineages exhibit intense phases of increasing taxonomic diversity. These phases correspond to post-extinction radiation in the strict sense of the term. For some organisms, the post-extinction radiation phase will be so intense that the biodiversity of the group will be much greater than the level seen before the extinction. Other species, which were rare or even unknown before the extinction, may become particularly abundant in the fossil collections;

– step 3: back to normal. The extinction rate returns to the level which is typically observed outside of a mass-extinction episode.

This timeline (see Figure 3.7) has been the subject of numerous studies. The step which interests us most here – the radiation – may manifest itself in a variety of ways in the fossil record. Sometimes the recovery time (*R* – *C*, Figure 3.7) is short (case A, Figure 3.7). Other cases exhibit much longer recovery times (case B). These discrepancies can exist between different organisms but for a single episode of post-extinction recovery: some clades then show rapid recovery, and others slower recovery. Primary producers often recover faster than organisms of higher trophic levels. Within the same group, omnivores and scavengers also recover faster than herbivores and carnivores. Here we can see the complexity of this phenomenon. This means that the post-extinction recovery phase is not necessarily simply a return to normality, but it can facilitate a genuine revolution in terms of biodiversity, e.g. by restoring food webs based on different organisms.

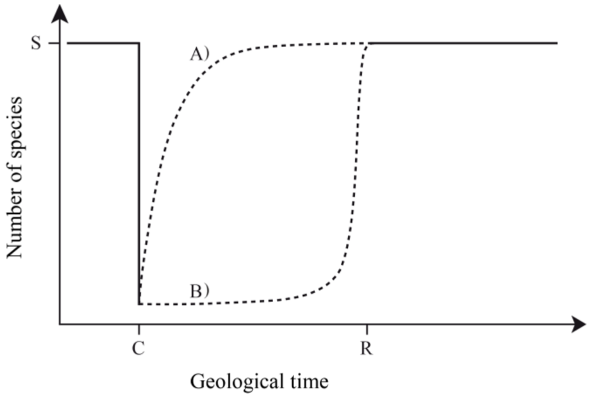


Figure 3.7. *Diagrammatic representation of the effects of a mass extinction on biodiversity (case of recovery to the initial level of biodiversity S). S: number of species before extinction. C: time of the mass extinction. R: when the post-extinction recovery has actually taken place. Recovery models inspired by [SOL 10]*

Beyond this timeline, today there are important issues that remain to be solved in the understanding of this type of radiation:

– it is often considered that the post-extinction radiation phase will be longer than the mass-extinction event itself. However, recent studies reveal instances of extremely fast post-extinction recovery [BRA 09]. We do not yet know precisely what regulates the post-extinction radiation rates;

– in regard to the range of taxa that survive the extinction (which do not die out totally or which emerge at that time), we are unable to determine, *a priori*, which ones experience post-extinction radiation. Not all survivors are guaranteed of major diversification phase! We can simply observe the facts, but without really understanding the causes.

4

Examples of Evolutionary Radiations

In this chapter, we shall explore a variety of cases of evolutionary radiations in the fossil record. The case studies are chosen for their exemplary value. The Cambrian explosion over 500 million years ago is striking because of the emergence of a particularly diversified abundance of life. The ammonites – a clade that lived for over 350 million years – are a good example of the degree of biodiversity that can be achieved in terms of successive diversifications. The radiation of flowering plants, at the start of the Cretaceous a little over 120 million years ago, is an essential example of delayed anatomical invention in terms of geological time, followed by a major diversification in the plant kingdom. Finally, non-rounded sea urchins show us that the loss of a feature may prove beneficial. This took place at the start of the Jurassic, around -190 million years ago.

4.1. A paleontological bestseller: the Cambrian explosion

Rarely has a subject had so much success with paleontologists. What are the events that took place on the boundary between the Precambrian and the Phanerozoic (see Figure 1.1), in the period ranging between -550 and -500 million years? The answer is that many upsets in the world's biodiversity occurred, and ultimately a remarkable radiation – so remarkable, in fact, that paleontologists call it the "Cambrian explosion" [CON 89]. The term "explosion" refers to the enormous variety of life forms that emerged at that time, and "Cambrian" refers to the Cambrian period, which marked the start of the Phanerozoic (see Table A.5). At this time, we witness a surprising and innovative turn, which laid the foundations for the biodiversity for hundreds of millions of years. Above all else, this change of direction was an instance of evolutionary radiation. We now have a better understanding of these events, although there are still some points which need to be illuminated and questions which need to be answered.

4.1.1. *Previously on Planet Earth…*

In order to fully comprehend the Cambrian explosion, it is useful to review the previous paleontological literature. Our knowledge of the Cambrian explosion is the result of a true paleontological saga. It began in 1909.

Before that, let us rewind a little. At the start of the history of geology and paleontology, paleontologists lived in a simple world! The history of biodiversity was divided into two. The Precambrian (literally the period before the Cambrian) was known for the absence or near-absence of life. The base of the Cambrian marked the beginning of the period whose primary characteristic was the presence of abundant biodiversity, known because of numerous fossil markers, including the traces of movements in marine sediments. This base corresponds to the Cambrian explosion, which we shall explore here. Very soon, though, the question of the absence of life in the Precambrian was raised in the paleontological debate. Was life present but "hidden" – i.e. invisible or not easily visible using the investigative methods of the time, or was it truly absent? Today, we actually know the answer to this question. We know that life did actually exist in the Precambrian – for at least 3.5 billion years. However, these lifeforms are rather less exciting in the eyes of paleontologists. Sometimes, that life can be detected only by chemical indicators (chemical tracers of life, fossilized in ancient rocks) rather than by direct discovery of fossils in the field. In most cases, Precambrian lifeforms are microorganisms, or larger forms but without skeletons. They usually prove to be rather enigmatic still. It is easy to understand that their preservation in the fossil record, on the one hand, and their detection by paleontologists, on the other, are far from certain. Certain lifeforms, though, are sometimes clearly visible. This is the case with stromatolites, which are chalky biogenic rocks (related to the activity of organisms), comprising ancient microbial communities, often dominated by bacteria, that develop in shallow marine or terrestrial environments. These microbial communities form biofilms and microbial mats that, firstly, trap sediments and, secondly, enable the organism to secrete biominerals (by biologically-induced mineralization), thus facilitating their fossilization. Over time, with the mineralization of microbial mats and the accumulation of sediments, these original communities eventually become fossilized, usually in the form of layered structures like piles of plates, stacked upside down, sometimes tens of meters high.

Alongside the stromatolites, there are deposits dating from the Precambrian which enable us to trace the existence of completely original lifeforms. In order to properly understand the Cambrian explosion, we need to examine this Precambrian biodiversity at length. The story starts around -3.5 billion years. However, the start of that story goes beyond the purpose of this book. We shall begin our examination at a much more recent point – between -575 and -542 million years. During this period, a community of very special organisms developed, always accompanied by stromatolites. We call these lifeforms the Ediacaran biota. The term “Ediacaran” here refers to a famous deposit in southern Australia where some such fossils have been discovered. The term “biota” simply refers to all of the organisms living during the same geological time period. Now, this community has been found on numerous paleontological sites the world over, far beyond Australia. In this biota, the lifeforms are known only because of fossilized imprints, which attest to the presence of soft-bodied organisms, sometimes exhibiting radial symmetry and sometimes bilateral symmetry. They vary in size; the largest individuals could grow up to two meters. These organisms are interpreted as having been filter feeders, and were usually anchored to the sea bed. However, three major innovations would affect this Ediacaran biodiversity:

– the emergence of mobility, at least 555 million years ago;

– the invention of biologically-controlled mineralization–biomineralization – around -550 million years;

– and last but not least of these innovations, the dawn of predation, at least 549 million years ago.

The zoological affinity of these Ediacaran organisms is, as yet, uncertain. In the view of certain paleontologists, they are the precursors to the zoological groups that we know today. For others, they represent an invention with no future – a sort of failed experiment in evolution, which left no descendants. More recently, specialists in these fauna have suggested that the Ediacaran biota corresponded to a mixture of species. Some of them have no descendants, whereas others show varying degrees of affinity with animals that are still known today, such as jellyfish, sponges, echinoderms, annelids, mollusks or arthropods [NAR 05].

From the start of the Cambrian onwards (particularly around -530 to -520 million years), biodiversity took a new intriguing turn – a new episode in our saga. In sedimentary rocks from that period, paleontologists have found numerous fossils – usually very small (less than a millimeter). These fossils, which vary greatly in shape, represent either complete shells of organisms or separate elements of the armor of a larger organism. Once again, their zoological affinities have yet to be determined. Some are similar to brachiopods or mollusks, whilst others are rather enigmatic.

4.1.2. *The strange biodiversity of the Cambrian*

The episode to which we now turn our attention is the Cambrian explosion in the strictest sense of the term. It is marked by the diversification of lifeforms, some of which have mineralized skeletons or tests. It relates to the diversification of the animals (metazoans) in the marine environment. It is from the end of the lower Cambrian that fossils become abundant, morphologically varied and similar to the organisms found in the Phanerozoic. Sometimes optimal, the conditions for preservation of fossils play a major role in this paleontological saga. We have an ever-improving understanding of the events at the start of the Cambrian, thanks to deposits of exceptional quality: *Lagerstätten* (see Chapter 2). The Chengjiang site in China is recognized for the huge diversity and phenomenal quality of the fossils found there. This deposit, which was discovered in the 1980s, is a sort of open book on marine biodiversity at the time. However, it is on another paleontological deposit of exceptional quality that we shall base our paleontological saga. This deposit, located in the Canadian Rocky Mountains – specifically in Yoho National Park – is known as the Burgess Shale deposit. The most recent studies date this deposit in the middle Cambrian, around -505 million years. The episode of its discovery – which began in 1909, and is the start of our saga – is well known. It is described in ample detail in an authoritative publication by Stephen Jay Gould [GOU 89]. Readers of this book are wholeheartedly advised to read Gould's to expand their knowledge of this Cambrian radiation. From this story, where myths and truths are interwoven, planted firm in the collective imagination of paleontologists the world over, we shall only cite a few elements that are helpful for the understanding of the Cambrian explosion.

In late August 1909, the paleontologist Charles Doolittle Walcott (1850–1927) discovered the first fossils of soft-bodied organisms in the Burgess shale. He organized them systematically into known zoological groups – mainly belonging to the arthropods. Thus, to begin with, the analysis of these Cambrian lifeforms did not attract attention. The conclusions of the study are indeed modest. The lifeforms in the Cambrian are no more than variations of the lifeforms that were to follow. There, one might imagine, the story would end… but it does not.

The debate over the Cambrian explosion took a particularly dramatic turn with the reinterpretation of the fossils found in sedimentary rocks from the Cambrian. In the 1960s, in order to compile a view of the paleontological heritage, new campaigns of excavations took place in the Burgess Shale. From the 1980s onwards, paleontologists began to study these fossils. Certain studies were inconsequential: the organisms found at Burgess demonstrate clear anatomical affinities with known animals. Others would rock our view of biodiversity and its history to the core: on occasion, it is impossible to find a connection between the fossilized organisms found at Burgess and any known zoological group. Nevertheless, these are indubitably animal organisms, often showing bilateral symmetry, sometimes rather large (the largest measuring around a meter), whose preservation in fossil form is astonishing. *Anomalocaris*, the predator described in Chapter 1, who roamed the oceans of the Cambrian, is one such specimen! Hence, the conclusions fly in the face of those reached by Walcott. Above all, the Cambrian explosion is characterized by phenomenal biodiversity in terms of body plans (anatomical organizations). It combines known groups (arthropods, mollusks, brachiopods, etc.) with others that are anatomically different, which have no long-term descendants. Note that the excellent conditions of fossilization support this result: in this case we cannot cite mediocre conditions of preservation that mask important anatomical features and prevent us from obtaining robust results. The fossils are wonderfully preserved: it is clear that some of them bear no resemblance to anything that is known elsewhere.

What conclusion can be drawn, then, about this Cambrian explosion? This evolutionary radiation pertains primarily to animals. More specifically, it is the emergence of large groups of animals. Each of them is characterized by a particular body plan. In the classification of organisms (see Chapter 2), these major groups are recognized at the level of classes or phyla. Cuttlefish, whose anatomical originality we praised in Chapter 3 belong to the phylum of mollusks, and the class of cephalopods (Table 2.1). All mollusks share anatomical features which are unique to that phylum, such as the presence of a mantle (a tegument which secretes the chalky parts), or of gills of a particular shape. Cephalopods represent one of the classes of mollusks. All of them share specific features: a central nervous system, and a closed circulatory system. The Cambrian explosion corresponds to the establishment of nearly all of these major referential body types. This explosion is even more visible when we observe it in relation to the past 600 million years of the history of biodiversity (Figure 4.1). Practically all classes of animals around today have been known since the Cambrian. Nothing (or almost nothing) is known before that, and very few new body types would emerge later on. The Cambrian explosion is, undoubtedly, the event when the biodiversity of today's animals was established, by way of an evolutionary radiation.

It is that and so much more! Besides the body plans known from then on, as we have seen, the Cambrian explosion facilitated the development of major original body types that have produced no descendants. Thus, it is also characterized by immense biodiversity in terms of anatomic organizational plans. For [GOU 89], this diversity of body plans was greater in the Cambrian than it is today. If this hypothesis proves true (a little later on we shall see the points that remain to be resolved – that of counting body plans is one such point), then our entire overall vision of the evolution of biodiversity is called into question. We have all learned, at school or elsewhere, that the diversity of the organisms increases gradually over time. This hypothesis, referred to as the growing diversity cone, is easy to understand. From a common distant ancestor, life diversified, so that there is a constantly increasing degree of diversity as time goes on. Represented on a spindle diagram, this hypothesis produces a cone shape, which becomes ever wider as we get closer to the present day (Figure 4.2a). On the other hand, Gould's hypothesis inverts the cone: the diversity is greatest in the Cambrian (owing to the Cambrian explosion), so that the spindle diagram is wider at its base than it is today (Figure 4.2b). Note that certain paleontologists opt for an intermediary hypothesis whereby the diversity increased over time, but very rapidly (during the Cambrian) and remained more or less stable from then on (Figure 4.2c). It should also be remembered that we are speaking, here, about the diversity of body plans rather than that of species.

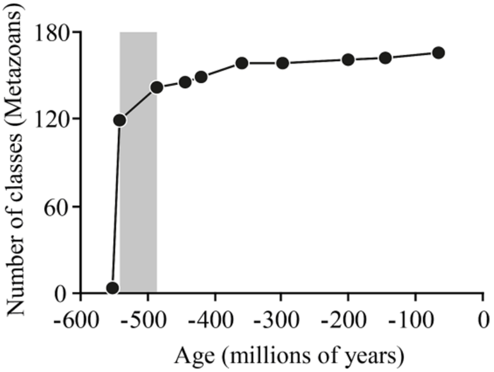


Figure 4.1. *Diversification in the number of classes of animals over the geological ages. The shaded area corresponds to the Cambrian period. The diversification at the Precambrian/Cambrian transition was sudden and spectacular, but thereafter the number of new classes is very low (number of classes according to [ERW 11]; geological ages according to [GRA 12])*

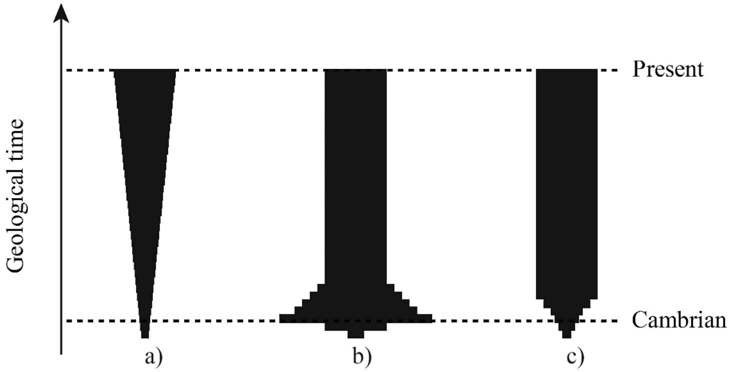


Figure 4.2. *Schematic representation, in the form of spindle diagrams, of the evolution of the diversity of body plans over the geological ages. a) Traditional model of the growing cone; b) inverted cone model (from [GOU 89]); c) tubular model*

4.1.3. *The causes of the Cambrian diversification*

The question of the cause of this major evolutionary radiation is by no means easy to approach. Remember simply that we are talking about events that occurred over 500 million years ago! To simplify somewhat, we can say that there are three categories of possible causes. One pertains to the organisms' environment (the physical, chemical, atmospheric, aquatic conditions, etc.). Another relates to their biological development (their growth). Finally, the third category relates to their ecology: the relations between the different organisms in their environmental context. These three categories are expressed below independently. However, increasing numbers of specialists are arguing for an integrated view of all these causes, which are probably interconnected in reality [SMI 13].

4.1.3.1. *Environmental causes*

The general idea is that the environment (the physical, chemical, atmospheric, aquatic conditions, etc.) favored the development of diversified and large lifeforms. The important factors cited by researchers specializing in this area include:

– the increase in the amount of oxygen in the atmosphere. This would have encouraged the emergence of large organisms, unlike in periods of low oxygenation, which would have prevented such organisms from being able to exist. In truth, this hypothesis is very difficult to verify, because we have an imperfect understanding of the minimum degree of oxygenation that would, theoretically, have been necessary for the development of the first animal lifeforms, and the chronology of the oxygenation of the Earth's atmosphere also remains unclear;

– the end of the so-called "snowball Earth" period (for a detailed view, see http://www.snowballearth.org). Between -2.2 billion years and -635 million years, there were various periods when the Earth was completely covered in ice, from pole to pole. What interests us here is the most recent episode – the "Marinoan" snowball Earth. The deglaciation that followed this episode occurred only a few million years before the emergence of the earliest large lifeforms (the Ediacaran biota). This deglaciation will have created the environmental conditions favorable for the diversification of the metazoans;

– the discovery of a chemical anomaly in the carbon contained in the rocks at the Precambrian/Cambrian transition. We interpret this type of anomaly as revealing a major disturbance in the environment – particularly the carbon cycle. This would have been a drastic environmental change, leading to a mass extinction. The Ediacaran biota would then have been exterminated, giving way to the innovations experienced by the Cambrian animals. This elegant explanation does not account for everything that we observe at this point of transition. In particular, it does not explain why life became so diversified after this point.

4.1.3.2. *Developmental causes*

These causes refer to the means of biological evolution, and more specifically to the development (growth) of the organisms. The most surprising point with which we are confronted is this extraordinary (in the original sense of the term – i.e. not ordinary) increase in the anatomical diversity of the organisms. As just mentioned, environmental effects alone can hardly account for this increase. The developmental hypothesis is based on scientists' discovery of the rules of construction in metazoan organisms with bilateral symmetry (the "bilaterians"). These rules are determined by homeotic genes, also known as architectural genes (the well-known *Hox* genes, which control the body plan along the anterior-posterior axis, offer a good example). We call them architectural because they are responsible for the general body plan of an organism. Simply put, this type of gene ensures that our organs are expressed in the right place in the body! Numerous experiments attest to this fact: altering these genes can lead to architectural defects – e.g. with legs being formed in place of antennas in *Drosophila* (fruit fly). Based on these fairly recent demonstrations, the developmental cause of the Cambrian radiation simply means that the constraints imposed by these genes were less stringent during the Cambrian than they now are, which facilitated the expression of numerous different anatomical paths. With time, these constraints are believed to have intensified, so that it became increasingly difficult to deviate from them. Therefore, it would no longer be possible (or at least extremely difficult) to create a new body plan. In fact, this new body plan is perfectly possible in theory and indeed in practice, but would be immediately eliminated by natural selection, so would have no chance of naturally being expressed in nature.

Recently, researchers have proven that this genetic organization of bilaterians (i.e. the presence of homeotic genes) greatly pre-dates the Cambrian radiation. Hence, it is not so much the presence of these architectural genes as alterations in their expression which may have led to the anatomical explosion observed at the very beginning of the Cambrian.

4.1.3.3. *Ecological causes*

We use this term to denote the causes which may apply if we consider the organisms in their living environment: both their biotic environment (the other organisms with which they coexist) and abiotic environment (the conditions in which they live). In order to understand these causes, it is necessary to use the concept of an ecological niche. Whilst its definition remains variable, it is nonetheless possible to intuitively understand essentially what an ecological niche is: it is a species' habitat and the relations between that and the other species present – e.g. in a food chain. In the case of the Cambrian radiation, the development of mineralized parts (or more generally biomineralization) may have given rise to significant alterations in the trophic relations. Animals capable of growing external skeletons could thereby protect themselves from their predators and, in turn, the predators would have to be inventive in order to be able to continue to hunt. In addition, those which were capable of colonizing the water column to achieve pelagic life would thus be protected against the benthic predators that ruled the sea bed. Conversely, certain organisms would develop the ability to live in the sediment on the sea floor. These endobenthic organisms developed mainly at the start of the Cambrian. The direct effect of their way of life was a mingling of the sediments of the sea bed: that is, they caused bioturbation. This colonization is known as the agronomic revolution (see [BOT 00]), in reference to the effects of human agriculture on soils. There again, the vertical colonization of the muddy sea bottom will have altered the trophic relations between organisms.

In summary, the various species seem to play "cat and mouse": they observe one another, and develop their own innovations in response to the innovations made by others (more specifically, natural selection favors those individuals which are best adapted to deal with the innovations of the other species with which they coexist). Assuredly, this is a major cause of anatomical innovation. In other words, the Cambrian radiation period saw the establishment of ecological niches in the context of an “ecological void”, where each individual took their place in a habitat and in the context of a trophic relation. Consequently, once all of these relations between organisms were established, it would be extremely difficult to find a new place in the ecosystem. In the view of certain paleontologists, this accounts for the near absence of major anatomical innovations since the Cambrian (see Figure 4.1).

We can easily see, here, that the three causes of the Cambrian explosion, far from contrasting with one another, are closely linked. The reasons for this Cambrian explosion, therefore, are probably a mixture of environmental, developmental and ecological effects.

4.1.4. ***Areas of uncertainty***

At the end of the symbolic episode *The Return of the Jedi*, released in 1983 bearing the number VI in the *Star Wars* cinema saga, we discover the true identity of Darth Vader – Luke Skywalker’s father. However, it was only with episodes I, II and III, the last of which (*The Revenge of the Sith*) hit theaters over 20 years later in 2005, that we truly come to understand his human story with the name Anakin Skywalker, his Jedi training, and his troubled destiny. Much like this space opera, our paleontological saga (of the Cambrian explosion) plays on the geological ages and the dates of paleontological discoveries. The story starts in 1909, at Burgess in the Cambrian, but the events that precede Burgess – e.g. the existence of the Ediacaran biota – would not be discovered until much later (around the end of the 20th Century). However, it is crucial to understand that biota in order to be able to examine the Burgess Shale in its historical context, just as episodes I, II and III of *Star Wars*, released recently, are crucial to understand episodes IV, V and VI, released so many years before. Also, just like *Star Wars*, the Cambrian explosion is littered with characters and events which also have areas of uncertainty – e.g. the strange taxa found in the Cambrian. The characters need to be illuminated by new episodes in the saga so that we can truly understand their importance. Undoubtedly, new discoveries will help us to gain a clearer picture of the events of biodiversity that took place around that time. Let us say that whilst numerous episodes of the paleontological saga have already been released, we are still missing two or three to perfect our understanding of the Cambrian explosion. Amongst these areas of uncertainty, there are two that are particularly worthy of attention – likely starting points for new episodes in the paleontological saga:

1) *Is the diversification of body plans in the Cambrian an optical illusion?* As we have seen, the striking point about the Cambrian explosion is the emergence of diversified animal life. This demonstration is based on the counting of body plans (see Figure 4.1). In the view of certain scientists [LEV 08], paleontologists have fallen into a trap: that of labeling every strange, new fossil they find as representing a new, previously-unknown body plan. The consequence of this would be an artificial inflation of the biodiversity at the start of the Cambrian. When these strange animals are re-evaluated, some see them, in fact, as a mixture of derived and ancestral organisms of the main anatomical groups known later on. The existence, at the same moment in geological time, of organisms exhibiting ancestral body plans with others whose body plan is more derivative is completely normal. This does not mean that these derived and ancestral organisms emerged at exactly the same time. In the biodiversity of the world today, the group of cephalopods, which we briefly mentioned in Chapter 3, includes both derived forms (whose body plan is recent) such as cuttlefish, and ancestral forms such as the nautilus, whose body plan has been in existence for at least 450 million years. It is possible that the same was true in the Cambrian, with some of these strange forms potentially being ancestors of groups that emerged later on. They have certain features that are similar to these subsequent groups but which may have been underestimated in our analysis, and others which the line would lose later on but whose originality would have had us scratching our heads. If paleontologists have actually fallen into that trap, then the biodiversity from the start of the Cambrian would be less than we believed it was. The likely model of evolution of biodiversity at the Precambrian/Cambrian boundary would, undoubtedly, be an increase, but only up to a level comparable

to (not greater than) that which would prevail later on (model C in Figure 4.2);

2) *Is the geological age of the fossils the geological age of the radiation*? This question touches on the problem of sampling of the fossil record – a topic which we discussed in Chapter 2. Paradoxically, it is by genetic analysis that the fossil data come to be criticized! This is a paradox because today, our scientific methods are unable to find the genetic characteristics of the animals that lived in the Cambrian, as their DNA is not preserved. Without going into too much detail, let us simply acknowledge the work of the geneticists. They developed a method for analyzing the rate of genetic mutations undergone by modern organisms (i.e. those which are alive today), which enables them to calculate the probable geological age of the common ancestor of two modern species. This method, known as the molecular clock method, is not entirely immune from bias – particularly because the rates of mutation vary over the course of geological time. Nevertheless, it does provide interesting input into the debate concerning the Cambrian radiation. If we accept the hypothesis upon which the method is founded, we discover that the ages of appearance of the major body groups in the fossil record are always more recent than the ages determined by the molecular clock technique. In other words, if the molecular clock is correct, the taxa found at the start of the Cambrian have ancestors from before the Cambrian – i.e. in the Precambrian. The Cambrian radiation would, in fact, be Precambrian! Let us remain optimistic about the paleontological data. The most recent and robust estimations provided by the molecular clock finally show (after publications of much more ancient ages resulting from incorrect calibration of the tool) that these ancestors would have a geological age corresponding to the advent of the Ediacarian biota (around -575 million years – see section 4.1.1). Thus, we have a temporal hole of around 30 million years – a period which is disconcertingly long in relation to our own human history, but is relatively short in relation to the age of the Cambrian explosion. However, the very-numerous samples taken in the field have never confirmed the presence of diversified fauna of marine metazoans in the Precambrian. It is unlikely that we have simply missed it, as paleontologists so relentlessly search for it in the field. It is much more probable that if the taxa did already exist at this point, their

ability to biomineralize would come much later, near to the Precambrian/Cambrian boundary. Thus, before that boundary, fossilized remains are rare because the organisms did not have a skeleton that could be easily fossilized. The Cambrian explosion would then reflect the explosion of skeletons or tests constructed by groups of organisms which had already coexisted for several million years.

Finally, what conclusion can we draw for our paleontological saga? We know that the Cambrian explosion pertains to animals: this was assuredly an evolutionary radiation. Taking place around 540 million years ago, it is characterized by the establishment of numerous body plans. It is then that the typical organization (which is still in place today) of relations between organisms was established, with each organism being woven into a particular environment and a food chain. However, this saga still has some surprises in store for us. Its exact chronology, and its extent in terms of invention of new body plans, are two examples of this.

4.2. Cascaded radiations: the case of ammonites

If we had to choose only one group of organisms for which evolutionary radiations have been fundamentally important, it would be the group of ammonites (see Figure 2.1). The history of these marine mollusks is marked by alternating extinction and radiation events. Compare the spindle diagram of the ammonites (Figure 4.3) to that of birds (Figure 2.8(b)) or that of teleostean fish (Figure 3.4). What is particularly striking is the lack of regularity in the ammonites – they were a group with which something was always happening! Sometimes the number of families was high (around -370, -250 or -110 million years). These moments of significant biodiversity were interrupted by sudden bottlenecks (reductions in biodiversity) that mark extinction episodes. The last of these events – the Cretaceous/Tertiary mass extinction – was absolutely fatal for them: at this point, the ammonites died out, leaving no descendants.

Ammonites were cephalopods with a chambered outer shell. The smallest adult specimens have a shell measuring five millimeters in diameter; the largest known to date had a diameter of around two meters. There is no doubt that they are linked to present-day cephalopods. One such modern cephalopod (the nautilus) has a shell that is, anatomically, very similar to that of the ammonites. Other modern cephalopods (such as ram's-horn squid and cuttlefish) have embryonic shell structures (i.e. the structure of the shell that forms initially when the animal is in the embryonic state) which are remarkably similar to those of the ammonites. Analysis of the ammonites' morphological features – particularly their embryonic features – and comparison with those of the cephalopods of today, shows that the ammonites were more closely related to present-day coleoidea (squid, cuttlefish and octopuses) than to the nautilus. Ammonites also have anatomical features that are unique to them (once again, elements of their embryonic shell) that distinguish them from other cephalopods. Therefore, they constitute a clade.

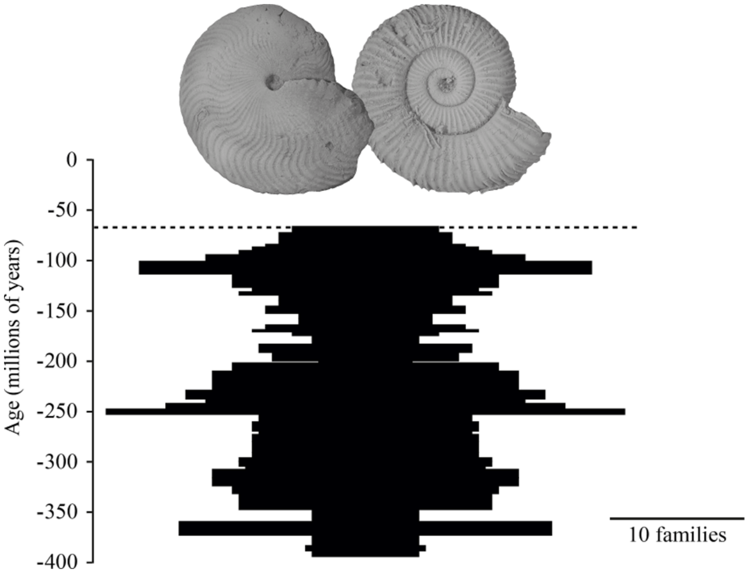


Figure 4.3. *Evolution in the number of families of ammonites over the geological ages, presented in the form of a spindle diagram (number of families according to [BEN 93], geological ages according to [GRA 12]). The dashed line indicates the Cretaceous/Tertiary mass extinction event, which saw the total extinction of the ammonites. Illustrated specimens: see Figure 4.5(e) and 4.5(c) (photos by P. Neige)*

By these phylogenetic links, and also by a number of very well preserved fossils, we can reconstruct an image of what this now-extinct animal may have looked like. In terms of an outline, imagine a squid in a shell. This external shell plays the double role of a buoyancy system and protection against predators. The fossil record of ammonites is very well known – firstly because the fossilized specimens are abundant, and secondly because they are frequently used for dating of sedimentary rocks. We mentioned this earlier (in section 2.2): thus, they have been extensively studied. Hence, our databases on the ammonites are excellent! Here, we shall look at just two examples of evolutionary radiations in the ammonites. The first took place 250 million years ago; the other, more recent, 175 million years ago.

4.2.1. *A post-extinction radiation: the example of the Permian/Triassic boundary*

With an estimation of around 90% of marine species and 70% of land-dwelling species wiped out, the Permian/Triassic mass extinction sounds like a frightful example of reduction in biodiversity. It is even greater than the extinctions recognized throughout the rest of the geological ages (see Figure 1.2). The ammonites were particularly badly affected by this event. In 2008, the British paleontologist Michael J. Benton (who created the historic paleontological databases – see section 2.4.2.1) devoted a whole book to the event, with the evocative title: “When Life Nearly Died” [BEN 08]. What interests us here is not so much the mass extinction as the events which followed in its wake. How did the Earth’s biodiversity recover after such a major extinction? Slowly? With difficulty?

At the end of the Permian (and the end of the Paleozoic – see Table A.3), i.e. just before the mass extinction, all the continental landmasses were grouped together in a single “super continent”: Pangea, surrounded by an immense ocean – Panthalassa. The land was populated by tetrapods: amphibians with varying degrees of specialization and numerous amniotes of variable size. Mammals, for their part, did not yet exist. Alongside the vertebrates lived varied arthropods and plants – particularly conifers (flowering plants had not yet appeared – see section 4.3). The biodiversity of marine animals essentially comprised cephalopods (ammonites and nautiluses), brachiopods (benthic filter-feeders with a shell, composed of two valves), crinoids (echinoderms with a stem, one side of which was anchored in the sediment and the other was connected to a calyx with arms), coral, ostracodes (small crustaceans that live between two valves, which they secrete), vertebrates (we find numerous agnatha – jawless fish – sharks and others teleostean fish), or foraminifera (single-celled animals that secrete a calcified test that is often fossilized), such as fusulinids, which would die out totally in the Permian/Triassic mass extinction. Aside from the organisms present, marine biodiversity at the end of the Permian was characterized by the frequent presence of reefs, which gathered varying quantities of all sorts of organisms such as sponges, algae, bryozoans and of course, corals, though these specimens were quite far removed, morphologically speaking, from the corals found today.

The French paleontologist Arnaud Brayard and his colleagues carried out a detailed study of the phenomena that affected the ammonites during this extinction event [BRA 09]. The originality of their work lies in the conducting of numerous studies in the field, and in the construction of a new paleontological database with excellent temporal calibration. The database catalogs, the FAD and LAD, of all genera of ammonites collected in 77 sedimentary basins for 25 time slices of varying duration, but all calibrated by a numerical age (expressed in millions of years). The study extends from around -300 million years (at the end of the Carboniferous, a little before the Permian – see Table A.4) to -200 million years (near the very end of the Triassic). In other words, it is a precise analysis of a total period of 100 million years. Therefore, it is a prime-quality sample of the fossil record, which enables us not only to examine the mass extinction events (situated at -252 million years) but also – and it is here that the study makes its true impact – those of the post-extinction evolutionary radiation.

In ammonites, the Permian period was characterized by several oscillations in the number of genera, ranging between 30 and around 70 (Figure 4.4). The Permian/Triassic mass extinction is clearly marked, by a very stark decrease in the biodiversity of the ammonites, which dropped to less than ten genera. What happened next is truly surprising. Evidently, after such a decrease, but in the absence of a total extinction, the ammonites had ample chance to recover their level of biodiversity. However, this recovery – this evolutionary radiation – is particularly important for three reasons:

– the level of taxonomic diversity achieved at the end of this radiation, following the phase of post-extinction recovery (see section 3.2.3), massively surpassed that which was present before the crisis, with over 100 genera in the different sedimentary basins. This demonstrates that the biodiversity of a group of organisms (here the ammonites) after their recovery phase can be higher than the initial level recorded before a major mass extinction event;

– the rate of post-extinction recovery is far, far greater than that which was traditionally envisaged. Often, paleontologists believed that these recovery phases were slow. In the case which interests us here, certain paleontologists estimated a period of around five million years. The study to which we refer here shows a far shorter recovery period. This recovery occurred in the space of, at most, two million years (Figure 4.4). This is a long time in respect of our human history, but is very short in terms of the macroevolutionary events of such amplitude;

– the post-extinction recovery pertained to a single phylogenetic group of ammonites, called Ceratitina. These ammonites, which are recognizable by the shape of their suture line, exhibit very great shell diversity in the Triassic. They first appear in the fossil record at the end of the lower Permian. For 20 million years, they remained fairly low-key in terms of biodiversity, with at most 20 genera in the different sedimentary basins throughout the world. Although other groups of ammonites perished in the Permian/Triassic mass extinction, Ceratitina suddenly diversified just after this extinction, experiencing this major and rapid evolutionary radiation from the start of the Triassic onwards.

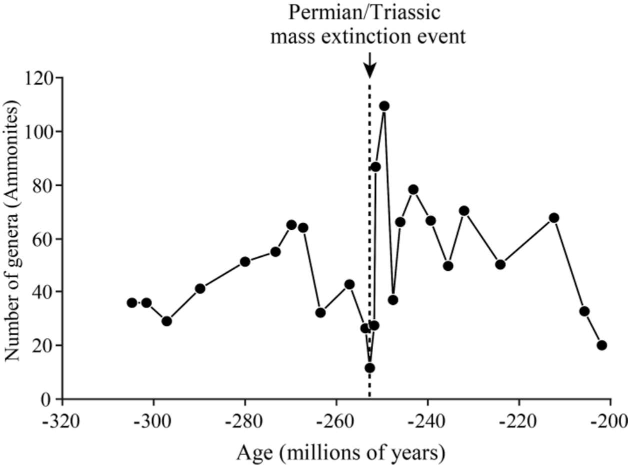


Figure 4.4. *Evolution in the number of genera of ammonites over the geological ages (number of genera and geological ages modified from [BRA 09])*

This post-extinction radiation teaches us a great deal about the way in which biodiversity works. To begin with, a group of organisms may exhibit modest diversity for a portion of their history, and then become hugely diversified (that is what is at the very heart of this book: evolutionary radiation events) and largely dominant, owing to an event independent of their history (here a mass extinction). Let us return to the image of the story of biodiversity resembling a piece of theater (see Chapter 1). Here, we see a change in the billing of the actors on the scene: an actor who played only a small role before the mass extinction becomes the lead actor in the subsequent part of the story. In addition, a post-extinction evolutionary radiation may be particularly quick. The intensity of an extinction, therefore, tells us nothing about the rate of post-extinction recovery. The fact that a mass extinction event is particularly potent does not necessarily mean that the ecosystem will take a long time to recover from it.

4.2.2. *An adaptive radiation: the example of the lower Jurassic*

The second example discussed here involves the same group of organisms (ammonites), but this time at the Lower/Middle Jurassic boundary – around 75 million years more recent than the Permian/Triassic extinction event we have just examined (in section 4.2.1). Between this extinction and the lower Jurassic, ammonites went through a second major extinction (at the Triassic/Jurassic boundary, 201 million years ago), followed by a second-order mass extinction (the so-called lower Toarcian extinction, at -182 million years). Our new story begins just after this extinction.

In a recent study that I conducted with two other paleontologists [NEI 13], we examined the history of the ammonites in the lower Jurassic. Unfortunately, it was not possible to use numerical geological ages (in terms of millions of years) throughout our study. Therefore, we used the standard division into chronozones, typically used by paleontologists (see section 2.1). Our study covers the end of the lower Jurassic (nearly all of the Toarcian – see Table A.2) and the very beginning of the middle Jurassic (the base of the Aalenian stage – see Table A.2). We know the total duration (9 million years) and we have a given numerical value for the age, carefully calibrated for the midpoint of the period of interest (-175.6 million years). This period is divided into eight slices of time of varying duration, as the durations cannot be precisely calculated for the moment. To clarify our ideas, let us say that on average, each of them has a duration of a little over one million years (eight slices of time, totaling nine million years). In a database, we cataloged all the species of ammonites known in each of these temporal slices for the various marine deposits of the world, relevant to that epoch. These species exhibit great variation in the shape of their shell (Figure 4.5). The strong point of our study lies in the taxonomic precision used – that of the species – but also in the way in which the data are processed. Indeed, we have studied both the number of species over time for the ten natural groups of that epoch (clades A-J in Figure 4.6) but also their morphological disparity. We saw previously that this morphological component was important in appreciating the different types of radiation. To recap, a high degree of morphological disparity, accompanied by a high degree of taxonomic diversity, is a strong indicator of adaptive radiation (see section 3.2.1).

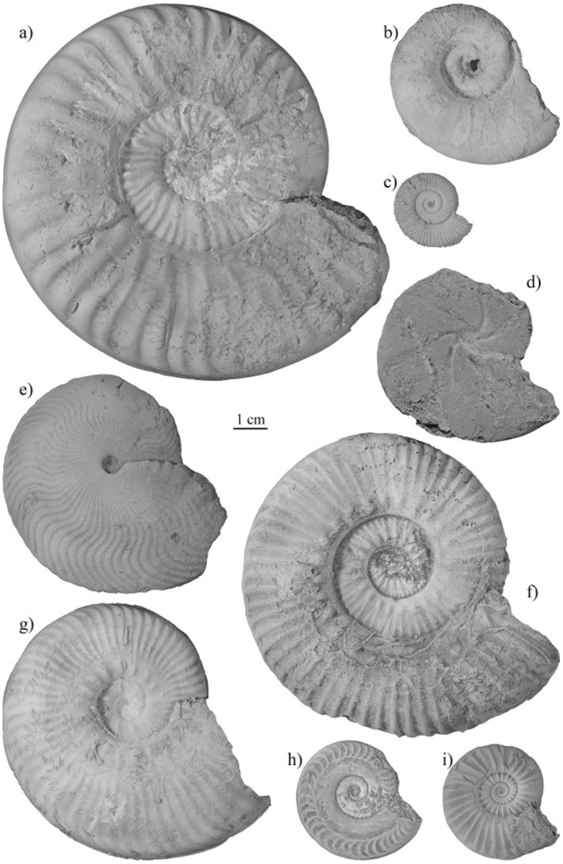


Figure 4.5. *Various ammonite shells from the lower Jurassic: a)* Denckmannia *(UBGD 278904), b)* Lytoceras *(UBGD 278905), c)* Dactylioceras *(UBGD 278906), d)* Calliphylloceras *(UBGD 278907), e)* Polyplectus *(UBGD 278908), f)* Hammatoceras *(UBGD 278909), g)* Haugia *(UBGD 278910), h)* Hildoceras *(UBGD 278911), i)* Dumortieria *(UBGD 278912). P. Neige's collection; various origins (photos by P. Neige)*

The results confirmed some of the predicted points, but also brought some surprises. Overall, the period in question corresponds to an immense change in the ammonites (see Figure 4.6). Most groups were successively extinguished (groups C, D, E, G, H and I). Another clade, which specialists call Hammatoceratidae (in spite of its name, for our purposes, it is group J in Figure 4.6), became largely dominant, increasing from only one species at the start of the period under study to around fifty, only nine million years later. This obviously fits the definition of an evolutionary radiation. Also, this increase in the number of species was combined with an increase in morphological disparity (Figure 4.6). Thus, over the course of its history, group J is represented in the fossil record by increasing numbers of species but also by increasing numbers of different shell shapes. In all likelihood, what we are witnessing here is a case of adaptive radiation. Although we do not yet know the whole story, we can suppose that these species adapted to new ecological surroundings.

One of the major surprises is the story of group C (formally known as Dactylioceratidae). The ammonites in this group are easily recognizable out of all the ammonites present during this period. Invariably, they lack a very specific, characteristic anatomical feature: the keel – a sort of strip or layer of shell in positive relief which, in other ammonites, is situated exactly on the axis of bilateral symmetry. This group is known in fossil records pre-dating our study, but it exhibits particularly impressive evolution during the time period studied here. Starting with a modest number of species (in chronozone t1 – Figure 4.6), this group diversified enormously (in terms both of species and morphology) for the next period (t2). Hitherto, this shows nothing out of the ordinary – simply an indicator of adaptive radiation. Yet the next chapter in the story, which corresponds to the definitive extinction of that group, is surprising. Very suddenly, during period t3, these ammonites were afflicted by a massive extinction of species (their numbers dropped from 62 to 17 species, which represents an extinction rate of over 70%), which had little impact on their morphological disparity (Figure 4.6). After that point, these ammonites disappeared totally without leaving any descendants. Our surprise is easy to understand. In this example, we see the juxtaposition, within a very short period of time (2-3 million years) of two major phenomena in macroevolution: evolutionary radiation and definitive extinction. What is surprising here is the order in which these two events occur: first the radiation and then the total extinction, just afterwards! Remember that, previously – and fairly logically, in the final analysis – for the example of the Permian/Triassic mass extinction event, we observed the opposite order: a mass extinction (but not a complete extinction, otherwise the story would end), followed by the radiation of a group that survived that extinction event. In the case of this group C, the logic is reversed. Also, we can draw an essential lesson from this: an evolutionary radiation does not necessarily ensure a long history after that radiation! Dactylioceratidae illustrate this point perfectly: they died out very suddenly, only a very short time after their radiation.

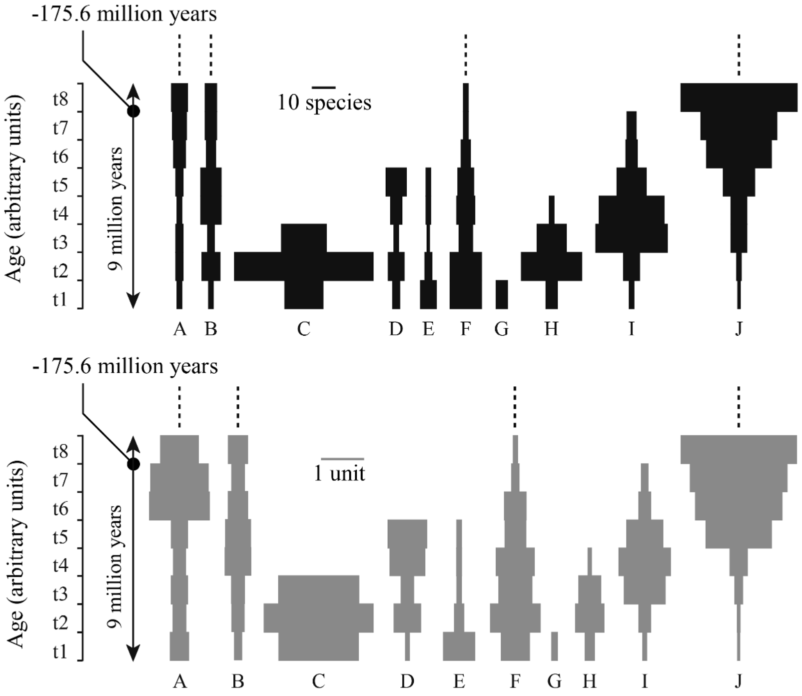


Figure 4.6. *Evolution of the biodiversity of ammonites in the lower Jurassic (ages t1-t7) and middle Jurassic (age t8) presented in the form of spindle diagrams. a) Number of species. b) Morphological disparity (number of species and morphological disparity modified from [NEI 13]; geological dating taken from [GRA 12])*

How, then, are we to understand the differences in the behavior of the two groups we have just studied: group J, which diversifies ceaselessly (both in terms of number of species and morphologies) and group C which, after a period of diversification, died out suddenly, leaving no descendants? This is a difficult question to answer. However, we do have a technique on which to base an investigation. It involves the morphological analysis of the groups of ammonites. As we saw earlier, morphological disparity is a measure of the diversity of body shapes. Between the two clades (C and J) studied here, there is significant morphological disparity. In order to quickly visualize a set of morphologies (e.g. the shape of the shell for each species in groups C and J), we often use a mathematical representation thereof. Let us say simply that having measured certain characteristics of the shell of an ammonite (diameter, aperture breadth, etc.), we are able to simplify it mathematically by reducing it to two or three numerical parameters representing morphological features. Then, it is possible to plot the morphologies (by way of the morphological parameters) in a body form space (a Euclidean space) using more or less complicated statistical techniques (in the case of interest to us here, it is Principal Component Analysis (PCA) which is used).

In order to properly understand this idea, it is necessary to make a comparison. Everyone knows how to read a geographical map. On such a map, you can find, say, the different cities in the region. The closer two cities are on the map, the closer they are in reality too. The same principle applies with a morphological map. Unlike with a geographical map, this space is morphological rather than geographical. In a morphological space, a form of ammonite is marked by a dot. Two dots near to one another indicate morphological proximity; two dots very far apart signify great difference. Dots grouped together in a region of the space share fairly similar morphological features (for a more in-depth comparison, see [DAV 04]). Thus, by constructing the morphological space for the species of ammonites studied, and more specifically, visualizing groups C and J, we can compare them, and easily tell whether or not they resemble one another. The answer (looking at Figure 4.7) is that they do not resemble one another – far from it! Two differences can be noted:

– the absence of involute morphologies (with external curves that overlap greatly with the internal curves of the shell) in group C, whose species remain strictly located in the right-hand part of the morphological space (Figure 4.7c);

– the broader distribution of group J, whose species are located in all quadrants of the morphological space (Figure 4.7d).

In the present case, it seems that the inability of species in group C to evolve to have more involute shell shapes leads them to extinction. On the other hand, the high capacity of the species in group J to evolve in all areas of the morphological space appears to lend them a certain advantage. Yet this explanation is only partial: we do not yet know precisely why certain groups of ammonites are morphologically constrained (group C, for example) but others less so (e.g. group J).

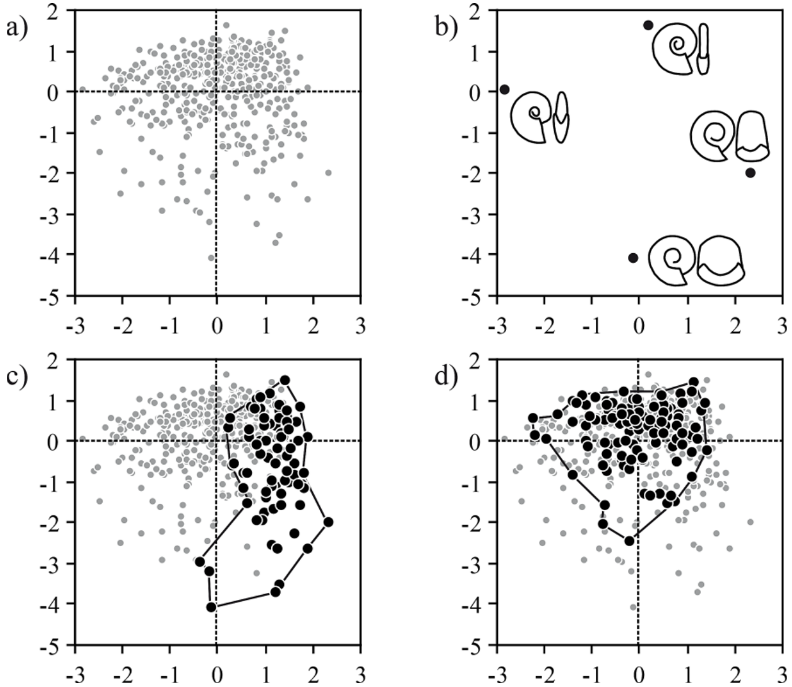


Figure 4.7. *Morphological space of ammonites from the lower Jurassic (modified from [NEI 13], with previously-unpublished data)*

COMMENTS ON FIGURE 4.7.– a) Morphological space of all ammonites studied. The axes represent the morphology of their shells (main components 1 and 2, 82% of cumulative variance). Each gray dot represents a species. The closer two dots are to one another, the more similar are the morphologies of the ammonites that they represent. b) Illustration of four extreme morphologies (lateral view and view of the aperture). The shapes on the right in the morphological space are evolute (the external curves of the shell do not overlap greatly with the internal curves); those on the left are involute (the external curves greatly overlap the internal ones). The shapes at the top are compressed (thin), whereas those at the bottom are depressed (thick). c) Visualization of the morphologies of group C, represented by black dots, all situated on the right-hand side of the morphological space (the gray dots, once again, represent all of the species studied). d) Visualization of the morphologies of group J, distributed throughout the whole of the morphological space (with the gray dots representing all of the species studied).

4.3. Floral success: the emergence and radiation of flowering plants

It is difficult to precisely examine the emergence and radiation of flowering plants. Their fossil record – particularly at the start of their history – is relatively poor, for the obvious reason of their poor ability to become fossilized – at least for the flowers that are characteristic of them. For example, “The Fossil Record 2” database [BEN 93] (see section 2.4.2.1) catalogs 259 families of angiosperms today. Only 154 of those (i.e. only 60%) have a proven fossil record – a record for which we have elements to prove their existence in the past. The 105 other families in that database are only known today. Two interpretations are open to us. The first is to consider that the 40% of families of angiosperms for which there is no fossil record have appeared very recently. The second is to consider that the database is incomplete. All specialists in the field are in agreement as to the second interpretation.

The fossil record of flowering plants is, indubitably, incomplete. Yet there can be no question of omitting this example from a book on evolutionary radiations in the fossil record. They were the last major group of plants to have emerged over the course of the geological ages. For many, this even represents one of the rare cases of emergence of a major body plan, relatively late on, in terms of the whole history of biodiversity. Opinions vary (see below) as to whether it was the middle of the Triassic or the start of the Cretaceous (i.e. between -225 and -140 million years), but in all cases, the proposed date of emergence is much later than the last major event for animals. Remember that nearly all groups of animals have been known since the Cambrian, around -500 million years (see Figure 4.1). This case of the evolutionary radiation of flowering plants is a real triumph. In today's world, there are no less than 270,000 species (some estimates suggest up to 400,000), spread throughout all living environments: land, freshwater and marine. They come in a variety of shapes and widely varying sizes. The number of species is comparable to that of pteridophytes (which include ferns): about 10,000 species, or gymnosperms (which include pines): about 1,000 species – though these two groups of plants are far more ancient. Several paleontological discoveries made over the past fifteen years offer us a clearer view of the emergence, evolutionary radiation and colonization of environments by flowering plants.

4.3.1. *In search of the first flower*

Flowering plants (also called angiosperms or Magnoliophyta) constitute a natural group (a clade), as is attested by molecular and anatomical arguments. The most emblematic anatomical feature is the presence of a flower that contains the plant's reproductive organs. There are various solutions available for scientists to address the question of the age of the first flowering plants and, thus, to study their initial evolutionary radiation. Paleontologists base their arguments on fossilized remains (see [WIL 14] for a fuller discussion). Depending on the anatomical trait examined – pollen grains, leaves or even flowers – the interpretation is more or less open to debate. The age often put forward for the origin of flowering plants, at -125 million years, is supported by fossils of excellent quality, found in exceptional deposits in Liaoning Province in China. This was where the fossils of the genus *Archaefructus* – a small herbaceous freshwater plant, with dissected leaves, whose flowers were probably the only part protruding from the water – were discovered. This deposit (a *Lagerstätte*) has yielded a number of fossils of exceptional quality, including – amongst other organisms – insects, birds, feathered dinosaurs (see section 1.2), mammals, and also these flowering plants called *Archaefructus*. It was only in 1998 that a Sino-American team offered the first description of *Archaefructus* [SUN 98]. This genus is now known for three species which exhibit a few anatomical differences, all three of which show anatomical features typical of angiosperms – notably the presence of two types of fertile flower parts: carpels (female reproductive organs) and stamens (male reproductive organs). In numerous angiosperms today, the carpels are fused together to form the pistil. The title of Sun *et al.*'s article is explicit: "In Search of the First Flower: A Jurassic Angiosperm, *Archaefructus*, from Northeast China" [SUN 98]. However, the reality does not quite correspond to this title.

Early on, it was demonstrated that the deposit containing these fossilized remains dates from the start of the Cretaceous, around -125 million years, rather than the Jurassic as initially supposed. The taxonomic position originally proposed for *Archaefructus* is also subject to caution, because that fossil has a number of peculiar differences in comparison to the typical flowering plants of today. In particular, *Archaefructus* does not have sterile external parts (petals and sepals). The interpretation of the structures growing on the germinative axis of the plant (the part that has the reproductive organs) is being debated amongst paleobotanists. The debate relates to what a novice might call small anatomical details; in fact, it is not quite so simple! Not only do we need to recognize these details on 125 million year-old fossils, we then need to attach meaning to them – i.e. interpret them in relation to the details observed in flowering plants today. Here, we shall not go into the finer details of these interpretations, but it is necessary to linger over a few elements that are crucial to the understanding of this debate, and thus appreciate the different possible solutions for the phylogenetic position of *Archaefructus*. The dating of the origin of flowering plants partly depends on this! One of the points of disagreement is how to interpret the absence of bracts in *Archaefructus*. In angiosperms, bracts are typical anatomical elements, located between the leaf and the flower, which sprout at the joint between the flowers and the stem. These bracts have the shape of a leaf or a petal, and may play a protective role. Sometimes they have spectacular shapes. If you have ever eaten artichokes – at least the part that we tend to call the leaves or the petals – then you know what bracts are. In actual fact, the part that we eat is neither leaves nor petals, but bracts!

The first interpretation of *Archaefructus* proposed a distribution of the (distal) carpels and the (proximal) stamens along the length of the stem. One of the peculiarities of this plant is the absence of bracts associated with the elements or carpels or stamens. According to this interpretation, based on the absence of bracts, the germinative axis of *Archaefructus* corresponds to a single, bisexed flower, but divided into several parts, and nude (i.e. without petals and sepals). In the view of the authors of this interpretation [SUN 98], each separate part cannot be a flower, because it does not have a bract. This genus could, therefore, represent a particular line that is at the basis of the group of flowering plants. *Archaefructus* would be what we call a “sister group” to the angiosperms, i.e. it would not be an angiosperm in the strict sense, but a sort of close cousin – a good representation of the ancestral group of the angiosperms. In other words, *Archaefructus* and all the angiosperms would possess a coming ancestor. However, this interpretation of the fossil remains is not the only possibility. In the eyes of other specialists [FRI 06], the germinative axis is a bisexed inflorescence (a set of flowers) made up of unisexed and nude flowers: flowers with pistils (female parts) on the distal part of the axis, and others with stamens (male parts), in a more proximal location. For them, the absence of bracts cannot be a deciding factor in the interpretation: *Archaefructus* could have lost its bracts secondarily, just like some of the angiosperms in today’s world – proof of adaptation to an entirely aquatic way of life. This interpretation as an inflorescence greatly alters the phylogenetic position of *Archaefructus*, which then becomes a member of the angiosperms in its own right, a close relative to the group of nympheas, at the base of the phylogeny of the angiosperms, including water lilies amongst other plants that we know today. In another species of the genus *Archaefructus*, between the distal area with carpels and the more proximal area with stamens, paleobotanists have been able to demonstrate the presence of a small bisexed flower, again without a bract, comprising two carpels and a stamen [QIA 04]. This discovery, along with other anatomical elements, does not resolve all of the phylogenetic uncertainties relating to *Archaefructus*, but it favors a position within the clade of angiosperms, unlike with the initial interpretation, which proposed a more ancestral position. Depending on whether we take one or other of the interpretations, therefore, the date of origin of the angiosperms is variable – around -125 million years, or a little more recent, in the case of an interpretation of *Archaefructus* as a sister group to the angiosperms, or over -125 million years, with no exact date as to when, if *Archaefructus* is interpreted as being close to nympheas. Indeed, if *Archaefructus* is an entirely separate angiosperm, then the origin of the group pre-dates it by quite some way.

Besides the fossilized remains of flowers, by analyzing fossilized grains of pollen, we are able to propose different ages for the origin of the angiosperms. The oldest proven angiosperm pollen dates from the Valanginian (at the start of the Cretaceous – see Table A.2), around 139 million years ago.

Quite apart from the debates about the fossilization of flowers and the interpretation of the anatomical details, genetic analyses suggest ages of the origin of angiosperms by the molecular clock method (see section 4.1.4). This method, which enables us to calculate numerical geological ages for the common ancestor of two taxa known today, thus provides some additional input into the debate concerning the origin of flowering plants. According to the methods and phylogenies used, the ages proposed and argued range between -240 million years (marking an origin from the middle Triassic – see Table A.3) and -150 million years (for an origin at the end of the Jurassic – see Table A.2). In a very exhaustive study published recently, using the molecular clock method, Bell and his collaborators proposed a date of origin between -199 and -167 million years [BEL 10]. This proposal deviates somewhat from the ages determined by the fossil record, by at least 30 million years (-139 million years for the most ancient pollen). However, the dates proposed by [BEL 10] for multiple lineages of angiosperms are fairly close to those given by the fossil record for those same lineages. This convergence is encouraging. Note, however, that a study published in 2014 proposes more ancient origins, between -240 and -225 million years (in the Triassic), with a date of diversification of the Mesangiosperms (a clade including almost all the angiosperms alive today) in the middle or upper Jurassic [ZEN 14]. Although very significant progress has been made in the past 20 years, it is indisputable that there is still an unknown area in the exact chronology of the apparition and diversification of these flowering plants.

4.3.2. *Radiation and dominance of angiosperms*

The first plants that were adapted to life on land (we speak of the terrestrialization of plants, in contrast to aquatic life) date from the middle Ordovician (around -470 million years). They are known only by the presence of sorts of pods containing one, two or four spores. The first complete fossils of terrestrial plants are somewhat more recent, dating from -425 million years. As we have seen, flowering plants appear in the fossil record around -139 million years, i.e. nearly 330 million years later. Thus, they came to exist in a world that was already largely colonized by other plants. Nevertheless, they would diversify at an incredible rate.

There are relatively few studies in the specialized literature that enable us to track the number of species (or of any other taxonomic rank) of flowering plants. As we have seen, their fossil record must be viewed with circumspection. Certain authors have offered analyses of the fossil record of plants (all groups included) which enable us to examine their evolution on a large scale, but they too stress the still-incomplete nature of the available data [NIK 94]. In the specific case of angiosperms, the study by Lidgard and Crane, published in 1988 [LID 88] is able to trace some general outlines (Figure 4.8). In their study, only the remnants of macrofossils are considered. The more ambiguous fossils, remnants of wood, roots, or remains whose taxonomic attribution is uncertain, are excluded from the analysis. Although, even in this case, the fossil record needs to be examined with caution, we can draw two informative elements from this study (see Figure 4.8):

– the major increase in the number of species of angiosperms from about -100 million years (i.e. at the start of the upper Cretaceous);

– the inversion of the dominance in more or less the same age between angiosperms and other plants: they became more varied (in terms of the number of taxa) than all the other plants.

Thus, in only a few million years since their first appearance in the fossil record, angiosperms have diversified greatly. At the start of the Cenozoic (-66 million years), they would be dominant in nearly all environments, and present over a vast geographical area. This represents a typical example of evolutionary radiation!

4.3.3. *Why such success?*

Understanding the precise reasons for such evolutionary success remains a complex exercise, and there are many competing hypotheses. An important point to be resolved is the specification of the appearance of the earliest flowering plants, as well as their living environments. Today, specialists believe that the first flowering plants were probably herbaceous (rather than arborescent) in form, with an aquatic mode of life. The arguments employed to justify this point of view are various. For example, the theory’s proponents point to the rarity of fossilized remnants of angiosperm wood from the start of the Cretaceous, whereas the fossil traces of gymnosperm wood are common, which indicates originally herbaceous forms. In addition, the fossilized remains of the leaves of the earliest flowering plants are small in size, which is indicative of herbaceous plants with a rapid lifecycle. These observations concur with the hypotheses of phylogenetic relations based on molecular analyses, showing that the groups present today that are closest to the earliest flowering plants – e.g. nympheas – are aquatic.

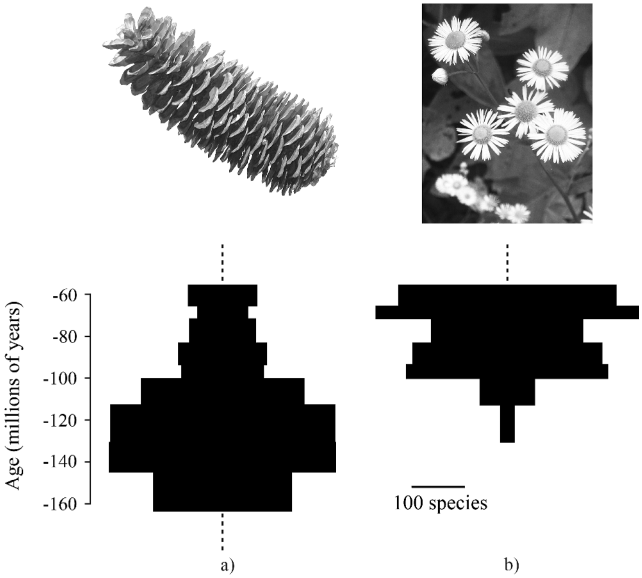


Figure 4.8. *Evolution of the biodiversity of plants over the course of the geological ages, presented in the form of spindle diagrams. a) Number of plant species with the exception of flowering plants. b) Number of species of flowering plants (modified from [LID 88], geological ages according to [GRA 12]). Specimens illustrated: cone of a conifer, photographed in Yosemite National Park, USA; flowers of angiosperms, photographed on the island of Hokkaido, Japan (photo by P. Neige)*

Aquatic and herbaceous in origin – however, how are we to account for the phenomenal radiation that has led to clear dominance of angiosperms (in terms of number of species)? The answer appears to be linked just as closely to the characteristics of these plants as it is to those of the gymnosperms, which were dominant to begin with. To make things a little more complicated, it is likely that organisms connected to these plants (such as pollinating insects) also had a role to play. For the sake of ease, here we shall discuss a few of the factors that have been put forward as being responsible for the evolutionary radiation of the angiosperms (environmental, ecological and climatic factors). The most recent studies, though, tend to support the combination of various explanatory factors, rather than the dominance of only one [AUG 14].

For certain scientists, this major change (this major evolutionary radiation) is the result of positive feedback between angiosperms and environment. To sum this hypothesis up in simple terms, suffice it to say that angiosperms form litter that produces nutrients which can be more easily reused for the development of the next generation of plants (gymnosperms, for their part, do not produce this favorable litter). Coupled with their faster growth rate, the ready supply of nutrients would be a crucial element for angiosperms to colonize and soon come to dominate numerous ecological media. In the eyes of other specialists, the radiation was caused by the variation in the level of CO_2 in the atmosphere (we speak of the partial pressure of atmospheric CO_2), which was originally very high at the start of the Cretaceous (around eight times higher than it was before the industrial development of the modern world), and dropped later on. This decrease in the level of CO_2 would have created arid environmental conditions – at least during certain periods of the year. In the view of Jennifer McElwain and her collaborators [MCE 05], angiosperms, because of their anatomical organization – especially their water transport system – would be better adapted to these harsher conditions (particularly in the case of limit water supply) than gymnosperms. Other specialists espouse the hypothesis that more frequent fires played a part. With the drop in the level of atmospheric CO_2 during the Cretaceous, and the accompanying increase in oxygen levels, fires would occur more frequently on the landmasses. In these authors' view, angiosperms encourage fires (by their production of flammable biomass) and would, in return, have an advantage after fires, because of their excellent capacities for colonizing environments (by their rapid reproduction). At the opposite end of the scale to this hypothesis of fire, some lend importance to the role of cold events recently discovered to have taken place during the Cretaceous. Once again, the hypothesis is founded on the fact that angiosperms are better adapted to these conditions than gymnosperms, and once again, everything hinges on the water transport system in flowering plants in these extreme living conditions.

Finally – and this will be our final case study of the likely cause (although of course there are others in the literature in the field), certain authors associate the radiation of angiosperms with pollinating insects. This is the hypothesis of a coevolution between flowering plants and insects. There are many arguments to suggest that the earliest angiosperms were insect-pollinated (the alternative would be wind pollination): presence of stamens with short anthers (the anthers are the end parts of the stamens, which produce the pollen), relatively large pollen grains, relatively low number of grains of pollen, etc. This hypothesis of the role of insects is also based on the comparison of the fossil records of angiosperms and insects. If the hypothesis is true, then the association of insects and angiosperms must be beneficial for both protagonists – in other words, the coevolution must encourage a "co-radiation". Therefore, we should observe a radiation in the insect kingdom alongside that of flowering plants. However, just as the fossil record of angiosperms is far from perfect (they do not easily fossilize), that of insects is little better, which renders the comparison tricky at least! Nevertheless, there are a few interesting points for comparison [LAB 93]. Certain groups of pollinating insects (hymenoptera and lepidoptera) show radiation that is in general synchrony with that of the angiosperms. Others (coleoptera and diptera) exhibit diversification beginning earlier than that of the angiosperms, sometimes with adaptations for pollination that even pre-date the origin of the angiosperms. These cases are interpreted as adaptations to allow the insects to feed on gymnosperms. More worrying still, the number of insect families over the geological ages has been increasing almost constantly since the Triassic, after the Permian/Triassic mass extinction (see section 3.2.3), with the notable exception of the middle of the Cretaceous – the moment when the angiosperms experienced their radiation [LAB 93]. Thus, this idea of a "co-radiation" is far from being proven beyond a doubt. However, it does seem fairly certain that insects played a part in this major evolutionary radiation of the angiosperms, even though numerous questions still need to be adequately answered.

4.4. Not-so-round sea urchins!

For a non-specialist observer, all sea urchins are round. Their primary characteristic, like all other echinoderms (the group to which they belong) is anatomic organization that demonstrates pentameral symmetry. Sea urchins belong to a class of echinoderms called

Echinoidea. They all live in a marine environment. The five-part symmetry is clearly visible in starfish and brittle stars, but also in sea urchins if we examine their tests carefully. In sea urchins, the term "test" denotes the rigid armor of the organism, which comprises a set of individual calcite plates. Indeed, this armor is not a shell *per se*: it is an internal skeleton (covered by muscles and skin), as is found in vertebrates! This test comprises five sets of four columns of plates arranged alternately: a double column corresponding to the ambulacral area (of which there are five), and then a double column corresponding to the interambulacral area (unsurprisingly, once again, there are five). The ambulacral areas have plates with pores which allow the animal to extrude its podia – small sensory organs that are also involved in other functions, such as locomotion, feeding and respiration. The test of sea urchins is covered with spines, also called radioles, which may be very different in form from one group to another. If you find a sea urchin test without its spines – a so-called nude sea urchin – the outer surface of the test is covered with numerous tubercles that are more or less pronounced (Figure 4.9(a)). They serve as the point of insertion and articulation of the spines on the test. A sea urchin test has two major perforations (Figure 4.9(a)): a small hole on the upper surface (the apical face) and a hole that is generally larger on the other side (the oral face). This opening on the oral side may include a structure inside the test, which also has five-part symmetry: the Aristotle's lantern. The term denotes the general shape of this structure (lantern-shaped) and the name of the first scientist to describe it (the Greek philosopher Aristotle). The Aristotle's lantern is the sea urchin's masticatory apparatus. It is made up of up to 50 small elements including five teeth, which are all moved by around 60 muscles. It is not firmly fixed to the test, but linked to it by a membrane and muscles, so that in general, it does not remain in the sea urchin's test during the fossilization process. The Aristotle's lantern surrounds the inlet to the urchin's digestive system. The perforation associated therewith is called the peristome. On the opposite side (i.e. on top of the test), we have the outlet from the digestive system: the anus. It opens by way of a membrane – the periproct – which is, itself, encircled by around ten plates associated with the functions of reproduction, test growth and balancing the pressure within the sea urchin. All of this forms the apical system. The thickness of the test varies from one species to another. However, it is generally round when viewed from an apical perspective.

We call those organisms that fit this description “regular sea urchins”. They are regular in the sense that they possess a test with perfect five-part radial symmetry. There are others, though: so-called “irregular” sea urchins – sea urchins that are not so round! They too have this five-part symmetry (with five ambulacral areas and five interambulacral areas), but they also display bilateral symmetry (see Figure 4.9b). This bilateral symmetry alters their general shape: some of them become heart-shaped, others lantern-shaped, and some even coin-shaped: these are flat sea urchins, which may or may not have indentations. Such is the case of the famous “sand dollars”: irregular sea urchins that are sometimes very round and extremely flat, much like a dollar coin.

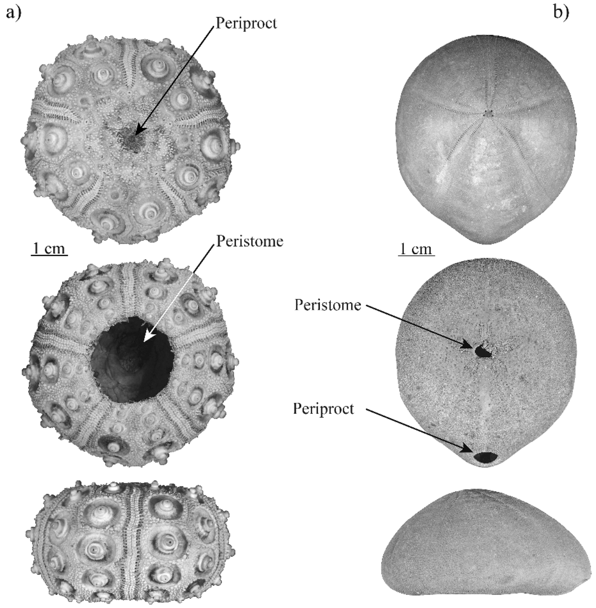


Figure 4.9. *General morphology of the tests of sea urchins. a) Regular sea urchin – example of the genus* Ctenocidaris *(UBGD 278913, T. Saucède’s collection). On this specimen, the Aristotle’s lantern has not been preserved. b) Irregular sea urchin – example of the genus* Echinolampas *(UBGD 278914, B. David’s collection, MUSORSTOM 6 campaign). Top: apical view, middle: oral view, bottom: lateral view (photos by P. Neige)*

The set of the morphological changes undergone by irregular sea urchins, in comparison to their regular ancestors, is impressive, going far beyond their general shape. Their periproct migrated out of the apical system toward the posterior side of the apical face, sometimes reaching the very edge of the test, or even (in certain cases) the oral face. In parallel, the animal's mouth (the peristome) changed in size and shape. It became smaller, and may be found to have an arched shape. In many cases, it moved away from the anterior side of the oral face. Other innovative strategies include the reduction in size but increase in number of the spines, a reorganization of the apical system, and the emergence of new mechanisms for collecting particles to feed.

In a study published in 2007, Thomas Saucède, a paleontologist specializing in sea urchins, and his colleagues, re-examined the origin of these strange irregular sea urchins [SAU 07]. Their study contributed to a fuller understanding of how this surprising morphology came to be. It also confirmed a more long-standing idea: the irregular sea urchins constitute a coherent natural group. That is, they constitute a clade, all descended from the same, exclusive common ancestor (see section 2.4.1.2). As we saw earlier (in section 3.1), it is important to study evolutionary radiations on the basis of clades (rather than on the basis of truncated groups). This ensures the analysis is coherent. The phylogenetic analyses and the order in which sea urchins occur in the fossil record are formalized beyond dispute: irregular sea urchins derived from regular sea urchins (therefore, note that the latter do not constitute a clade: they do indeed all have a common ancestor, but one which is not exclusive to them: that animal is also the ancestor of irregular sea urchins). This major evolutionary event (the emergence of irregular sea urchins) dates from the start of the Jurassic, around -190 million years, attested by a number of characteristic fossilized species.

4.4.1. *Parallel worlds*

Sea urchins appear in the fossil record at the end of the Ordovician, around -450 million years, and are still in existence today (on the basis of a re-evaluation of the anatomical features, some specialists believe that the most ancient forms from that geological period are not really sea urchins in the strictest sense of the term [DAV 99]. "True" sea urchins, therefore, appeared later on, during the Silurian – see Table A.5. Irregular sea urchins, as we have seen, first appeared in the fossil record at the start of the Jurassic. Today, it is estimated that there are, more or less, the same number of species of regular sea urchins as there are species of irregular sea urchins [SMI 84]. If we look at the general line of evolution of irregular sea urchins over geological time (which we can do by counting the number of families over the geological ages), we can see a double tendency (Figure 4.10(a)): a rapid diversification at the very start of their history (with the number of families tripling – this is the initial evolutionary radiation), coupled with a more long-term tendency of gradual increase of the number of families. The originality of the radiation can be seen in the comparison with so-called "regular" sea urchins (Figure 4.10b). The regular urchins suffered a drastic reduction in diversity in the wake of the Permian/Triassic mass extinction event. During the Triassic (between -252.2 and -201.3 million years) they exhibited only modest diversification. In the view of certain specialists, this in fact only represents an imperfect fossil record. At the start of the Jurassic (around -201.3 million years) we see an increase in the number of families of regular sea urchins. This observation can be interpreted in two different ways. If we consider the low number of species in the Triassic as a reality of the biodiversity of that period, then this increase corresponds to a major evolutionary radiation. If, on the other hand, we consider the low number of species found in the Triassic as a taphonomic bias, then this increase corresponds simply to a change in the conditions of fossilization, which became more favorable (and in this case, the increase in the number of species discovered would merely be an artifact). After that point, the number of families has remained fairly stable throughout the geological ages, right up to today. By comparing the two groups, we note that the radiation of the irregular sea urchins does not seem to affect that of the regular sea urchins. They retain a degree of taxonomic diversity (in terms of number of families) that is relatively stable over the geological ages from the Jurassic onwards.

The evolutionary radiation of irregular sea urchins can be seen by calculating their proportion (as usual, in terms of the number of families) in relation to the total number of sea urchins, with all categories being included equally (i.e. both regular and irregular sea urchins). The result is striking (see Figure 4.11). At the very beginning of the Jurassic, they still represented absolutely nothing (which is to say that they did not yet exist). In the middle of the Jurassic, irregular sea urchins represented around 30% of families. Between the beginning and the middle of the Cretaceous, they reached the level of 50% – i.e. they accounted for one out of every two families. At the start of the Cenozoic, they gained even more importance, reaching around 65%. Nevertheless, as we have seen, the number of families of regular sea urchins has not changed since the Jurassic.

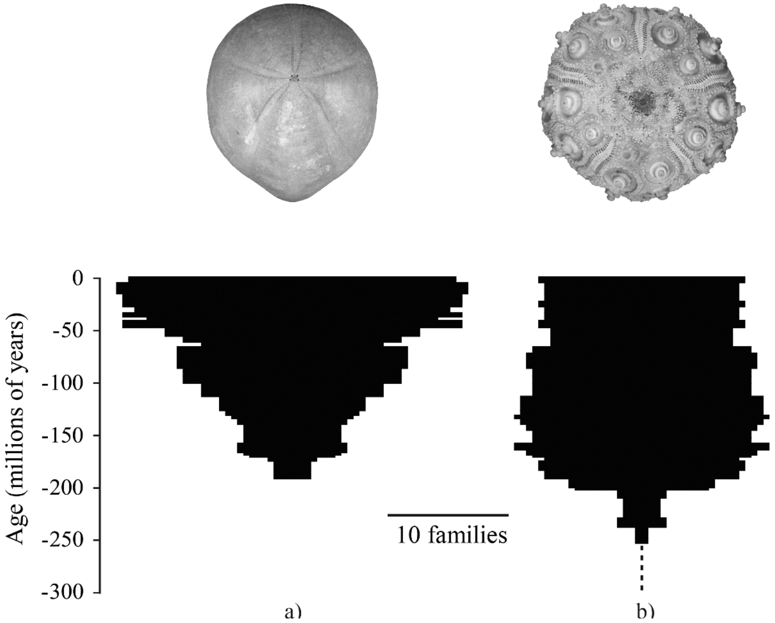


Figure 4.10. *Evolution of biodiversity of sea urchins over the course of the geological ages, presented in the form of spindle diagrams. a) Number of families of irregular sea urchins. b) Number of families of regular sea urchins (number of families modified from [BEN 93], geological ages according to [GRA 12]). Illustrated specimens: same individuals as in Figure 4.9 (photos by P. Neige)*

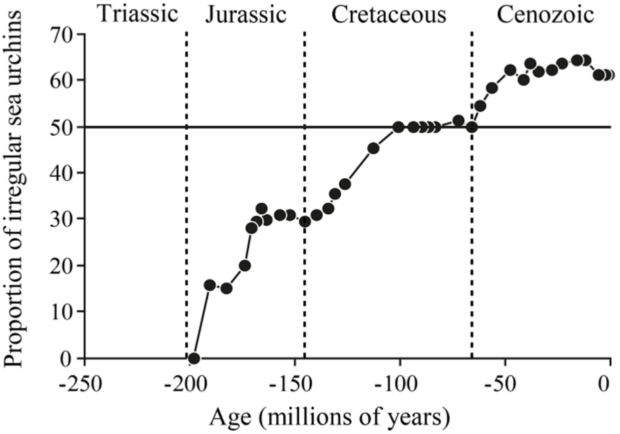


Figure 4.11. *Evolution of the proportion of irregular sea urchins (in terms of percentage of the number of families of all sea urchins) over the geological ages (number of families modified from [BEN 93]; geological ages according to [GRA 12])*

4.4.2. *Anatomical innovation as the cause of evolutionary radiation*

How come irregular sea urchins have experienced such success since the Jurassic, but seemingly without affecting the number of families of regular sea urchins? The answer is, in fact, relatively simple. Irregular sea urchins simply "invented" a new way of life in comparison to that of other sea urchins. The anatomical changes which affected them (see above) actually represent a profound alteration in the way in which these sea urchins live and feed. Hence, they are not competitors for regular sea urchins. This ecological upset has been largely studied by specialists, and can be summarized as comprising five stages [KIE 82, SMI 84]:

– evolution and miniaturization of the Aristotle's lantern;

– start of a change to their living environment: irregular sea urchins adapted to life on loose sea beds;

– start of adaptations to an endobenthic way of life (i.e. within the sediment on the sea floor): first using protective "coverage" of debris found on the sea bed (mineral elements or the remains of the shells of other organisms), and then actually burrowing into the loose material of the sea floor;

– diet change. Irregular sea urchins essentially feed from sediment, collecting food particles, normally with their podia and their spines, and then selecting the necessary nutrient elements in their core;

– increasing adaptation to constant feeding from sediments.

Hence, the evolutionary radiation of irregular sea urchins is a rapid increase in the number of taxa descended from a common ancestor. We have examined it here through the lens of the number of families, but studies on the number of species yield similar results. The driving force behind this phenomenon appears to be the adaptation of organisms to new ecological contexts: the exploitation of the layer of loose sediment on the sea bed. These characteristics correspond to the definition of adaptive radiation (see section 3.2.1). In order to be certain of it, though, we still need to demonstrate that this diversification was accompanied by an increase in morphological disparity – an idea which seems correct intuitively, but needs more formal quantification by quantitative analysis (see section 3.1.3).

Conclusion

The story of biodiversity – of which we have just examined a number of fragments – is a long series of sometimes-sudden events. Evolutionary radiations are a part of this story, as are extinctions. Very generally speaking, therefore, an evolutionary radiation is a massively positive balance between the appearances of taxa and their disappearance within a given clade. Thus, evolutionary radiations do not preclude the extinction of certain taxa. Remember the example of mammals (see section 1.2). A number of the groups of mammals involved in the initial evolutionary radiation (just after the Cretaceous/Tertiary mass extinction, 66 million years ago) died out and made way for others during that same radiation. Yet in the context of an evolutionary radiation such as this, the number of taxa that arise is much greater than the number of taxa that die out, so that ultimately, we see a definite increase in the number of taxa.

In Chapter 3, we explored the question of the causes of evolutionary radiations (see section 3.2). Then, we examined a few of these radiations (Chapter 4). The illustrative examples represent well-known cases of evolutionary radiations in the fossil record. Certainly, we could have given many more – each as fascinating as the next. However, it was necessary to make a reasoned choice. In this final part, we wish to supplement our study of this phenomenon of evolutionary radiation, seen in the fossil record, with three additional questions, which simultaneously draw this book to a close and put it in perspective:

– what are the consequences of evolutionary radiations for biodiversity?

– are all groups of organisms characterized by evolutionary radiation events?

– what lessons can we draw from this in regard to the future of biodiversity?

What are the consequences of evolutionary radiations for biodiversity?

There is no single right answer to this question. As we have seen, radiations are expressed at different scales – from the diversification, 2 million years ago, of the species of finches in the Galapagos Islands to the emergence of the prevailing body plans of the metazoans 550 million years ago. These two events are difficult to compare. In fact, they involve phenomena on two rather different scales.

The radiation of the finches, for instance, obviously belongs to the domain of microevolution (see section 3.1.2). Natural selection has played a major role in the process, in a very enclosed adaptive context (see section 3.2.1). That of the metazoans is a phenomenon of macroevolution. The first radiation impacts on the biodiversity in a very specific context (the birds on the Galapagos Islands), whilst the second affects biodiversity much more widely (i.e. the biodiversity of all the metazoans). Returning to the comparison of the story of biodiversity with a work of theater (see Chapter 1), the radiation of the finches marks the arrival of a new actor on the stage, but one who, as yet, has played only a very small role in relation to the scale of the history of biodiversity. It is difficult, if not actually impossible, to predict the fate of that actor (see section 1.1). On the other hand, the radiation of the metazoans completely overthrew the actors on the stage, and caused a massive shakeup in the relations between them.

Other radiations have different consequences again. That of mammals, for example, took place in the very specific context of events in the wake of a mass extinction. As is correctly pointed out by the American paleontologist David Jablonski [JAB 01], a mass extinction is a double-edged phenomenon: undeniably, it decreases the level of biodiversity, but in doing so it allows other life forms to diversify. In the particular case of the Cretaceous/Tertiary mass extinction, the number of families of mammals would only truly begin to rise after the extinction of the non-avian dinosaurs. This event seems, to us, to be a major one, because of the resulting rise of mammals – a group with which we are familiar (indeed one to which we belong). However, if we look more closely, the fact is that these two groups (non-avian dinosaurs and mammals) are fairly similar: both are amniotes (vertebrate animals which have a membrane – the amnios – which protects the embryo), and typically land-dwelling. Thus, the difference between the two groups in not so very great when viewed in relation to the diversity of the natural world! Hence, the scenario involves the replacement of one group by another, but in the same ecological and environmental context. In keeping with our metaphor, we could say that an actor that had been fairly minimal up to that point (mammals) took center stage, but without greatly altering the action of the "play". How true is this, though? It is not so certain that the changing roles did not greatly alter the course of events. Only a relatively short time ago (200,000 years at most), a species of mammal emerged that would considerably change the course of events: *Homo sapiens* – us! We shall look again at this point in the last part of this chapter. However, this well-known event of the radiation of mammals must not lead us to forget that the descendants of certain dinosaurs – namely birds – have also experienced a phenomenal radiation (see Figure 2.8 and [SAH 10, BEN 14]). Once again, the birds that came onto the scene, which are very diverse today, were and are very different from the avian dinosaurs of the Mesozoic.

The radiation of the angiosperms is a very particular case. It was not linked to a mass extinction, and is relatively recent in comparison to the radiation events that established the major groups of metazoans. However, it resulted in a considerable alteration of the environment of biodiversity on land. Furthermore, angiosperms have not only made their presence felt as a major element in biodiversity from the Cretaceous onwards; they have brought with them a cascade of events linked, in particular, to their reproductive system, which require pollination by other organisms (e.g. insects, birds or bats). Hence, this group was a completely new and totally unexpected actor stepping onto the stage, who would soon come to occupy a very important position, bringing other groups with them to center stage (pollinating insects, in particular).

Thus, it must be recognized that some evolutionary radiations are characterized by an impact which extends far beyond the exact moment of the radiation. The emergence of the metazoans took place 500 million years ago, but its effects can still be seen today. The inventions that determined the structure of biodiversity at the time – such as biomineralization or predation – have impacts which are still of importance today. Indisputably, these impacts are just as significant as those caused by mass extinctions. In the theater metaphor, we observe a total change of the players and the relations between them. The same is true of the radiation of the angiosperms. The play will never be the same again!

Thus, great or small, evolutionary radiations constitute major phenomena that impact the structure of biodiversity: they facilitate the diversification of the organisms and sometimes cause extremely extensive changes in the dominance relations between species or taxa.

Are all groups of organisms characterized by evolutionary radiation events?

The question posed here is very general. As we have seen, certain groups exhibit evolutionary radiations. These groups, at a particular moment in their history, diversified massively. This book focuses on these clades and on these events of sudden diversification – and rightly so: the phenomenon of evolutionary radiation is of crucial importance in the structuring of biodiversity, whether it be the biodiversity of today’s world or that of the past (see section entitled

"What are the consequences of evolutionary radiations for biodiversity?" above).

Yet this phenomenon, however important it may be, must not prevent us from perceiving another reality: that of groups which do not diversify, or at least not much. Today, for example, there are two groups of vertebrates that are relatively close from a phylogenetic point of view: crocodiles and birds. Both belong to a phylogenetic set called the Archosaurs, which also contains non-avian dinosaurs (which are all extinct – see section 2.4.1.2), pterosaurs (flying "reptiles" which also died out at the end of the Cretaceous) and a few other, lesser-known groups. These two close groups (crocodiles and birds) offer a good illustration of this contrast in diversity: whereas today, birds have become enormously diversified, with over 10,000 species (see the representation of their radiation – Figure 2.8(b)), crocodiles, on the other hand, are known in the world today to have only around 20 species (23, to be exact). This simple observation enables us to provide a response to the question posed in the title of this section: no, not all groups of organisms are characterized by evolutionary radiation events. More specifically, we can state that certain groups of organisms will never experience evolutionary radiations, whilst others display such radiations during certain periods in their evolutionary history. In the case of crocodiles, we must not attach too much importance to the measure of their current biodiversity. True, they may currently have only 23 species, but they undoubtedly had many more during certain periods in their long evolutionary history [MAR 98]. Crocodiles today project the image of relics, because they are the rare representatives of a group that has suffered numerous extinctions over the course of the geological ages. Much like the bias which can skew paleontological data (see Chapter 2), it must be admitted that, in this case, the data on today's biodiversity are also particularly poorly suited to depict the diversity of this group of Archosaurs. In actual fact, the data concerning biodiversity in today's world are fairly myopic! They offer us only a fuzzy, blurred image of the past. Fortunately, data gleaned from the fossil record can, in certain cases (see Chapter 2), correct this short-sightedness: they offer us a clearer picture of the evolutionary history of the groups.

Unlike the clades which we have studied in this book (those characterized by evolutionary radiations), or crocodiles, discussed above, other clades exhibit very low rates of morphological evolution throughout their history. That is, they are defined by low taxonomic diversity. They project an image of groups whose morphology always remains identical, or nearly identical, over the course of the geological ages. The coelacanths (marine vertebrates which resemble fish but have special fins whose bony anatomical organization is very similar to that of land-dwelling tetrapods), nautiluses (cephalopods with an external shell whose chambered part is perforated by a siphonal tube at the center) or indeed horseshoe crabs (marine chelicerate arthropods whose carapace is in the shape of a horseshoe) are known today by way of organisms that are, morphologically, very similar to their fossilized close relatives, sometimes hundreds of millions of years old. Some people call these groups "living fossils", though in truth, the term is not very appropriate:

– on the one hand, this term suggests that the same species endures over the geological ages, which is far from true: usually we observe a succession of species, whose morphologies could not be differentiated by a non-specialist;

– on the other, lack of morphological evolution does not mean lack of evolution: species can perfectly well evolve genetically but without modification of the form of the individuals.

Regardless of the name that we attach to them, these very little diversified groups exist. They demonstrate that the phenomenon of evolutionary radiation, although it is very widespread, is not at work for all organisms. The study of these little diversified groups would require an entirely separate book.

What lessons can we draw from this in regard to the future of biodiversity?

In order to understand this question, and answer it, it is necessary to perform a brief analysis of the state of biodiversity as it stands today.

It was in the 1970s that scientists began to believe that the biodiversity in the modern world was in crisis, and that that crisis was accelerating. Based on this newfound awareness, a scientific discipline emerged which is now very fertile: conservation biology. The very existence of conservation biology is closely linked to the recognition of this current phase of extinction of biodiversity, which is supposedly linked to certain harmful human actions (we speak of anthropic effects). Some even hold this to be the sixth mass extinction in the history of biodiversity, in reference to the previous five recognized by paleontologists in the fossil record (Figure 1.2). There is an abundant body of literature which examines, dissects, analyzes or indeed summarizes this current phase of extinction. We shall not add to it here. Let us simply state that estimations conclude that current extinction rates are between 100 and 1,000 times higher than what is typically observed in the fossil record. Today, for example, nearly 20% of amphibian species are on the list of endangered species.

Beyond the purely extinction-related aspects, the purpose of conservation biology is to study today's biodiversity and to protect it. In detail, activities in this field cover different aspects, which we can sum up here by way of four statements [SOD 10, PRI 14]:

– the biodiversity of species and ecosystems must be preserved – for reasons of human enjoyment (we love this diversity that surrounds us and particularly admire certain species), but also because this biodiversity has an intrinsic value. Sometimes this is an economic value, and sometimes an ethical value. The idea espoused here is that each species (or ecosystem) is an entity in its own right, and has the right to exist;

– premature extinctions (of populations, species or even whole ecosystems) must be avoided. It is necessary, here, to distinguish so-called "natural" extinctions from "premature" ones. Natural extinctions are those which we have discussed in this book. Paleontologists discover evidence of them, but they can obviously also affect biodiversity today. Over the course of the geological ages, there is a constant background of extinctions (besides sudden and rare events such as mass extinctions and second-order mass extinctions – see Figure 1.2). Humans did not yet exist at the time of these extinctions, therefore we cannot be held responsible for those events! In the lexicon of conservation biology, premature extinctions are those caused by human actions. The extinctions are said to be premature because we consider that the species dies out before its probable extinction date if humans and our actions did not exist;

– ecological complexity must be maintained. Species do not exist independently of one another. They are interconnected (e.g. by relations of predation or symbiosis). Beyond species and populations, therefore, it is ecological complexity which is important;

– biological evolution must continue. Let us state simply that the organisms whose stories we have explored in this book are fascinating. They exist because they have been fashioned by evolution. To allow biological evolution to continue is to facilitate the emergence of increasingly original organisms. In order to achieve this, it is necessary for genetic diversity to be preserved and the capacity for dispersion of species to be ensured. In the context of a species conservation policy, this differentiates the approach of preservation in captivity (when the organisms are cut off from their natural evolutionary processes) from an approach conducted in the natural environment.

Why, though, should we be concerned for today's biodiversity and why should we wish to preserve it given that, as we have seen, evolutionary radiations compensate for extinctions? Should not evolutionary radiations enable biodiversity to re-establish itself after this current phase of extinction? Remember that in this book, we have demonstrated that a fundamental feature of biodiversity is its ability to diversify. It does so in many different circumstances: e.g. because of an extinction, or indeed by adaptation to a different ecological context. It may do so quickly and intensely, in which case we speak of an evolutionary radiation. Of course, biodiversity sometimes decreases – sometimes even very suddenly – in mass extinction episodes (see Figures 1.2 and 3.7). However, we have also noted that the post-extinction episodes of diversification (post-extinction radiations) for their part are also rapid and intense – sometimes even more rapid and intense than the extinction itself. In summary, biodiversity is intrinsically capable of diversifying and therefore withstanding all sorts of damaging events. Is there nothing to worry about, then? In fact, things are not quite so simple. In order to properly understand them, two points already touched upon in this book are worth summarizing here:

– the time scales studied are not the same between the phase of extinction of biodiversity observed today and the extinctions and evolutionary radiations observed through fossil data. Paleontological data, although now much more reliable than before, cannot be directly transposed onto the current biodiversity crisis. On a long timescale, it is true that radiations compensate for extinctions. The first conclusion of this book, therefore, is that biodiversity – i.e. the diversity of the living world, which has endured for over 3.5 billion years on Earth – is not really in danger. It has experienced very numerous extinction episodes – some of them intense – and has always come through the other side, one way or another! Indeed, in certain cases, it has recovered quickly. However, as readers must have understood, for paleontologists, the concept of passing time is unusual. It is not comparable to human time. Thus, a rapid recovery of biodiversity after a mass extinction (see section 4.2.1), no matter how intense, may still take a period of around two million years! This is a brief instant on the scale of geological time or the history of biodiversity, but an eternity in relation to the human frame of temporal reference. This will be the second conclusion to this book: whilst biodiversity has the ability to diversify again and again, even after an intense extinction, it requires a huge amount of time in relation to our human frame of temporal reference – for instance, ample time for our own species to become extinct. This crisis of biodiversity that we are observing today could, therefore, lead to the premature extinction of numerous species (some such extinctions have already occurred): mammals, birds, amphibians, all sort of insects, plants, mollusks or other life forms;

– in addition (and this serves as the third conclusion to this book), biodiversity always recovers, but the consequences of post-extinction evolutionary radiations are significant modifications to the “cast” involved in the “play”. Put differently, if the phase of extinction of biodiversity today were to continue until the world’s biodiversity reaches levels similar to those experienced during the mass extinctions over the course of the geological ages, not only could the post-extinction recovery phase take a million years or more, but also the biodiversity that would characterize that future world would be enormously different to that which we know today. If our species does manage to endure, there is no guarantee that it will always play such a dominant role on the ecological stage.

In this context, taking account of the three conclusions we have just drawn ((1) biodiversity as the diversity of the living world is not in danger; (2) its ability for diversification is strong and rapid in comparison to the history of life on Earth, but extremely long in relation to a scale of human reference; and (3) post-extinction evolutionary radiations always cause significant alterations of the dominance relations between organisms), we can thus estimate that the risk of extinction exists for a set of species (potentially including our own one). Biodiversity, though, considered as diversity of life, is guaranteed a long future, marked by numerous events of diversification (some of them precipitous), which will be examples of evolutionary radiations. Finally, to paraphrase the paleontologist Stephen Jay Gould [GOU 91], the fragile entity in this long-term story – that of biodiversity through the geological ages – is undoubtedly humans, and some of the species that surround us (which represent certain species in the existing biodiversity). Our planet, however – our Earth – will survive us. So too will biodiversity, with new species. There can be no doubt, then, that life will continue for a very long time on our planet, and will diversify by way of that mechanism which we have observed throughout this book: the phenomenon of evolutionary radiation.

Appendix

Era	Period	Epoch	Stage	
Cenozoic	Quaternary	Pleistocene	*-2.59* *not detailed*	
	Neogene	Pliocene		*-5.33*
		Miocene	Messinian	*-7.25*
			Tortonian	*-11.63*
			Serravalian	*-13.82*
			Langhian	*-15.97*
			Burdigalian	*-20.44*
			Aquitanian	*-23.03*
	Paleogene	Oligocene	Chattian	*-28.1*
			Rupelian	*-33.9*
		Eocene	Priabonian	*-37.8*
			Bartonian	*-41.2*
			Lutetian	*-47.8*
			Ypresian	*-56*
		Paleocene	Thanetian	*-59.2*
			Selandian	*-61.6*
			Danian	*-66*

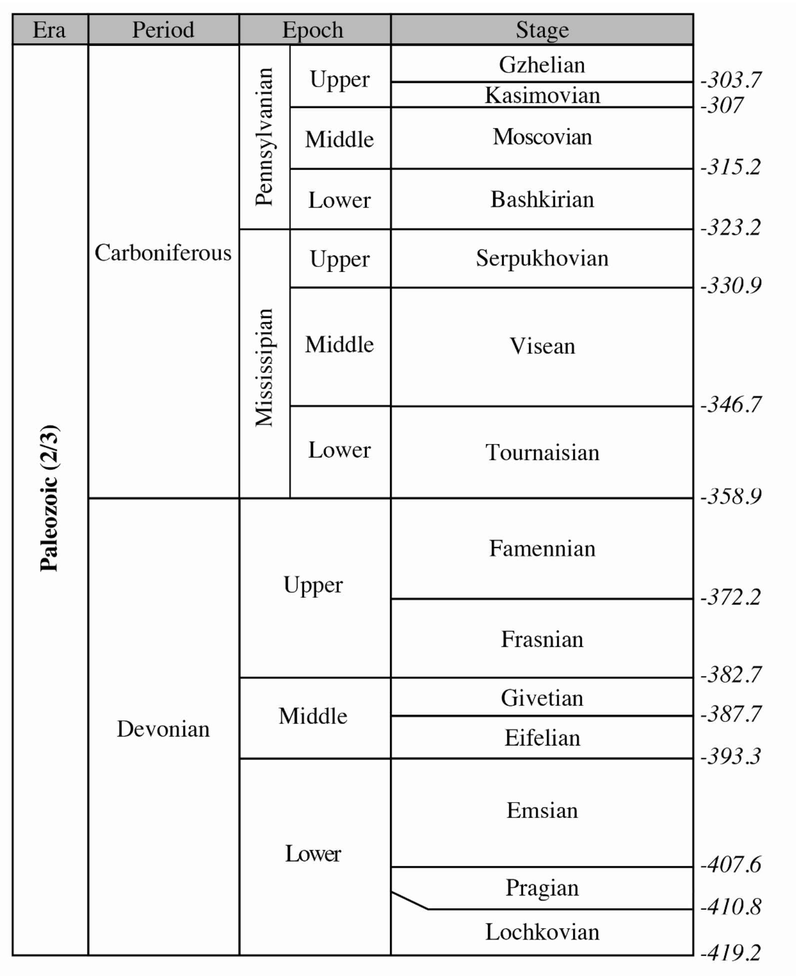
Table A.1. *Standard division of geological ages (Cenozoic). Geological ages (millions of years) according to [GRA 12]*

Era	Period	Epoch	Stage	
Mesozoic (2/2)	Cretaceous	Upper	Maastrichtian	*-72.1*
			Campanian	*-83.6*
			Santonian	*-86.3*
			Coniacian	*-89.8*
			Turonian	*-93.9*
			Cenomanian	*-100.5*
		Lower	Albian	*-113*
			Aptian	*-126.3*
			Barremian	*-130.8*
			Hauterivian	*-133.9*
			Valanginian	*-139.4*
			Berriasian	*-145*
	Jurassic	Upper	Tithonian	*-152.1*
			Kimmeridgian	*-157.3*
			Oxfordian	*-163.5*
		Middle	Callovian	*-166.1*
			Bathonian	*-168.3*
			Bajocian	*-170.3*
			Aalenian	*-174.1*
		Lower	Toarcian	*-182.7*
			Pliensbachian	*-190.8*
			Sinemurian	*-199.3*
			Hettangian	*-201.3*

Table A.2. *Standard division of geological ages (Mesozoic, 2/2). Geological ages (millions of years) according to [GRA 12]*

Era	Period	Epoch	Stage	
Mesozoic (1/2)	Triassic	Upper	Rhaetian	-209.5
			Norian	-228.4
			Carnian	-237
		Middle	Ladinian	-241.5
			Anisian	-247.1
		Lower	Olenekian	-250
			Induan	-252.2
Paleozoic (3/3)	Permian	Lopingian	Changhsingian	-254.2
			Wuchiapingian	-259.8
		Guadalupian	Capitanian	-265.1
			Wordian	-268.8
			Roadian	-272.3
		Cisuralian	Kungurian	-279.3
			Artinskian	-290.1
			Sakmarian	-295.5
			Asselian	-298.9

Table A.3. *Standard division of geological ages (Mesozoic, 1/2, Paleozoic, 3/3). Geological ages (millions of years) according to [GRA 12]*



Era	Period	Epoch		Stage	
Paleozoic (2/3)	Carboniferous	Pennsylvanian	Upper	Gzhelian	-303.7
				Kasimovian	-307
			Middle	Moscovian	-315.2
			Lower	Bashkirian	-323.2
		Mississipian	Upper	Serpukhovian	-330.9
			Middle	Visean	-346.7
			Lower	Tournaisian	-358.9
	Devonian	Upper		Famennian	-372.2
				Frasnian	-382.7
		Middle		Givetian	-387.7
				Eifelian	-393.3
		Lower		Emsian	-407.6
				Pragian	-410.8
				Lochkovian	-419.2

Table A.4. *Standard division of geological ages (Paleozoic 2/3). Geological ages (millions of years) according to [GRA 12]*

Era	Period	Epoch	Stage	
Paleozoic (1/3)	Silurian	Pridoli		-423
		Ludlow	Ludfordian	-425.6
			Gorstian	-427.4
		Wenlock	Homerian	-430.5
			Sheinwoodian	-433.4
		Llandovery	Telychian	-438.5
			Aeronian	-440.8
			Rhuddanian	-443.8
	Ordovicien	Upper	Hirnantian	-445.2
			Katian	-453
			Sandbian	-458.4
		Middle	Darriwilian	-467.3
			Dapingian	-470
		Lower	Floian	-477.7
			Tremadocian	-485.4
	Cambrian	Furongian	Stage 10	-489.5
			Jiangshanian	-494
			Paibian	-497
		Epoch 3	Guzhangian	-500.5
			Drumian	-504.5
			Stage 5	-509
		Epoch 2	Stage 4	-514
			Stage 3	-521
		Terraneuvian	Stage 2	-529
			Fortunian	-541

Table A.5. *Standard division of geological ages (Paleozoic 1/3). Geological ages (millions of years) according to [GRA 12]*

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