Four Billion Years of Evolution

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Palaeontology is an historical science comparable to prehistory, archeology, and history, in that it deals with living beings from past times. The documents needed to write the history of life are the remains of organisms contained in geological deposits from the last four billion years. They are called "fossils."

The fields of study mentioned above are united by a common character, the establishment of a chronological scale that allows facts to be organized into a system, the aim of which is to study changes over time.

The geological and palaeontological time scales are based on two groups of facts. One is the principle of superposition. In a series of geological deposits, that is to say, in a group of sandy, clayey, or calcareous sediments of a dozen or a hundred meters or more that filled an old sea or lake, the lowest bed ("stratum") was deposited first. The bed above, deposited later, is younger but older than the following bed. The reduction in age continues until one reaches the highest beds. A spatial phenomenon is also a temporal phenomenon (Fig. 1).

The second group of facts is related to fossils. At the beginning of modern times, they were considered to be "inorganic products," From the eighteenth century on, geologists recognized fossils as the remains of living beings. Toward the end of that century, W. Smith, an engineer who built canals in central England and was a collector of fossils, observed that these remains did not always appear everywhere in identical groupings. In 1786, he found that, on the contrary, there were differences. In the lower bed ("lower" according to the concept of superposition), there was a suite of fossils different from that in the upper bed. This phenomenon was observed in all the following strata and throughout the region. Thanks to this discovery, it became possible to characterize sedimentary beds (strata) by their different fossil content and to estab-

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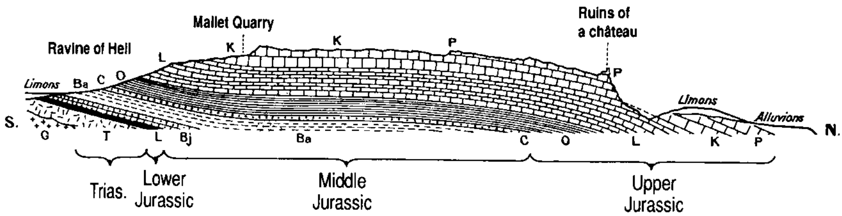

Figure 1: Crussol Mountain near Valence (Drôme) shows the superposition of limestone, chalk, etc., stratas with rich biotas different from the Jurassic and the Triassic. Thus can be found from top to bottom: the upper, middle, and lower Jurassic, and the Triassic. The depth of the Triassic-Jurassic layers: ca. 1000m; absolute age ca. 110 million years.

Table 1: Chart of the geological periods and their expanded biostratigraphic and paleobiotic subdivisions.

Nomenclature of Eras								Systems	Millions of Years (MY)
Tradtional	Geologic/Paleozoologic		Paleobotanic		Paleobiologic				
Quarternary	Phanerozoic	Cenozoic	Phanerophytic	Cenophytic	Phanerobiotic	Cenobiotic		Quarternary	--1.8
Tertiary								Tertiary	--65
Secondary		Mesozoic		Mesophytic		Mesobiotic		Cretaceous Jurassic Triassic	- 140 - 205 --250
Primary		Paleozoic		Paleophytic		Paleobiotic		Permian Carboniferous Devonian Silurian Ordovician Cambrian	- 290 - 355 - 410 - 438 - 510 --570
	Proterozoic		Proterophytic		Proterobiotic		"Precambr."	Algonkian	--2500
	Archaeozoic		Cryptophytic		Archaeobiotic			Archaean	--4000
Prebiotic Era									
Abiotic Era									
Definitive Solidification of the Earth's Crust									4600

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lish their subdivisions, based on the transformation of living beings through time. Smith became the founder of "biostratigraphy."

As a result, there developed a system of chronological subdivisions based on the palaeoflora and palaeofauna found in sedimentary rocks. After several decades, the great eras of evolution were established – Primary, Secondary, Tertiary and Quaternary or Palaeo-, Meso-, and Ceno- (or Neo-) zoic. Later, palaeobotanists added the Palaeo-, Meso-, and Neo-phytic (see table). These eras represent a series of fossil biotas (or biospheres), including all the animals and plants of a given time period.

In the course of establishing these eras, researchers recognized a second order of subdivisions, named "systems," beginning with the Cambrian – the oldest – and finishing with the Holocene for the last ten thousand years (see table).

Eventually, the sequence of eras and systems originally developed for Europe was easily applied to other continents. Of course, the systems themselves were subdivided. For instance, today the Jurassic is subdivided into sixty units, multiplying the already enormous series of palaeobiota.

The search for the oldest fossils (of the Precambrian era) began later, toward the end of the nineteenth century. The reason for this was the extreme rarity of organic remains in the older, as opposed to the most recent, beds. But the microscopic and ultramicroscopic methods of our century have improved the situation and opened the way to the discovery, analysis, and interpretation of such fossils, that, even so, are still rare and often problematic.

The Proterozoic and Proterophytic (Proterobiotic) era was preceded by an Archaeozoic and Cryptophytic or Archaeobiotic era (see table), and it is possible that this era itself was preceded by Prebiotic (Chemofossil) and Abiotic eras accompanying and immediately following the final formation of the Earth's crust.

The chronology of the history of the Earth and its organisms (see table) rests on a system of relative dating. The Secondary-Mesobiotic era is younger than the Primary- Palaeobiotic era and older than the Tertiary-Neobiotic era, and in the same way, the Jurassic system is situated between the oldest Triassic and the youngest Cretaceous (see table). After the stabilization of this relative chronology, geologists have tried a number of times to find a chronometry that would permit absolute dating – in years – of the history of the Earth. But the results were not precise (the figure

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given for a sedimentary marine series, for example, was derived from the speed of sedimentation in the oceans at the present time).

The discovery of radioactivity at the beginning of the twentieth century allowed the development of an absolute chronometry of geological time.

The table shows the absolute dating – in millions of years – of the eras and systems that have delivered the evidence of past life on the Earth. The Archaeobiotic began around 4,000 million years ago, the Proterobiotic around 2,500 million. The beginning of the Cambrian is dated at 570 million, the Triassic at 250 million, the Tertiary at 65 million, and the Quaternary at 1.8 million. The Earth's crust would date from 4,600 million years (see table).

The History of Life

The Archaean - Archaeobiotic Era

According to the most recent research, the oldest fossils come from a sandy sediment, extensively transformed by later orogenesis (phases in the formation of the relief of the Earth's Precambrian crust). This quartzite from southwest Greenland has an age of 3,800 million years according to radiometric dating techniques (Fig. 2).

These fossils are spherical cells of 0.5 microns and tubular cell fragments of the same size. They are the remains of cyanobacteria and iron bacteria that show (through mass spectrographic analysis) the presence of the photosynthetic isotope carbon 12 (^{12}C). The fossils probably come from an epicontinental shallow sea. They confirm the proposition that the origin of life is to be found in an aquatic environment.

The so-called *Fig Tree Group* of quartzites from Swaziland (southern Africa) are younger (3,200 million years). These rocks, also of marine origin, contain cylindrical filaments of bacterian appearance (*Eobacterium isolatum*) and have a globulous structure. Many similar microfossils are already known from the *Onverwacht* group from South Africa (3,700 to 3,500 million years old) and the Warawoona sediments from Australia (3,600 to 3,500 million years old). All these unicellular organisms are procaryote: the nucleus, the cellular core, is missing; they are "anucleobiont."

The plant thucholithes has been found next to cyanobacteria and other microbes in the fluvial and deltaic deposits containing gold and uranium in the screes (thucolithes) of Witwatersrand

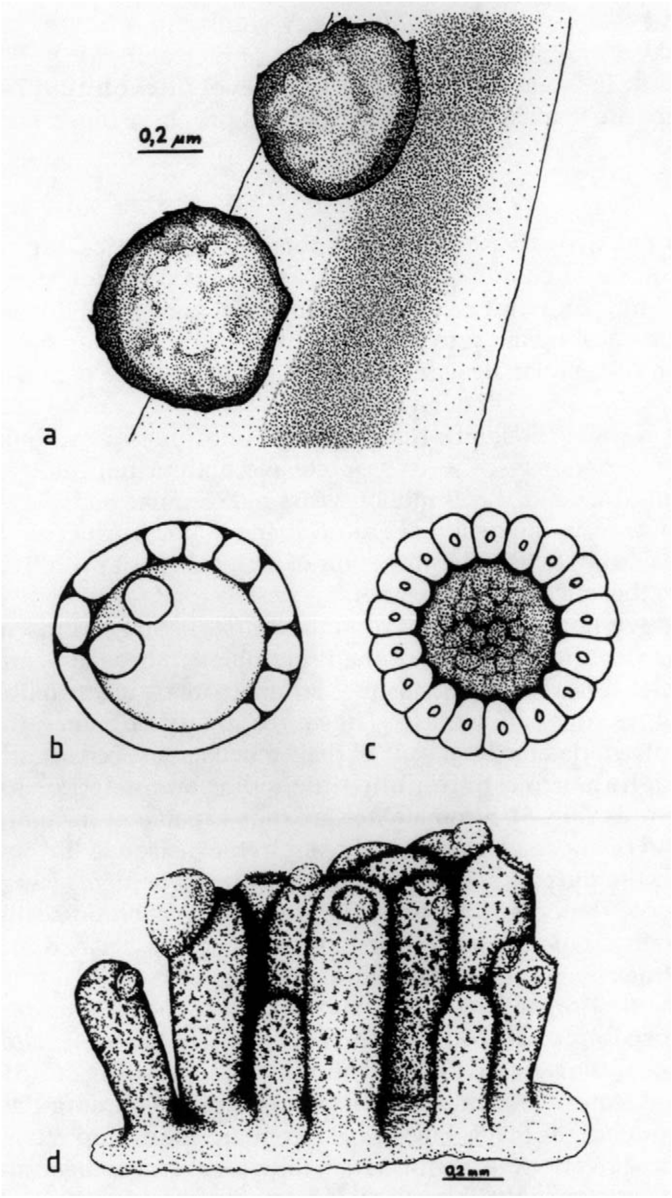

Figure 2: 2a: two spherical cells and a cellular fragment, comparable to iron bacterias. The oldest fossil from Greenland. 2b: *Eosphaera*, multicellular sphere with an internal concavity. 2c: Volvox, a recent green spherical algae for comparison. 2d: *Thucholithes*, a plant very similar to lichen; size of the colony: 14 x 10 mm.

(Transvaal, South Africa). It is very similar to a lichen, in other words, a multicellular plant. The size of the colony (Fig. 3) is 14 x 10 mm. It is an organism at a high level of evolution because lichens are symbionts between algae and primitive mushrooms.

Algonkian – Proterobiotic

This era already shows an important diversification. In the microflora of Gunflint (Ontario, Canada, 1,900 million years old), there are, for example, numerous forms of bacteria and cyanobacteria, almost identical to modern forms, next to filamentous globulous multicellular algae (*Eosphaera* , Fig. 4). But these organisms are also procaryote (without a nucleus).

In Karelia (Finland), there is a metamorphosed carboniferous bed (intermediary between graphite and anthracite), shungite, two meters thick and 1,800 million years old. Similar beds have been discovered in the region of Lake Superior (North America) and in the Bavarian forest. They are signs of an intense but primitive plant life in the epicontinental seas of this period.

As we have just seen, Precambrian fossils are microscopic in size. With the beginning of the Proterobiotic, there appeared, for the first time, larger organisms – stromatolites – measured in centimeters or even meters. These are groups of very prolific cyanobacteria able by means of their mucilage to secrete carbonate through their mesh, resulting in circular laminated or foliated structures (Fig. 5). Stromatolites are thus capable of forming rocks and, in many cases, even actual reefs. In the history of life on Earth, they were the first builders of reefs. Their environments were at the edges of the oceans, where they produced morphologically very diversified colonies in all the regions of the globe. To a great extent, the Proterobiotic is the age of stromatolites.

The first organisms with a nucleus inside the cells (eucaryotes) appeared around 1,500 million years ago. For example, alongside monocellular algae, the microflora of Back Spring (California, United States, 1,300 million years ago) produced a multicellular filamentous algae that is linked to a recent group (mycophyta).

These relationships with certain families of recent algae are even more obvious in the microflora of Bitter Springs (Australia, around 1,100 million years ago). Macroscopic algae appeared for the first time around 700 million years ago.

The first multicellular animals – metazoans – left only imprints

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or traces. A very diverse fauna has been found at Ediacara (Australia, 600 million years ago). The forms collected are very similar to medusas and other cnidarians and annelids (segmented worms). All these animals are characterized by the complete absence of skeletal tissue (carbonated, chitino-calcareous, acido-siliceous, and so on). Only imprints of the soft parts are known. Ediacaran fauna have been found in South Africa, northern Asia and in Europe (Scotland) in the same environment (coastal deposits), the same state of fossilization, and of approximately the same age. This invertebrate fauna from the end of the Proterobiotic (or Precambrian), with its worldwide distribution, bears no relation to the Cambrian fauna with which the Primary (or Palaeobiotic) era began. The origin and decline of the Ediacaran fauna are still a mystery.

The two "Precambrian" eras cover 3,430 million years (4,000 to 570 million years ago; see table). The Archaeobiotic and Proterobiotic eras thus comprise about 86 percent of the history of life on Earth!

When one takes into account this enormous length of time, the progress of evolution and organic diversification does not appear very intense. The great majority of Precambrian fossils show a very elementary level of organization. Nonetheless, there were already specializations of a high level. The Ediacaran fauna, for example, must have had a palaeontological history. To quote yet another example, the "evolutionary potential" of cyanobacteria and cyanophytes produced palaeobiological structures that – by their dimensions, by the extreme complexity of the reefs that were constructed (bioherms), and by their phylogenetic evolution – showed a high degree of specialization and diversification. In the absence of competition, they occupied an extraordinary collection of ecological niches around 2,000 million years ago. With the Cambrian, things began to change.

The Primary – Palaeozoological – Palaeobiotic Era

The Primary, Secondary, Tertiary, and Quaternary eras are grouped together under the name Phanerozoic (or in the palaeobiological sense, Phanerobiotic). This term suggests an almost infinite variety of fossils and biota. The Phanerobiotic periods played a decisive role in the reconstruction of the history of life on Earth.

The Phanerobiotic covers the last 570 million years of the history of life, that is to say 14 percent. The Primary (or Palaeobiotic) covers 320 million years, more than half!

The Palaeobiotic era is divided into six systems (see table), the oldest of which is the Cambrian. It should be emphasized that these systems are based on changing suites of fossils and thus of life and its biota.

The Cambrian

In Cambrian times, life was aquatic, as it had been during the Proterobiotic. That is why the plants are almost exclusively algae. As well as the cyanophytes (blue algae) already present since the Precambrian, one can find green algae (*Chlorophyceae*) and red algae (*Rhodophyceae*), belonging to highly evolved and specialized groups still present in the oceans today.

By contrast, the fauna is extremely diversified. From the beginning of the Cambrian, all the great plans of construction of the animal kingdom (phyla) were already present, except for those of typical vertebrates. These were foraminifera and unicellar radiolarians of microscopic size, multicellular metazoans like poriferans (sponges, archaeocyathids), coelenterates (the ancestors of corals, actinias, medusas, polyps), brachiopods (enclosed in a shell made up of two valves that are often rigidly hinged – or not hinged at all), arthropods (trilobites, crustaceans, arachnids), mollusks (bivalves, gastropods, cephalopods), echinoderms (ancestors of sea urchins, starfish, and ophiuroideas present in today's oceans and of many extinct groups), conodonts (small extinct animals with a chord, which is the anatomical predecessor of the vertebral column of later vertebrates).

The above examples have one characteristic: they possess more or less complete skeletons, which is the fundamental condition for the fossilization of animals. These skeletons were external, covering the soft parts of the body (foraminifera, brachiopods, arthropods, mollusks, radiolarians, sponges, echinoderms, coelenterates) or internal (conodonts). In addition, many marine sediments have preserved traces of the movements of these animals (sliding across the surface or burrowing and drilling into the sediments).

All the groups mentioned above (and all the others not mentioned) literally exploded from the beginning of the Cambrian. This was the greatest morphological and adaptive outburst in the history of life, and, in terms of the geological time scale, it happened rapidly. From then on, there was no real innovation, apart from that of the superior vertebrates. Naturally, this Cambrian world of living creatures evolved and was transformed even during the Cambrian period (60 million years) and in later times, when the ancient groups disappeared and were replaced by others. But these were evolutionary phenomena that occurred within the framework of the fundamental organizational plans: the phyla. For the palaeontologist, nothing is known about the first evolutionary phases of the phyla.

Palaeontologists think that in the early – certainly Precambrian – stages of evolution, no skeletal tissues were produced. But, as we have seen, the Ediacaran fauna, nonetheless, offered a model: in this case, a biota of metazoans without a skeleton and advanced morphological structures shows that there were sometimes possibilities for the fossilization of animals without hard skeletal tissue. Therefore, it is not improbable that the ancestors of the biota of the lower Cambrian, which did not have skeletons, might be found one day in marine deposits from the end of the Proterobiotic.

As we have just seen, all the great phyla of the animal kingdom were already present in this Cambrian palaeo-community, but it was nonetheless dominated by trilobites and brachiopods. Of the 3,000 known species, 60 percent are trilobites and 30 percent brachiopods.

Trilobites (*Trilobitomorpha*) were primitive, marine arthropods, exclusively fossils, known only in the Palaeobiotic (Fig. 3). Their name comes from the fact that their chitinous or chitinophosphatic shell is divided on the back into three parts by furrows, in the longitudinal as well as transversal directions. The transversal trilobation is produced by the head (cephalos) with the eyes, the body itself (thorax), and the abdomen. These last two parts are segmented. These were chitinous rings, typical of the phylum *Arthropoda*. The longitudinal trilobation is produced by two anteroposterior furrows. The central convex section covers the intestine, musculature, nervous system, and gonads. The lateral sections protect the bifurcated feet of the lower side (ventral, Fig. 7b). The head is a flattened capsule with the anterior section of the digestive tube, the mouth, the nerve center and muscles.

A fundamental and archaic characteristic separates the crustaceans (shrimps, crabs and crayfish) from the trilobites. The former and their ancestors possess a masticatory device ("mandibles"), which surrounds the mouth and is capable of cut-

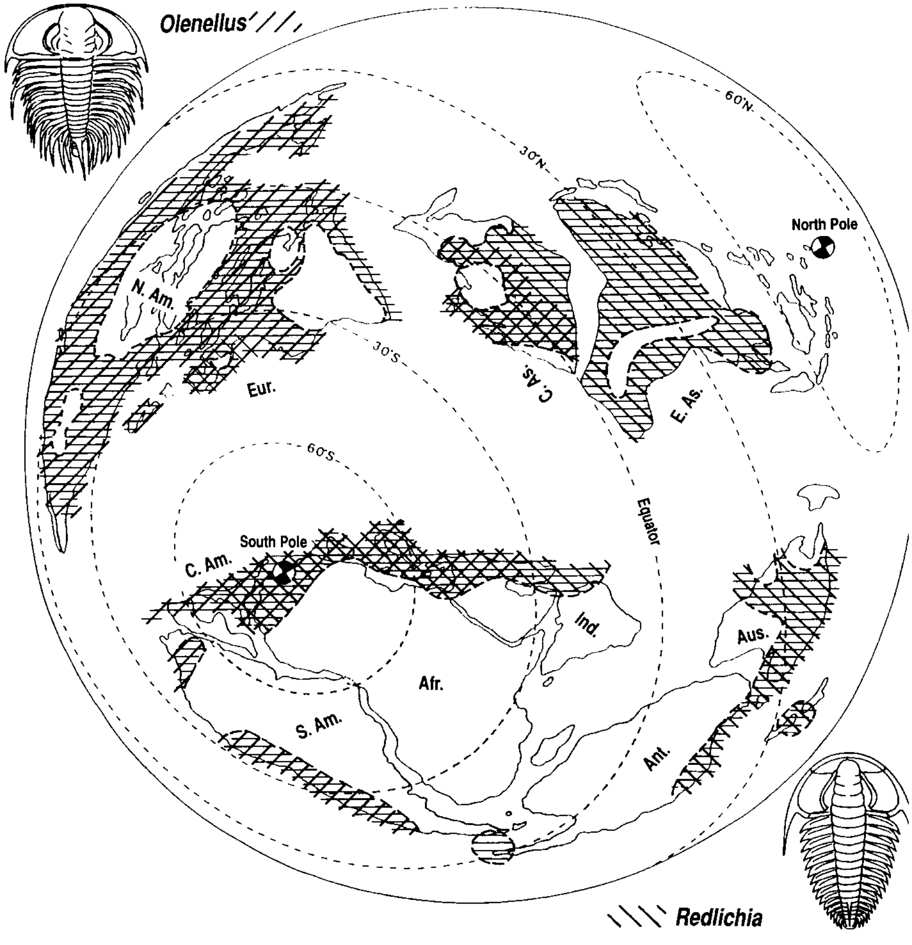

Figure 3: Two trilobites from the Cambrian period, *Olenellus* and *Redlichia* – very different in their ornamentation. They show a paleo-biogeographic difference; for the Cambrian, Olenellus characterizes a "zoogeographic province," the southern hemisphere; Redlichia, the same in the northern hemisphere; between them, mixed regions.

ting up or tearing large pieces of food. By contrast, trilobites do not have mandibles (*Mandibulata*) and can only eat small particles or mud, enriched by organic particles from the bottom of the sea. In passing into the digestive tube, the latter was digested and the sediment expelled. The trilobites' method of feeding was practiced for 320 million years. Competition from the certainly more efficient crustaceans was absent. Moreover, the dorso-ventral flattening of the body favored this way of life.

The other abundant element in the Cambrian fauna was the brachiopods, a small marine group that still exists today (250 species). Thus, they are of some considerable importance (7,000 species in the Palaeo- and Meso-biotic). They have a bivalve shell that protects the animal against nonorganic (water composition) or organic (enemies) aggression in the environment.

For an animal with bilateral symmetry and a longitudinal axis, there are two possibilities for the position of the two valves: they must cover the right and left sides or the dorsal and ventral sides. It was the latter variant that was realized by the brachiopods. Other bivalve groups appeared later – lamellibranchs, ostrachods, and a few other small groups – that generally developed right and left valves.

The orientation of the valves explains the difference between brachiopods and lamellibranchs, even though they have a few external similarities. Among the oldest brachiopods of the lower Cambrian, the two chitinophosphate valves are only linked by the soft muscular parts. This group still exists. Its most spectacular representative is the *Lingula* genus (Fig. 10a), which can be found today in the Pacific Ocean without any morphological modification of the valves (Fig. 10b). *Lingula* is an example of what is called a "living fossil." Palaeontologists have discovered a whole series of "living fossils" coming from more recent systems (for example, the coelacanth from the coasts of Madagascar). But *Lingula* is the oldest because it has survived for 570 million years. These examples show that the history of life is not exclusively a process of evolution, a phenomenon of permanent transformation. There are also stable forms lasting for tens of millions of years or more. But most brachiopods have calcareous shells with two valves linked by a hinge (the calcareous process – "teeth" – of the ventral valve interlocks with the corresponding sockets of the dorsal valve) at the posterior extremity of the shell. Through the action of the muscles, the valves open to communicate with the surroundings (feeding,

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breathing, action of the gonads) or close in case of danger (enemies, disturbed water). One can compare this morphological construction (two valves that open and close with the help of a hinge) to a spectacle case. This "spectacle case principle" can be found among the lamellibranchs and the ostrachods.

The brachiopods are immobile animals. They are fixed to the bottom of the sea, usually near the shore, either by a muscular peduncle that comes out between the valves at the posterior extremity, or directly by the posterior edge of the shell (Fig. 9). Because of this, the brachiopods belong to the benthic ecological community (from the Greek for "depth"). One distinguishes a vagrant benthos (from the Latin for "vagabond"), whose members walk or crawl on the bottom of oceans or lakes (trilobites being an example), from a sessile benthos (from the Latin for "sedentary"), whose members are fixed to the floor. The movements of members of this latter community are accomplished by their larvae. These belong to another aquatic community, plankton (from the Greek for "wandering"). These organisms are suspended in the water and are passively distributed by ocean or fresh water currents either for part of their life (like the larvae of brachiopods and other animals such as corals and sponges) or for their whole life, like permanent plankton (many plant-organisms and microscopic unicellular animals).

Compared to the richness of the trilobites and brachiopods, the members of the other Cambrian phyla play a secondary role.

There were already gastropods in the lower Cambrian. But their shells were not yet rolled up in the helicoidal fashion known later. It was subconic, not at all, or only slightly, rolled up. Lamellibranchs and cephalopods were rare. Echinoderms (*Homalozoa*), like sea urchins and starfish, possessed a peduncle, with which the internal skeleton, with its bilateral symmetry and formed from a capsule and adjacent plates of calcium carbonate, was more or less fixed to the floor. Half way between the sponges and the coelenterates (corals) appeared another, aberrant group confined for the most part to the lower Cambrian, and with almost worldwide distribution. These were the archaeocyathids. Their body was in the form of a goblet, a few centimeters tall, and fixed at the base (Fig. 11). Their skeleton was formed by two porous walls linked by radial and vertical partitions, a unique skeletal structure that has never been found in any other fossil or in recent metazoans. Their way of life also had a geological importance because, in the Cambrian seas, they formed veritable reefs of considerable extent. After the stromatolites of the Precambrian, archaeocyathids were the second reef builders in the history of life. They disappeared completely from the end of the Cambrian.

As opposed to the extraordinary diversification of the Cambrian fauna, the flora remained very poor, as in the Proterobiotic. It was composed entirely of algae. Thus, continents did not have any organic life, at least not of any group having fossilizable tissue.

The Ordovician and the Silurian

The Ordovician is the longest (72 million years) and the Silurian the shortest (28 million years) of the stages in the Palaeobiotic systems. It was during the Ordovician that, for the first time, calcium carbonate became the main substance in the composition of skeletons, whereas during the Cambrian (with the exception of the calcium carbonate of the archaeocyathids and of rare mollusks and echinoderms), chitin and chitinophosphate dominated (brachiopods, trilobites). During the Ordovician, trilobites reached maximum diversification. Among them there even appeared groups capable of curling up to protect themselves like contemporary wood-lice. Their main predators were the large arthropods, related to contemporary spiders and scorpions: giganturoidea, agile swimmers and carnivores. The Pterygotus genus had a length of more than 2 meters! Initially adapted to marine life, the giganturoidea are to be found in the lagoon environment toward the end of the Silurian. Their contemporary descendant is the well-known Limulus (mollusk crab) of the Carribean and the Indian Ocean, another "living fossil."

Among the brachiopods, forms with calcareous valves and posterior hinges began to dominate. Lamellibranchs, that were very rare in the Cambrian, were deployed in six orders with a multitude of species. They were equipped with two valves, covering the left and right flanks of their soft body, joined together by a dorsal hinge, thus realizing the functional principle of the spectacle case.

Typical corals, unknown in the Cambrian, were very widespread. Initially isolated forms, in the Silurian they constructed reef colonies. They replaced the rocks of the Cambrian archaeocyathids.

Cephalopods (related to contemporary cuttlefish such as sepia, squid, octopus, and so on), which had also been rare in the

Cambrian, began to develop in an extraordinary fashion. These fossilized forms were equipped with an external calcareous shell. Initially rectilinear (*Orthoceras*) or slightly curved cones predominated, with a living chamber occupied by the soft parts and the tentacles together with a funnel, and chambers partitioned in rows, called air chambers, filled with a gaseous substance. By their upward force, these last gave the creature the capacity to swim, as opposed to other mollusks that were originally benthic animals like lamellibranchs and gastropods. Giant forms of cephalopods existed with a shell length of 4.5 meters (*Endoceras*). Then, in the Silurian, coiled forms predominated in their turn, ancestors of the contemporary nautilus (*Nautilus*) of the Pacific Ocean.

Colonial organisms known as graptolites characterize almost uniquely the Ordovician and Silurian by their abundance. The graptolite is formed by a rigid stem, which is straight, curved, or branched, and a series of small chitinous cells (2 to 3 millimeters long) representing the individuals of the colony. These thecae were inhabited by small polyps (*Rhabdosoma*). Sometimes several rhabdosomes were united in a "megacolony" that carried a large floating structure in the shape of a dome. At the base of this pneumatophore are found small spheres, gonotheca, that produce the embryonic rhabdosomes. This construction was perfectly adapted to a planktonic life in the calm pelagic regions of the Ordovician and Silurian seas, far from the coastal zones. Graptolites have pterobranchia as recent relations, a group that is also related to the chordates, ancestors of the vertebrates.

It was already in the Ordovician that the first representatives of modern echinoderms (sea urchins, star fish, ophiuroidea, and crinoids of the contemporary oceans) were to be found. The first three of these groups belong to the vagrant benthos, crawling with spikes and arms along the floor, the orifice turned downwards. Crinoids were, for the most part, sessile attached to the bottom of the sea by a peduncle, the orifice turned upwards. The calcareous skeleton of the echinoderms is dominated by a pentaradial symmetry (like the five arms of the starfish or the ophiuroidea). But the embryogenesis of recent echinoderms shows that the larval stages have bilateral symmetry. Thus, pentaradiality is a derivative state. Ontogenesis (embryology) often reflects phylogenesis (the palaeontological history of the goup). Crinoids with a peduncle dominated the Palaeobiotic era. Today, they remain no more than a very small group among the echinoderms.

Clearly, the emergence of the first vertebrates in the course of the Ordovician is an important event. These were armored fish. Their axial skeleton was still cartilagenous, but the body was protected by an external bony skeleton, covered with scales or bony plates. These forms did not have jaws. The buccal orifice had a suction device analogous to that of the lamprey, to absorb mud from the sea bottom and to filter microbes and thin organic particles through the branchiae before transporting them to the stomach. The name agnath (from the Greek *a* , "without" and *gnathos*, "mandible") given to the group refers to this archaic form of construction. The bodies of the Ordovician agnaths were still covered with small scales.

In the Silurian, real armored agnaths appeared, equipped with very large bony plates on the anterior section of the body (*Pteraspis*), called the cephalic shield.

The first real fish (*Pisces*) existed alongside the agnaths. They had maxillae and articulated mandibles capable of catching and chewing larger prey. This evolving structure opened up new fields of nourishment, an important precondition for the future evolution of fish and tetrapods, including Man.

The flora was still exclusively marine. Calcareous algae, cyanobacteria, dominated, but new unicellular microscopic organisms appeared. These were acritarcha, which were very widespread and can be found up to the present day.

One does not find, in the Ordovician or the major part of the Silurian any more than in the Cambrian, continental deposits containing (plant and animal) fossils that are not of marine origin. It was at the end of the Silurian that the first remains of vascular plants (*Cooksonia*) began to appear. They are the oldest terrestrial plants. The group, named psilophyta, had neither leaves nor real roots (Fig. 4). The plants had subterranean shoots, rhizomes, from which ramified aerial shoots set out. The extremity of each shoot carried a sporangium in the form of a sac. Rhizomes with absorbent hairs and shoot made up a vascular system for the transport of water and foodstuffs. The purely marine ancestors – probably green algae (*Chlorophyceae*) – were surrounded with water and food, but, in order to survive on the Earth and in the air, they needed a vascular system to distribute these substances to all parts of the psilophyte. In addition, the vascular system performed the role of support tissue to hold itself up, something that had not been necessary for the ancestor algae with their upward aquatic forces.

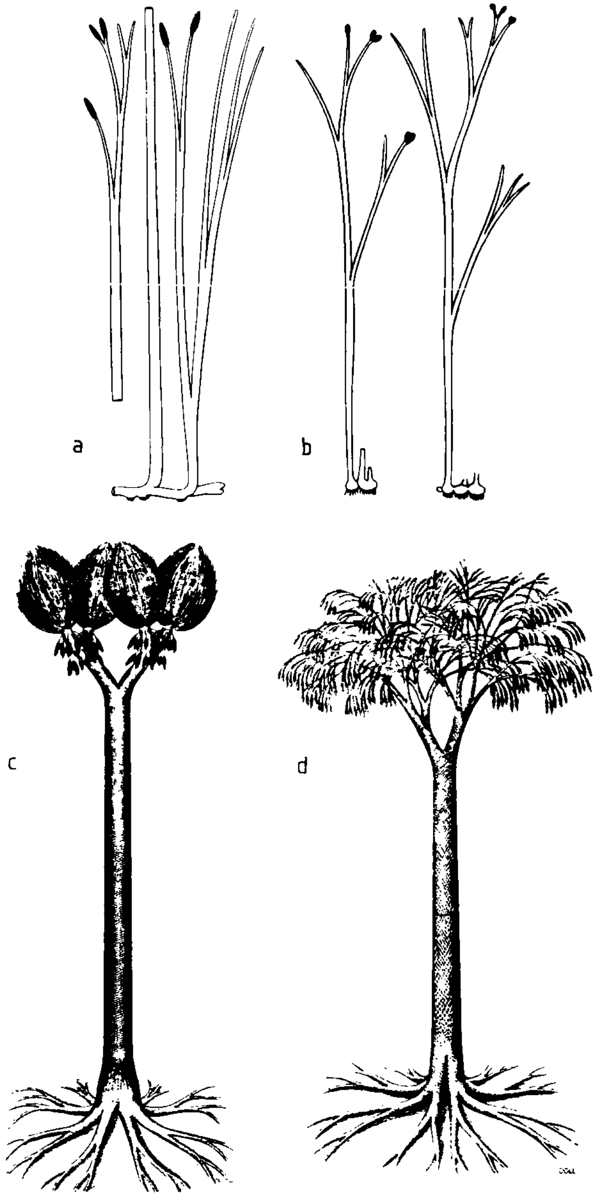

Figure 4: *Psilophyta*. 4a: *Rhynia* from the Devonian. 4b: *Horneophyton* from the Devonian (height: 25 cm). 4c: *Sigillaria* (licopsis) from the superior carboniferous (height: 30 m). 4d: *Lepidodendron*, another licopsis from the carboniferous with similar dimensions.

It was with the origin of the psilophytes at the end of the Silurian (410 million years ago) that the conquest of the terrestrial regions of the continents began. A plant covering was an indispensable precondition for the existence of more highly organized plants and for the first terrestrial animals.

The Devonian

The colonization of the continents made considerable progress during the Devonian (55 million years). The psilophytes reached their peak but were nonetheless extinct before the end of the system. Horsetails (calamites), club mosses (lycopods) and ferns (pteridophytes) developed from them. During the lower Devonian, these cryptogams were between a few centimeters and 2 meters tall. At the end of the system, genuine trees existed with heights varying between 8 and 20 meters. At this time, the first gymnosperms, ancestors of the conifers, appeared.

The Devonian vegetation, which was found on all continents, was a prelude to the development of terrestrial biota. The first snails (gastropods), freshwater lamellibranch, spiders, scorpions, and winged and wingless insects made their appearance.

Toward the end of the Devonian, a very important phenomenon occurred. The first terrestrial vertebrates appeared. The skeleton of these ancient quadrupeds, of which *Ichthyostega* (Fig. 5) was a typical genus, still contained several structures that were intermediary between those of fish and of amphibians (a caudal fin combined with the extremities of tetrapods to walk on solid ground; skull structure with fish-like characteristics). *Ichthyostega* have been found in East Greenland and in Australia. The discoveries indicate that these animals had a worldwide distribution as early as the Devonian.

The fish from which *Ichthyostega* descended were the crossopterygians that had developed lungs as well as their gills. With these lungs and their fins, equipped with a solid internal skeleton, they were capable of leaving the water and of venturing – even though slowly – on the land, for example, in order to abandon dried up lakes or rivers. One of their recent parents is the famous coelacanth (*Latimeria*).

Alongside these freshwater crossopterygians, there was a multitude of other fish, agnaths and "true fish" (*Pisces, Gnathostomata*). Without doubt, the largest of them was *Dinichthys*, which was 6

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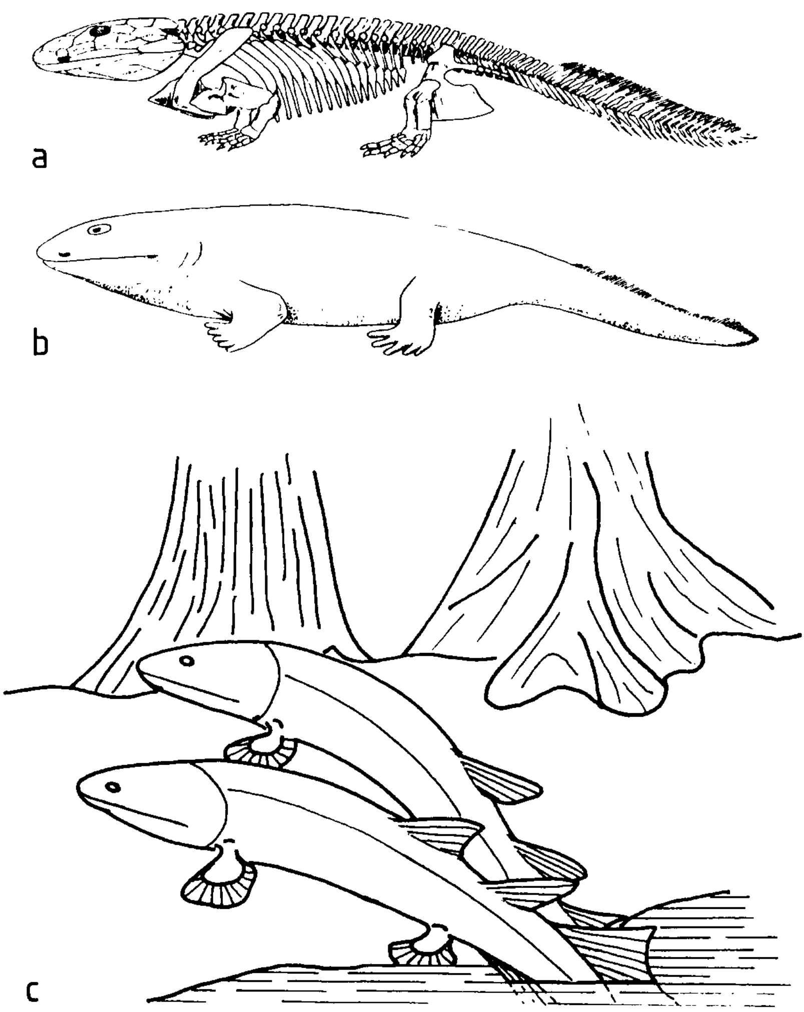

Figure 5: *Ichthyostega*. 5a: entire skeleton with tetrapodial extremities but with the remains on the end of a pisciform fin. 5b: reconstitution of the animal. 5c: crossopterygiens, getting out of the water.

meters long. It had bony protuberances that acted as teeth. But real teeth had already appeared among the ancestors of the selachians (cartilaginous fish) and bony fish.

Among marine invertebrates, there began the decline of the trilobites, after having reached their peak in the Ordovician. Graptolites became almost completely extinct. Devonian formations are characterized by brachiopods and echinoderms with peduncles. Corals, the third group of reef builders (after stromatolites and archaeocyathids), which, were already found in the Silurian, continued to develop during the Devonian.

There were important changes among the cephalopods. In the ancient Palaeobiotic, nautiloids dominated. During the Devonian, ammonites (ammonoids) appeared that lasted until the end of the Cretaceous, that is to say 300 million years (Fig. 6). Their main progressive characteristic was the greater complexity of the partitions between the successive chambers in the shell. This gave the shell a better resistance to the hydrostatic pressure of the water.

Conodonts were purely marine microfossils from 0.2 to 3 millimeters. Rare in the Cambrian, very widespread in the Ordovician and the Silurian, they reached their peak in the Devonian and the Carboniferous, became rare in the Permian, and disappeared at the Triassic. Devonian conodonts were shaped like combs, with more or less spiny plates and toothed bars. In fact, these were only isolated parts of a device made of calcium phosphate that surrounded the buccal orifice and served for the ingestion of nutritive particles, belonging to an animal with a soft body that could not be fossilized. Conodonts are very important to stratigraphers for marking the limits between eras and systems and for establishing correlations on a world scale, because they were very common and evolved quickly.

The Carboniferous

The Carboniferous (at 65 million years, one of the longest in the Palaeobiotic) is characterized by exuberant flora on all continents. The coalfields of the world almost all come from the Carboniferous, whence its name.

The group of vascular cryptogams like the horsetails (calamites), lycopods, and ferns (descendants of psilophytes) reached the peak of their evolution. They represent, especially the lycopods, the bulk of the marsh plants of the Carboniferous, the source of the coal in

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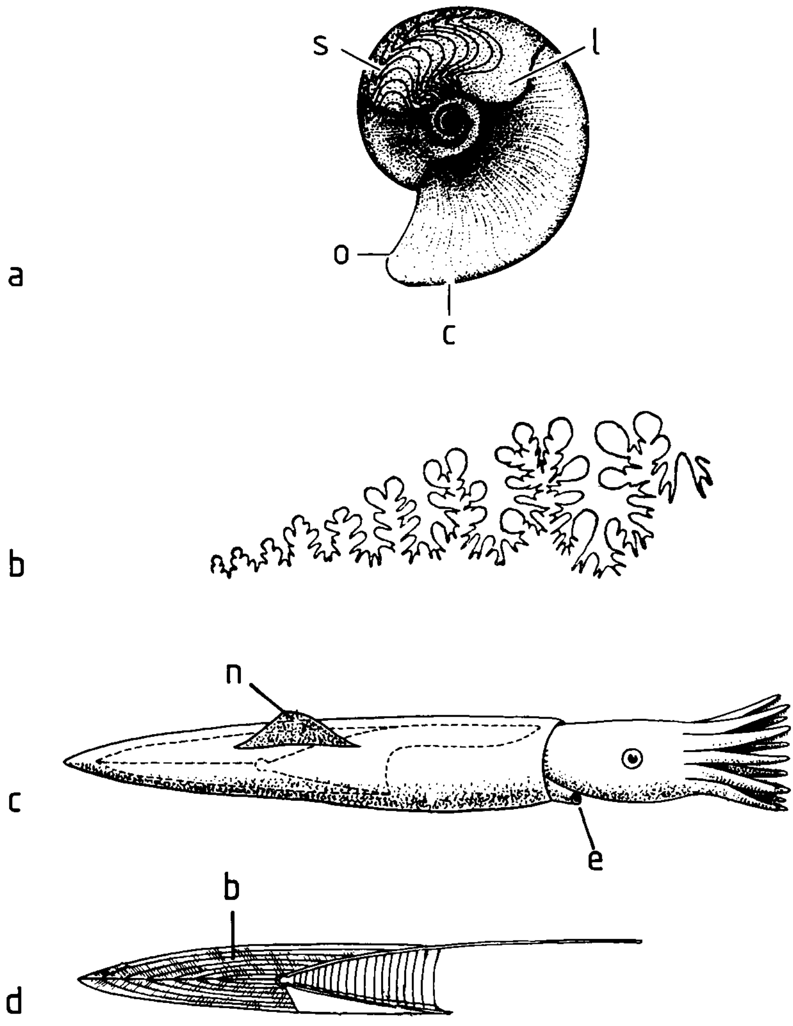

Figure 6: Cephalopod from the Jurassic and the Cretaceous. 6a: an ammonite shell (full scale). 6b: very complicated suture line of a jurassic ammonite (full scale). 6c: reconstitution of a belemite (full scale). 6d: internal skeleton isolated with the important rostrum element. (b) named by paleontologists "belemnite."

coal basins. The lycopods and horsetails reached heights of up to 30 meters and had trunks 2 meters in diameter. Ferns were also arborescent plants with a height of 10 meters (like their descendants in tropical regions today). The gymnosperms were represented by an extinct group, the pteridosperms. Toward the end of the Carboniferous, the first seed-bearing plants appeared in the form of conifers.

As a consequence of the spread and diversification of the flora, the continental fauna increased. There were already around 1,300 species of insects, including wingless forms (*Apterygota*) that were already known in the Devonian and winged forms (*Pterygota*). In the oldest forms, the wings could not be folded along the back (as in damselflies today). The best known insect, with a 75 centimeter wingspan, was the *Meganeura* genus. These "birds of the Carboniferous forest" (true birds did not appear until the Jurassic) had chewing devices and fed on plants and carrion.

The evolution of vertebrates continued on the continents. Amphibians predominated, with skeletons and skulls larger and more bony than those of salamanders and frogs today. They spent their entire juvenile stage in water, breathing by means of gills. When they became adult, they left the water and breathed by means of lungs. But they always had to remain close to an aquatic environment to lay their eggs, which did not yet have an envelope to protect them from drying out (*Anamnia*).

Along with these stegocephals (so called because of their completely ossified skulls, except for the eye and nose openings) the first reptiles emerged. They were at a higher stage of evolution, having better developed extremities, which gave the animals better mobility, and eggs enveloped in a hard membrane (*Amnios*, like those of birds and of the first mammals).

The agnaths and placoderms disappeared. As a consequence, the ichthyofauna of the Carboniferous does not seem all that strange to us. Marine ganoids and selachians predominated, including numerous species with flat teeth for breaking the shells of mollusks and brachiopods.

Among marine invertebrates, the trilobites were reduced to a few evolutionary lines. Beside the foraminifera of microscopic size known since the Cambrian, megaforms came into existence: fusulinids (genus *Fusulina*), ranging in size from a grain of wheat to a pea, they then formed into real rocks.

The Permian

During the Permian (40 million years), gymnosperms – that is to say the conifers, the ginkgoes, the Egyptian palms (*Cycadales*) – gained an ever greater supremacy over the cryptogams that dominated in the Palaeophytic. This means that the Mesophytic had already begun in the middle of the Permian, unlike the Palaeozoic (see table). In fact, the Permian Palaeobiotic is subdivided into in an upper part with gymnosperms and a lower part in which the cryptogams still dominated. The Mesophytic extends into the Triassic and the Jurassic up to the middle of the Cretaceous (see table).

The diversification of vascular plants on the continents, which had already begun in the Carboniferous, continued during the Permian. Palaeobotanists have identified four plant provinces on the great continental mass known as Pangaea. On the continents of the southern hemisphere grouped together under the name of Gondwana (after Gond, an Indian people), was found the flora of Gondwana. It was characterized by *Glossopteris*, a pteridosperm, that was totally lacking in the provinces of the northern hemisphere. On the other hand, the great lycopods (*Sigillaria* and *Lepidodendron*) that can be found in the North were absent from the Gondwana region. They were replaced by other genera like calamites and ferns.

In Australia, Africa, South America, and India, the strata containing the Gondwanian flora were covered by glacial deposits (moraines) with a depth of 1,000 meters over a distance of 1,000 kilometers. This was the result of significant glaciation of the southern hemisphere in the Carboniferous and the Permian. The small hard leaves and the rings of the gymnosperms reflect this cold climate, a product of past glaciation.

On the other hand, on the northern continents – that is the three provinces known as the Euro-American, the Angaran (after the river Angara that flows into Lake Baikal in north-eastern Asian), and the Cathaysian (after Cathay, the ancient name for China) – a more or less warm temperate climate dominated under which certain cryptogams and pteridosperms developed, for example the pteridosperm *Gigantopteris* in the province of Cathaysia.

Climatic and geological events – the formation of the supercontinent Pangaea through plate tectonics, the birth of mountain chains, the great glaciation of Gondwana, the climatic changes of

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the northern part of Pangaea – obviously influenced the continental fauna. For example, insect evolution "invented" the chrysalid phase that allowed it to survive in unfavorable climatic and feeding conditions.

In the Permian, reptiles underwent an enormous evolution. It was their first apogee. As in the plant biotas of Pangaea, it was marked, above all, by a great diversity of forms that were able to colonize a great variety of ecological niches. One can find the roots of the great saurian lines of the Mesobiotic, the mammalian reptiles that, at the boundary of the Triassic and the Jurassic, produced the first mammals and – for the first time in the history of the tetrapods – the return from a terrestrial life to an aquatic life, accomplished by the Mesosaurus genus.

On the other hand, marine fauna changed little. It continued under the conditions of the Carboniferous. Alongside the ancient goniatites, there appeared groups with more undulating and more complicated sutures. Trilobites became almost completely extinct. Brachiopods remained more or less stable with their "dorso-ventral spectacle case," except for the genus Richthofenia. Normally, shells of brachiopods were flat and fixed by the ventral valve to the bottom of the sea (Fig. 9). In Richthofenia, the ventral valve was extremely elongated and takes the form of a cone, attached by the point. The dorsal valve became opercular (there is here a curious convergence with certain polyparies and rudistids). The functional purpose for this "construction" was to reach a higher level in the water, where plankton food sources were less scarce than at the bottom.

The megaforaminifera, the fusulinids, and their relatives, the schwagerinidae, were also widespread in the warm seas of the Equator. Nonetheless, both groups became extinct at the end of the Permian.

The Secondary – Mesozoic – Mesobiotic Era

In the absolute chronology of the history of life, the Mesobiotic extends for 185 million years. A complex of systems known as Phanerozoic or Phanerobiotic lasted 570 million years from the Cambrian to the present (Holocene) (see table). That is to say that, with its 185 million years, the Mesobiotic comprises 32.5% of the Phanerobiotic (with its 320 million years, the Palaeobiotic comprises 56% of the Phanerobiotic).

The Triassic

The marine fauna of the Palaeobiotic was characterized by the great diversity of trilobites, graptolites, and brachiopods in its older phase and by goniatites in its later phase. All these groups had disappeared by the beginning of the Triassic (45 million years, see table) either through extinction, like the first two, or through evolution, like the last two. Ammonites are the dominant fossil guides, not only for the Triassic, but for the whole Mesobiotic. The characteristic point of recognition is the degree of complexity of their sutures, traces of the insertion of the partitions on the wall of the shell. In the ancient goniatite, for example, this same suture shows only one simple undulation.

In the majority of Triassic ammonites, these undulations were already very complicated. Like the goniatites, ammonites could float and swim, eating microscopic animals or larger organisms. The increasing complexity of the suture increased the stability of the shell in the face of hydrostatic pressure, allowing the animal much more flexibility in its dives. Thanks to this evolution, these mollusks prevailed over the brachiopods. However, a few lines of the latter survived and developed into a multitude of species in the Triassic and in the Mesobiotic (for example, the terebratulids and the rhynchonellida).

The ancient echinoderms, which had dominated during the Palaeobiotic, had their last representatives in the Permian. There remained only sessile crinoids with their peduncles. They were accompanied by echinoids (urchins), which were able to move thanks to the numerous spines on which the animal walked as though on stilts, and starfish (asteroids) capable of crawling by means of their arms.

Among fish, ganoids and selachians predominated. In their external appearance, they look rather like modern forms. The bodies of the ganoids were only covered with compact scales with a coating of enamel.

The flora of the Triassic seas contained green algae that produced a calcium carbonate skeleton (calcareous algae). They built great rocky reefs, notably in the eastern Alps.

The continental flora was dominated by gymnosperms. The giant cryptogams of the Permocarboniferous had disappeared. But it was the 1 to 2 meter tall lycophita (club mosses) that, through their morphology, showed adaptation to arid habitats (comparable to the modern cactus). For example, they can be found in the lower Triassic in France and Germany.

The stegocephalians – large amphibians (skull length: 1 meter), with heavy proportions and short limbs, living on the edges of lakes and lagoons – had a last flourish but became extinct toward the end of the Triassic, without leaving any descendants. The first dinosaurs and the first turtles appeared. Other groups returned to an aquatic way of life, precursors of the ichthyosaurs and plesiosaurs of the Jurassic, for example.

Among mammalian reptiles, evolution was so advanced that, toward the end of the Triassic, the mammiferous type had almost reached its definitive level of organization.

The Jurassic

With the beginning of the Jurassic (65 million years, see table), an important event occurred among the ammonites. Many genera of the Triassic, which were often extremely specialized, became almost totally extinct, with the exception of 3 lines (the genus Phylloceras, for example, crossed over the Triassic-Jurassic boundary and became the source of a second great wave of diversification of ammonitic fauna in the seas of the Jurassic and Cretaceous). The causes of this phenomenon are still unknown. Already represented by the precursors of the Triassic, belemnites were another group of cephalopods that were very widespread in the Mesobiotic. In their external appearance, they were very like the cuttlefish of today (genus sepia), with a head, tentacles, a funnel, and lateral fins, but the posterior section was equipped with a rostrum. This is a long calcareous body in the form of a cigar that carries additional lateral fins. These rostrums are all that remains of the belemnites.

During the Jurassic, sea urchins appeared that had retained the pentaradial base structure but with a distinctly bilateral shape to the capsule. These bilateral sea urchins were descended from "regular" forms. Regular sea urchins lived in coastal environments with hard sea floors, as they do today. Bilateral symmetry seems to have been an adaptation to silty environments into which these sea urchins buried themselves, eating mud, whereas regular sea urchins, walking on the ground by means of their spines, were provided with maxillae to seize larger objects (small bivalves, gastropods, algae, and so on).

Among marine fish, the first modern teleosts appeared. They had a completely ossified vertebral column that replaced the cartilaginous structure of their ancestors. On the other hand, the scaly shield of a ganoid of the Palaeobiotic and the Triassic was reduced. The teleosts lived alongside selachians in reduced numbers, but with special adaptations. These were the ancestors of today's rays, for example, with a flattened body and pectoral fins enlarged into the shape of wings. After the mesosaurs of the Permian, there was, in the Mesobiotic oceans, a second case of terrestrial reptiles returning to marine life – the ichthyosaurs whose external aspect bore an almost perfect resemblance to that of a dolphin, with an enormous caudal fin, an essential organ of propulsion, but in the vertical position. Another kind of adaptation that also had precursors in the Triassic was that of the plesiosaurs. Their even limbs were very developed and transformed into oar-like limbs for swimming, which must have played the main role in movement, as with turtles. Along with these marine forms, which became extinct at the end of the Cretaceous, there existed crocodilians that, since the Tertiary, were confined to continental waters.

On the continents, the reptiles reached a second apogee. Various dinosaurs dominated the continental regions (Fig. 7). Among them were predators with sharp and pointed teeth that hunted herbivores with small teeth. There were some groups of giants among the herbivores. The genus *Diplodocus* could reach a length of 30 meters and weigh more than 40 tons. Diplodocuses have been found in the upper Jurassic of North America, East Africa, and China. They were spread almost everywhere around the globe, and these giants existed 70 million years before the extinction of the last dinosaurs, at the end of the Cretaceous.

In the Jurassic, the reptiles, called pterosaurs, also succeeded in conquering the air. The fourth digit of their anterior extremities became extremely elongated and supported an alar membrane, a sort of fold of skin, that was inserted in the lateral sections of the body (Fig. 8). But at this time, there also appeared an ancient member of the class of birds – the *Archaeopteryx*. It was discovered in a lagoon deposit in southern Bavaria. It had the skeleton of a bipedal reptile, the size of a small chicken with a long tail, but equipped with genuine feathers. The ancestors of these two experiments were small bipedal reptiles, probably from the Triassic, whose forearms were free and not used for quadrupedal movement. This was the fundamental precondition for the transformation of anterior extremities into new constructions used for flying.

Finally, the evolution of mammiferous types, which had begun during the Triassic with the "mammalian reptiles," was almost completed. Small pantotheres, the size of a mouse and weighing 100 grams, were probably twilight and nocturnal animals, which were thus able to establish themselves in niches that were inaccessible to the dominant great reptiles.

The Cretaceous

As in the Jurassic, the continents were dominated by large dinosaurian reptiles during the Cretaceous (75 million years, see table). Among them were many bipedal forms. Among European dinosaurs, the genus *Iguanodon* is the best known. In an ancient valley of the lower Cretaceous in Belgium near Bernissart, a score of skeletons of this animal have been discovered. They had a height of 5 to 6 meters in a standing position, and their length exceeded 10 meters. They were fully adapted to the bipedal stance, with their tail acting as a balance, not touching the ground while they ran. Their teeth, reminiscent of those of today's iguana, are an indication of an herbivorous way of life. There are many comparable genera of *Iguanodon* in America, Africa, and China. One of their predators was the largest carnivore that had ever existed, the tyrannosaur, whose size exceeded 15 meters. Its enormous skull was armed with long, pointed teeth. Alongside the bipeds, there were also descendents of Jurassic quadrupeds, strange forms like stegosaurs, with large bony plates on its back, or triceratops, with three bony horns on the top of the cranium that terminated at the back in a large bony collar. This may have protected the neck of the animal from attacks by predators.

The pterosaurs underwent considerable increases in size at the same time. At the end of the Cretaceous, there were animals with a wingspan of more than 7 meters (*Pteranodon*). The pterosaurs fished, living near the coasts and capturing their prey while skimming across the surface of the sea.

During the upper Cretaceous, there still existed the first true birds. They did not have a tail but had jaws equipped with teeth (unlike modern birds with their horny beaks).

During the Cretaceous, the evolution of the basic structures of the two great groups of mammals that were to dominate the Tertiary period was realized: the marsupials (contemporary

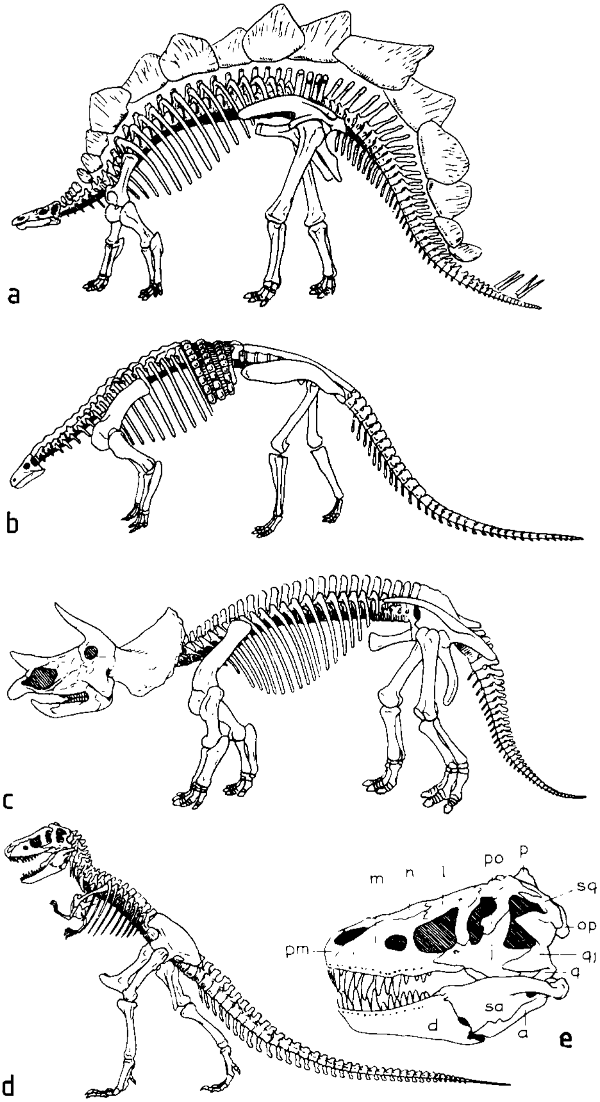

Figure 7: Dinosaurs from the Jurassic and Cretaceous eras. 7a: *Stegosaurus* (length approx. 8 m). 7b: *Nodosaurus*, with a bony band on the carcass (length, 2.7 m). 7c: *Triceratops*, superior Cretaceous. The *Triceratops* outlived the other dinosaurs.

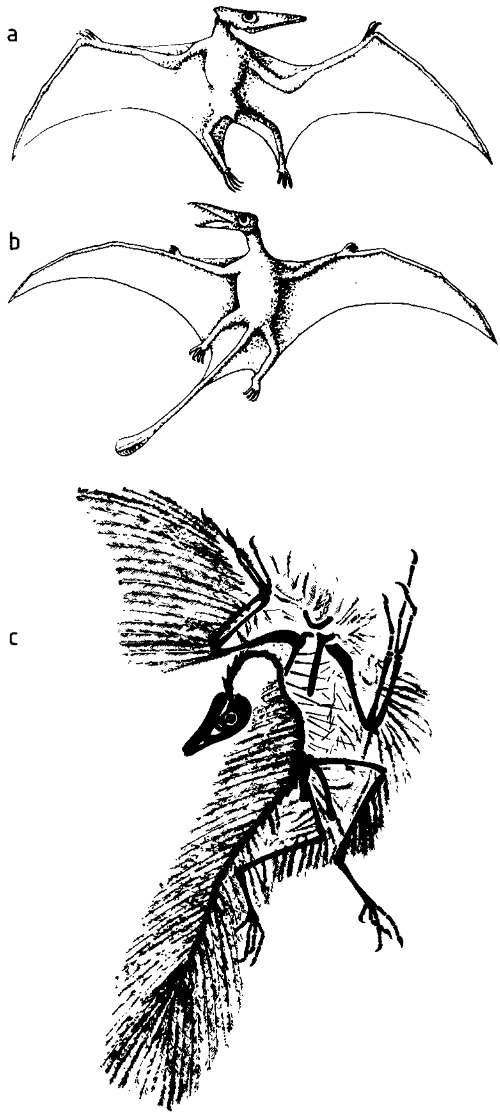

Figure 8: Pterosauriens and *Archaeopteryx*. 8 a, b: Pterosauriens with membranous wings. 8a: *Pterodactylus*, genus without tails (length 10 cm). 8b: *Ramphorhynchus* with a long tail. 8c: *Archaeopteryx*, how the skeleton looked immediately following the death of the animal (full scale). The feathers undoubtedly indicate a bird.

dasyures, kangaroos, koalas, opossums, and so on) and the placental mammals (all other types of mammals where the foetus developed completely in the uterus).

Also, at the end of the Cretaceous, there were already marsupials, insectivores (contemporary hedgehogs, shrews, moles), primates (contemporary lemurs, simians, hominids), "carnivores" and ancient ungulates. All these groups were undoubtedly still small in size and were at an archaic level of organization.

On the continents, an important transformation took place among the plants. While a flora of ferns and gymnosperms, known since the Triassic and the Jurassic, still characterize the lower Cretaceous, at the beginning of the upper Cretaceous, there appeared – almost everywhere around the globe – angiosperms (having flowers, scents, and seeds). Modern groups were already in existence, for example, beech, willows, plane trees, laurels, magnolias, and so on. The reasons for this sudden worldwide appearance are still unknown. In any case, the existence of plants of this kind favored, or even provoked, the blossoming of insects and birds during the Tertiary.

Thus the great transformation of the flora was achieved before the great change in the animal kingdom. The Cenophytic began around 30 million years before the beginning of the Cenozoic. An identical phenomenon was observed at the end of the Primary era (p. 87).

Fundamentally, the marine fauna was a continuation of the Jurassic fauna. Among bony fish, teleosts definitively became predominant. As for ichthyosaurs and plesiosaurs, they were, from this time on, confronted by a new competing group, members of the enormous family of lizards adapted to marine life, the mosasaurs, carnivorous reptiles with a body elongated to 12 meters and extremities transformed into paddles.

Ammonites and belemnites showed the same richness as in the Jurassic, but toward the end of the Cretaceous, they diminished rapidly, becoming extinct before the end of the Tertiary.

An "aberrant" group developed among the lamellibranchs, the rudistids. They had one valve (the right) that was cylindro-conic, enlarged and fixed to the bottom (quite unlike the bivalves). The other valve (the left) was small and flat and acted as a lid. Hippuritacea were very widespread in the Mediterranean area in the upper Cretaceous and may have exceeded 40 centimeters in length. At this time, they formed very extensive reefs in the warm seas of the area in question. Hippuritacea were remarkably analogous to the brachiopods of the Permian group *Richthofenia*. Here one valve (the ventral) was fixed and elongated into a cone, the other valve (the dorsal) was a flattened lid. Many solitary corals show a similar evolution toward an elongated and conic skeleton. The functional purpose of these "evolutionary convergences" was probably to reach higher levels at the bottom of the sea in order to obtain richer and more specialized food sources.

Foraminifera, which were known since the Palaeobiotic, were extremely important microfossils in the Jurassic and Cretaceous. Along with ostracods, they were very abundant and very varied in the rocks of these systems, and thus represent important tools for the geologist. The Cretaceous is the second system in which large foraminifera (macroforaminifera) are in evidence. The flattened shells of the *Orbitolina* group sometimes reached a significant size (up to 6 centimeters in diameter). It is interesting to note that the permanent companions of the foraminifera since the Cambrian, the microscopic, unicellular radiolarians with their siliceous skeletons, never reached the same large dimensions.

The Cenozoic – Cenobiotic Era

The Cenozoic (or Cenobiotic) lasted for 65 million years. Some time ago, the two traditional eras, Tertiary and Quaternary, were reunited into the idea of the Cenozoic era. But they have reappeared as the Tertiary and Quaternary systems in recent chronologies (see table).

At 65 million years, the Cenobiotic is the shortest of the three great eras of the 570 million year Phanerobiotic (the Palaeobiotic, 320 million years; the Mesobiotic, 185 million years). In percentages, they represent 56.1 percent, 32.5 percent, and 11.4 percent.

These differences have nothing to do with a kind of acceleration in the evolution of life, but they reflect a history of palaeontological research in the first half of the nineteenth century. The founders of palaeontology and historical geology (or biostratigraphy) were fascinated by changes in the composition of fauna, especially marine, such as the sudden appearance of all the phyla of skeletal invertebrates at the beginning of the Cambrian, which is the definition of the boundary between the Proterobiotic and the Palaeobiotic (in today's notation, the beginning of the Phanerobiotic); or the extinction of the trilobites at the end of the Permian (even up to the present, no Triassic trilobite has been found) and the appearance of ammonites at the dawn of the Triassic, denoting the boundary between the Palaeobiotic and the Mesobiotic; or the extinction of ammonites, belemnites, great marine reptiles (ichthyosaurs and so on), terrestrial dinosaurs, and pterosaurs, and the explosive evolution of placental mammals at the beginning of the Tertiary, indicating the boundary between the Mesobiotic and the Cenobiotic.

For the founding fathers of palaeontology, these were great breaks that provided the reasons for the division into eras. But they did not have any real arguments in terms of their extent in absolute time. It was only with the development of an absolute chronology and radiometric dating that the temporal disharmonies have become evident.

The Tertiary

For a long time, the Tertiary (65 million years, see table) has been subdivided into five stages.

Quaternary	
Pliocene	Neogene (22 million years)
Miocene	
Oligocene	
Eocene	Palaeogene (43 million years)
Palaeocene	
Cretaceous	

The three lower series have been grouped together as the Palaeogene and the two upper series as the Neogene.

As we have seen, the beginning of the Tertiary was marked by important changes in many groups of the animal kingdom. The most spectacular phenomenon was the rapid expansion of mammals. There are a variety of reasons for this. They are vertebrates with a constant temperature that have a body covered with hair, making them less sensitive to changes in temperature and climate. They are adapted to a variety of ways of life and to all sorts of food, thanks to an enormous diversity of chewing devices. Another characteristic gave mammals a rapid preponderance in their aquatic, terrestrial, or aerial ecological niches: the extraordinary development of their central nervous system.

The extinction of many reptiles at the end of the Cretaceous left vacant many niches that mammals were able to occupy from that time on. In addition, the worldwide withdrawal of the oceans at the end of the Cretaceous created new terrestrial regions, available for colonization.

The evolution of Tertiary mammals shows at least two phases of expansion. The first covered the Palaeocene and the Eocene. The second began in the Oligocene and continues today. Among placental mammals (*Eutheria*), the insectivores were in a privileged position to give birth to other orders. But from the end of the Cretaceous, the first primates appeared. Like the insectivores, they were small animals that already showed signs of a high level of evolution in the cranial region.

Beside these groups, a large quantity of *Eutheria* existed during the Palaeocene that had no equivalent in recent fauna. These animals are grouped under the name condylarths (*Condylarthra*), already known in the late Cretaceous, with others under the name of creodonts (*Creodonta*). The first are generally considered to be herbivores or omnivores, the others to be carnivores. Both groups have very short extremities with five digits, like contemporary carnivores (lion, dog), but with enormous heads relative to their bodies, and, by contrast, very small brains. The condylarths were characterized above all by teeth that were less adapted to cutting, and more to grinding, suitable for herbivorous or omnivorous feeding. The size of these animals was no greater than that of a wolf. Toward the end of the Palaeocene and in the lower Eocene there lived larger animals (up to 3 meters long like a small African rhinoceros), descendents of the condylarths called pantodonts, whose teeth indicate that they were herbivores.

Thus, three groups existed in the Palaeocene: a) small omnivores and herbivores (insectivores, primates), b) herbivores/omnivores and medium sized carnivores (condylarths and creodonts), and c) large herbivores (pantodonts).

To achieve the 3 meter size of the pandodonta *Coryphodon* of the upper Palaeocene, which was descended from the oldest pantodonta, the tetraclaenodon of the middle Palaeocene, which was the size of a sheep (1 meter), evolution "needed" 6 million years. By comparison, the evolution of the horse from *Hyracotherium* (beginning of the Eocene, size of a fox) to Equus (early Pleistocene) took 50 million years.

The flourishing of mammals during the first expansion not only produced a community *sui generis*, but opened up possibilities for speeding up evolution. Whatever the reasons for this phenomenon, the vacancy of ecological niches must have been favorable to this acceleration.

In the Eocene, several groups like the large pantodonts and some creodonts continued to evolve alongside the dinocerata (Fig. 9). These were also large animals with three pairs of bony processes on the skull that could reach 4 meters in length (*Uintatherium*). Extremely specialized, they became completely extinct at the end of the Eocene.

Among the last condylarths (ancient ungulates), there were two groups whose locomotive devices underwent an interesting morpho-functional transformation – a reduction in the number of digits. The feet of the condylarths had five digits. The reduction of the lateral digits (I–V) and the elongation and erection of the central digits considerably increased the speed of movement, that is to say, the capacity of these herbivores to escape the attacks of their enemies.

During the Eocene, evolution brought into existence two solutions of this kind. The perissodactyls (the modern rhinoceros, tapir, horse) had a tendency to an unequal symmetry of digits II, III, and IV, through the strengthening of digit III (the central) and through the shortening of digits II and IV. By contrast, the artiodactyls showed an even symmetry through the elongation and enlargement of two digits, III and IV (the middle),with digits II and V (the lateral) remaining, but smaller in size.

The most famous of Eocene perissodactyls was the genus *Hyracotherium* , with which the evolution of the horse began in North America. At the same time, a dozen other groups existed in Eurasia and North America that had a perissodactyl structure of the extremities, among which were large, heavy forms (titanotheres) and others resembling the hippopotamus in their proportions (amynodontidae).

In general, Eocene artiodactyls were small animals with teeth similar to those of condylarths. Nevertheless, a multitude existed, particularly in Europe, but the majority became extinct during the Eocene.

However, at the end of this epoch, one still finds animals the size of a donkey (*Anoplotherium* in the gypsum quarries of Montmartre).

Within the carnivores, creodonts dominated. They were very varied, and, toward the end of the Eocene, the first modern forms

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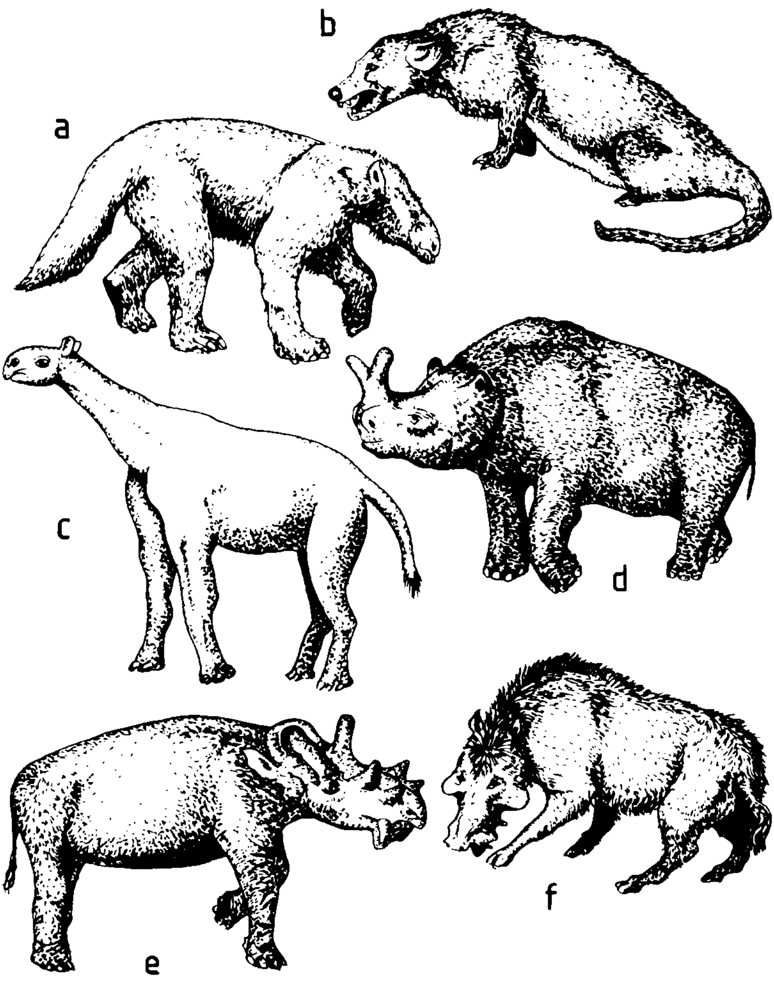

Figure 9: Mammals from the first phase of radiation of the ancient Tertiary era (Paleogene). 9a: *Barylambda*, Paleocene, archaic form, herbivore (length ca. 2 m). 9b: *Mesonyx*, eocene, archaic carnivore (ca. 2 m). 9c: *Indricotherium*, gigantic rhinoceros from the Oligocene (the largest terrestrial mammal). 9d: *Brontotherium*, Oligocene, with the dimensions of a rhinoceros . 9e: *Uintatherium*, Eocene, large form with three pairs of bony protuberances on the skull. (length 4 m). 9f: *Archaeotherium* (length of skull 60 cm), with the general appearance of a gigantic pig. 9c–f: herbivores.

appeared. They were still small, about the size of a marten.

Rodents also acquired a special importance at this time. At the beginning of the Eocene, they resembled squirrels. But an extraordinary diversification occurred in a very short time. There was a first expansion during the Eocene, followed by a second at the beginning of the Oligocene, characterized by an advanced dental structure.

The Eocene was also the time of the appearance of the first marine mammals. These were the cetaceans (ancestors of contemporary whales and dolphins). The jaws of these early forms were still equipped with strong teeth. Because their carnivoroid teeth were of considerable size (the skulls reached between 60 and 120 centimeters in length), and because the anterior extremities were transformed into fins, it has been suggested that these ancient cetaceans replaced the great aquatic saurians – like the ichthyosaurs, plesiosaurs, mosasaurs, and marine crocodiles of the late Cretaceous – in their ecological niches.

Among primates, a primitive group has relatives today – the lemurs of Madagascar. They existed in Europe and the United States. Other forms known in the two regions since the Eocene are related to the little tarsier with enormous eyes that today lives in Malaysia. But in the Eocene, true monkeys (superior primates) had not yet appeared.

At the beginning of the Eocene, an important palaeo-biogeographic event took place – an exchange between the mammalogical faunas of Europe and America via a northern route consisting of Greenland, Spitsbergen, or Norway. According to the theory of plates, the North Atlantic had not yet opened up. There was solid land between the northern parts of America and Europe that allowed reciprocal migrations. But it was above all Europe that was enriched by new groups (*Hyracotherium* , for example).

Taken together, the mammals of the Oligocene show a profound modernization. A whole series of ancient groups, typical of the Palaeocene and Eocene, became extinct while new forms appeared that were the ancestors of most of the groups that exist today. The second phase of expansion, which would bring into existence recent mammalogical fauna, began with the Oligocene.

In this way, Europe was invaded by many groups belonging to the perissodactyl and artiodactyl groups. This immigration from Asia, called "the great divide," included, for example, the ancestors of the rhinoceratidae, the great artiodactyl (*Anthracotherium*, an ani-

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mal typical of the European Oligocene), of modern tapirs, of wild boar, and of ruminants (contemporary deer, antelopes and so on), though these last did not yet have antlers or horns.

In North America and Asia, the Oligocene was also an epoch of modernization of the mammalogical fauna. In America, there was the spectacular and well known evolution of the horse and of the camel. In the Eocene, camels were small, but they reached enormous dimensions with extended necks like those of giraffes. During the Pliocene, the camelidae emigrated to southern America, where they remain as llamas. Another branch crossed the Bering Strait to Asia and Africa, where one finds the two contemporary forms.

The fauna of southern America has a very different history. There, the Palaeocene was dominated by condylarths that had migrated from North America. During the Eocene, an almost total geographic isolation developed that produced many groups of "ungulates" that had nothing in common with those of North America or Eurasia. They all became extinct during or toward the end of the Tertiary. Only one example typical of South American mammals still exists: the edentates. Known since the Palaeocene, they produced the armadillos, sloths, and ant-eaters of today. Another unusual characteristic of the Tertiary fauna of South America is the complete absence of genuine carnivores. Their role has been filled by marsupials that have probably been in existence on the continent since the Cretaceous. The modernization of the current South American fauna took place at the end of the Pliocene as a result of North American immigration.

The important element of the second phase was the appearance of rodents and lagomorphs (the ancestors of hares and rabbits). Among the Oligocene rodents, there were ancient groups that have become extinct, but also the roots of Neogene and contemporary groups (mice, hamsters, dormice, squirrels).

During the Miocene, the modernization of the mammalogical fauna continued through the evolution of Oligocene lines as well as through the appearance of new immigrants, for example the mastodonts in Eurasia (ancestors of the elephants) and higher primates coming from Africa. As for tridactyl Equidae, first the genus *Anchitherium* and then the genus *Hipparion* came from North America via Beringia. A great event also occurred among the ruminant artiodactyls, the appearance of the first forms equipped with horns, simple at first but, later, forked. The first horned ruminants, precursors of the antelopes, gazelles, goats, sheep, and cattle, also appeared, grouped together under the name of bovidae.

Carnivores, already well represented during the Oligocene, showed some similarities with the ancestors of dogs, hyenas, and mustelines as well as with extinct forms like the large amphicyonidae, a cross between the dog and the bear. Typical bears began their evolution during the Miocene. Typical among the big cats were "felines with 'saber tooth' upper canines" (*Machairodus*). Rodents continued to diversify.

The Pliocene was a relatively short period of approximately 4 million years that had a fauna almost identical to that which exists today. Even so, one can observe important palaeo-biogeographic events during this period. The mammalogical biotas of South America continued to show signs of isolation, with the exception of the transatlantic passage of rodents from Africa to the Brazilian coast during the Miocene. And at the end of the Pliocene, the Central American isthmus united the northern and southern parts of the continent and allowed an enormous migration from the North to the South. This included genuine carnivores, horses of the genus *Equus*, tapirs, camels of the llama group, a certain group of cervidae, a few mastodons, and hamsters, which contributed to the formation of the characteristic community existing today in the South American continent.

At the opposite extreme from the South American continent, Australia had been separated from the rest of the world since at least the beginning of the Tertiary. This prevented invasion by the higher mammals (*Eutheria*). Only marsupials invaded this continent and adapted to a whole series of different ecotypes. Besides the best known Australian marsupials, the herbivorous kangaroos, there exist many other small herbivores, some tree-dwellers (the koala), and burrowers, hunted by flesh-eating types such as the largest, the Tasmanian wolf, or small species that copied the small cats, martens, or otters of the world of *Eutheria*. Certain Quaternary deposits have produced giant herbivores, the size of a rhinoceros, (*Diprotodon*) that are now exinct.

Mammals were certainly the dominant animals in the terrestrial biotas of the Tertiary. The great dinosaurian, terrestrial, aquatic, and aerial reptiles characteristic of the Mesobiotic became extinct, but turtles, crocodiles, lizards, and snakes crossed over the boundary between the Cretaceous and the Tertiary and represent today the modest remnants of the reptilian era of the Mesobiotic.

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Birds acquired a multitude of forms. Practically all the modern orders were already in place parallel to the development of angiosperms (flowering plants), indicating a sort of co-evolution.

In the seas, the teleost fish continued to dominate, but even so, the selachians produced giant forms (12 meters long) with teeth 12 centimeters long. Brachiopods, which had been fairly common in the Cretaceous, were reduced to an almost insignificant state. Their ecological niches were occupied by gastropods and bivalves that prospered especially in the warm oceans. Thus, these two groups become the first "guide fossils" for the five subdivisions of the Tertiary – Palaeocene, Eocene, Oligocene, Miocene, and Pliocene. At present, it is rather the foraminiferas and other planktonic microfossils of plant origin that play this role.

For the third time in the history of microscopic unicellular animals, macroscopic groups appeared. Among them are to be found the nummulites of the lower Tertiary, whose flat or lenticular discs had a diameter ranging from a few centimeters to 12 centimeters (Fig. 10). Their spiral shells were subdivided into a large number of chambers, separated by partitions. Benthic animals, they dwelled on the floors of warm seas, especially in the Eocene. For example, the coarse limestone on which Paris is built is full of nummulites.

The Quaternary

The Quaternary is the shortest of all the Phaneroboitic systems, with a duration of 1.6 million years (see table). When the term originated in 1829, geologists had no precise ideas about what an absolute chronology might have been.

The Quaternary is subdivided into the Pleistocene (that followed the Pliocene) and the Holocene (the latter with a length of 10 thousand years, encompassing the present).

This period of time is too short for any fundamental transformation to have taken place. Only mammals showed some evolution among rodents, carnivores, ungulates, and elephants.

This evolution was influenced by an interesting phenomenon. During the middle and upper Pleistocene, glaciation has been recorded several times in the north of the Eurasian and American continents. In Europe, the glaciers of the high nordic mountains advanced, on several occasions, as far as the great North European plain. The glaciers of the Alps advanced, in their turn, as far as the

Danube. These multiple glaciations were interrupted by interglacial phases, when the glaciers contracted.

The mammals of the Pliocene adapted, little by little, to these climatic changes. During these periods of glaciation, reindeer, mammoths, large cave bears, musk oxen, blue foxes, and lemmings lived in central and southern Europe. Other species like the chamois, ibex, and marmot had already taken refuge in the Alpine mountains. The mammoth and the cave bear are extinct. The companion of the mammoth, the woolly rhinoceros, also became extinct.

The habitats of the interglacial biota were very different. Among mammals, one finds species adapted to life in the forest like the wild boar, roe deer, red deer, European bison, fox, badger, brown bear, wild cat, squirrel, and lynx. Among this "warm" fauna, one can also find forms that have since become extinct like the *Rhinoceros kirchbergensis*, *Elephas antiquus* and the aurochs. This contrast between the "cold" and "warm" faunas, which is also reflected in the flora and fauna of the terrestrial gastropods, began to become apparent during the middle and especially later Pleistocene. During the early Pleistocene, the contrast was less marked.

In tropical and subtropical regions, there was a related change. There were periods of rain (pluvial) and periods of drought (interpluvial) that, nonetheless, do not coincide exactly with the glacial and interglacial periods of the northern regions.

The maritime biotas were also affected by climatic changes. For example, during the early Pleistocene, bivalves and gastropods lived on the English coast that are found today in the vicinity of Iceland and Greenland (*Cyprina islandica, Astarte borealis, Cardium groenlandicum, Yoldia arctica*). At certain times, "cold" species, such as *Cyprina islandica* and foraminifera *Hyalinea baltica*, even reached the Mediterranean. In addition, on the coast of Schleswig-Holstein in Denmark, deposits from an interglacial sea have been found that contain "Lusitanian" mollusks, that is to say, forms that live today in the geographical latitude of Portugal, which were therefore more demanding from the thermal point of view.

Finally, the Pleistocene is obviously unique in that it witnessed the development of Man and his cultures.

The contemporary geological period, the Holocene, began with the retreat of the glaciers in the northern hemisphere. The animals and the vegetation of the last glaciation (the Wurmian glaciation)

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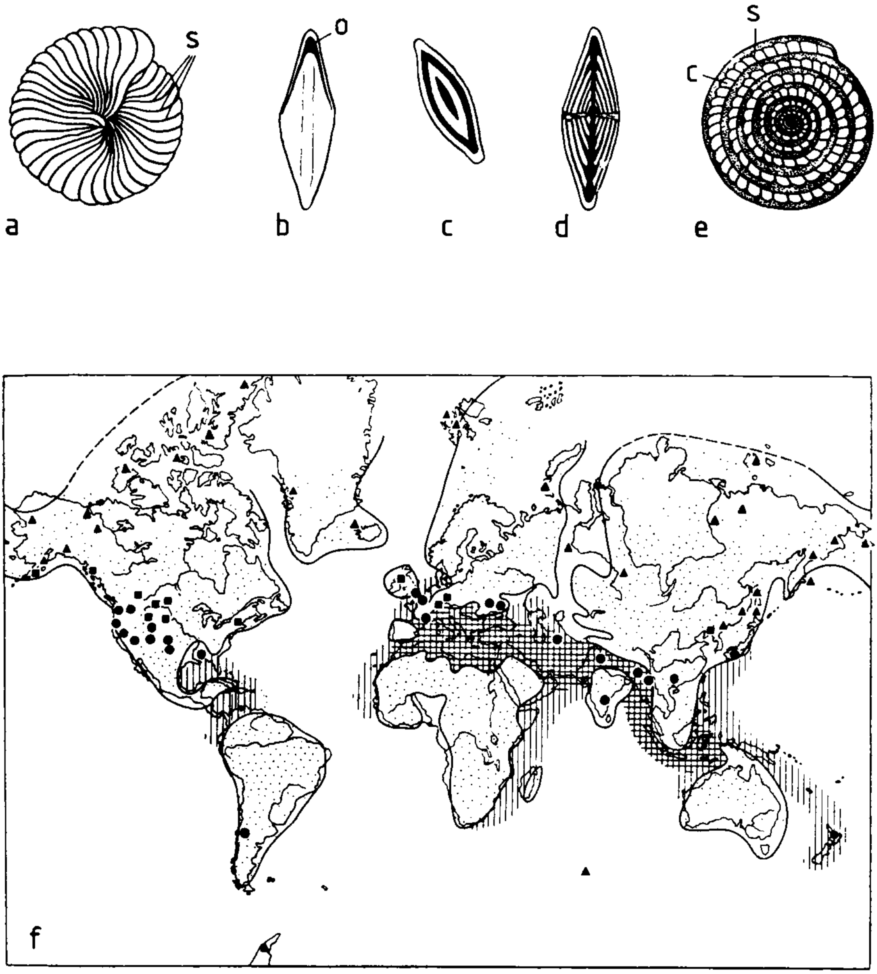

Figure 10: Nummulites and their distribution in the Eocene. 10a: shells, in diverse sections (enlarged). 10f: world map of the Paleogene with the distribution of nummulites, combined with the characteristics of continental vegetation. Vertical lines indicate the distribution of nummulites; dots, subtropical flora; squares, transient floras; triangles, temperate floras. The coincidence between the distribution of the nummulites and the subtropical floras is obvious.

followed the ice sheet and the melting Alpine glaciers retreated to their contemporary habitat. And the forest from the more southerly regions encroached little by little into the empty lands.

* * *

Unesco's program on Man and the Biosphere (MAB)

– The flora and fauna of the world today have been called the biosphere in close relation with the lithosphere and the atmosphere. From the point of view of historical palaeontology, the recent biosphere is the evolutionary product of earlier biospheres (palaeobiospheres).

– The aim of historical palaeontology is to decipher these palaeobiospheres with their palaeobiotas and to reconstruct ecological conditions ("ecosystems") within the long-established framework of classical systems like the Tertiary, Triassic, Devonian, and so on.

– Fossils are the documents. It is well-known that not all the organisms of past worlds have been preserved. For example, plant and animal organisms without skeletal tissue have very little chance of being fossilized. The mineralogical transformation of fossil-bearing strata by certain geodynamic agents or the covering of these strata by later deposits can also prevent or delay access to the documents. It is necessary to make allowances for the gaps encountered in the documentation.

– In this way, the deciphering of the palaeobiospheres remains more or less fragmentary. Nonetheless, palaeontology shows that the palaeobiotas were much more numerous than those of the recent biosphere, and that organisms that became extinct and have disappeared form an enormous, differentiated biomass compared to that which exists today.

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