PALEOZOIC HISTORY

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Summary

The Paleozoic era is marked by an unprecedented boom of invertebrates and a subsequent spread of higher plants, fishes, and amphibians. Not only individual plant and animal groups, but also whole ecosystems developed, and still other new habitats were colonized. We may well say that some habitats, such as coral reefs, were created by living organisms only during the Paleozoic. At the dawn of the Paleozoic, complex communities of multicellular organisms lived exclusively on the bottoms of shallow seas, while other environments were characterized by only very simple ecosystems or contained practically no life at all. By the end of the Paleozoic, shallow seas as well as ocean waters, seafloor sediments, lakes, rivers, and dry land were densely inhabited. The formation of soil cover greatly enhanced the multitude and variety of life on land.

The Paleozoic lasted 340 million y, which is more than the Mesozoic, Tertiary, and Quaternary together. It is subdivided into six systems, with the first four—the Cambrian, Ordovician, Silurian, and Devonian—called Lower Paleozoic, and the last two—Carboniferous and Permian—called Upper Paleozoic. Some authors subdivide the Paleozoic into Lower (Cambrian to Silurian), Middle (Devonian), and Upper (Carboniferous and Permian).

Representatives of all the major animal phyla appeared at the very beginning of the Paleozoic, during the Cambrian: sponges, coelenterates, brachiopods, molluscs, arthropods (such as trilobites), echinoderms, and the earliest Chordata. In some cases, a long time elapsed after the appearance of the first representative before the whole group spread to reach a wider distribution. For example, the first rare occurrences of demonstrable vertebrates date to the upper Cambrian, but a real boom began only some 100 million years later. Trilobites represent more than half of the known Cambrian fossil taxa. However, their proportion progressively decreases with time. They became insignificant by the Upper Paleozoic and finally became extinct at the end of the Paleozoic. Nautiloid cephalopods were highly important from the Ordovician to the end of the Paleozoic. Corals became significant in the Silurian, fish in the Devonian, amphibians and insects in the Carboniferous, while reptiles became one of the leading groups in the Permian. Crinoids prevailed among Paleozoic echinoderms. Graptolites, ranked within the phylum Hemichordata, were of high importance in the Ordovician and Silurian, forming small bushy or rod-like colonies floating at or near sea surface. Plants underwent a tremendous advancement during the Paleozoic. The photosynthetic process was still limited to algae and blue-green algae living in the sea during the Proterozoic and early Paleozoic. From the mid-Paleozoic, however, the first sporophytes started to penetrate onto dry land, with some of the oldest colonized habitats being near-shore swamps. Soon thereafter, a continuous plant cover developed in all regions with favorable temperatures and sufficient water supply. Arborescent forms of lycopods (club mosses), sphenopsids (horsetails), and ferns appeared in the Upper Paleozoic but the latest Paleozoic was dominated by gymnosperms, precursors of today's conifers. Marshes densely intergrown by these plants accumulated large amounts of organic matter which later transformed into coal.

The evolution of living organisms and their coexistence and distribution over the globe were also controlled by the changing positions of continents—plates of continental lithosphere. In the Paleozoic, the present blocks of South America, Africa, Arabia, India, Australia, and Antarctica were united, forming a single, large continent called Gondwana. This continent was situated in the region of the South Pole but at certain times it extended up to the temperate zones. The remaining continental blocks, such as the Canadian Shield, Baltic Shield, Siberian Shield, and the core of the present China, were located near the equator and characterized by a warm climate. In the course of the Paleozoic, Gondwana moved (drifted) north and its collision with other continents resulted in orogenic processes.

The Paleozoic era was characterized by fluctuations in temperature and in the chemical composition of the atmosphere. Cold periods are evidenced by signs of glaciation, warm periods by large extents of coral reefs (built not only by corals, but also sponges, algae, and microorganisms). Two instances of mass extinction were recorded in the Paleozoic: the mid-Paleozoic (Frasnian–Famenian) extinction, which primarily affected shallow marine species, and the extinction at the Paleozoic–Mesozoic boundary, which marked the extermination of a number of groups. Besides these mass extinctions, many smaller-scale extinctions are known to have occurred. Such events were probably driven by sea level and climatic changes due to continental drift and uplift of mountain ranges. The largest extinctions are frequently associated with collisions between Earth and large meteorites or asteroids, but there is no evidence for such events in the case of the Paleozoic extinctions.

The Paleozoic history thus shows the emergence of a series of novel evolutionary forms of life, but also the gradual establishment of large ecosystems and natural habitats generated by living organisms. It is obvious that the individual evolutionary steps were interconnected. For example, by creating new habitats (tropical forests, soil), plants gave the other organisms an opportunity to colonize these areas and consequently create new evolutionary lineages. The dispersal of insects, amphibians and reptiles would have been impossible without terrestrial plants.

1. General Characteristics

The Paleozoic era occupies a time interval of 300 to 340 million years and is the longest era of the Phanerozoic. The Paleozoic is subdivided into six systems, with the first four—the Cambrian, Ordovician, Silurian, and Devonian—called Lower Paleozoic, and the last two—Carboniferous and Permian—called Upper Paleozoic. (Outside Europe, the term Middle Paleozoic is frequently used to refer to the Devonian system.)

1.1. Evolution of Life in the Paleozoic

The Paleozoic is characterized, in contrast to the Precambrian, by an expansion of fauna and flora. All animal phyla appeared as early as the earliest Paleozoic, (so called Cambrian explosion): Porifera (sponges), Coelenterata, Bryozoa (sea mats), Brachiopoda (lamp shells), Mollusca, Arthropoda, Echinodermata, and the oldest vertebrates (Vertebrata) all appeared during the Cambrian.

During the Paleozoic, major evolutionary changes of fauna and flora took place, resulting in a different paleontological record in different systems of the Paleozoic. Some characteristic features in the evolution of animal life are the history of trilobites throughout the Paleozoic, the spread of tetracorals (corals with fourfold symmetry) from the Silurian to the end of the Paleozoic, the spread of nautiloid cephalopods from the Ordovician onwards and ammonoid cephalopods from the Devonian, the evolution of fish beginning in the Silurian, and the global distribution of amphibians in the Carboniferous and of reptiles in the Permian. It is important to bear in mind, however, that the first appearances of these groups usually considerably precede the period of their overall spread. For example, the first rare occurrences of vertebrates date to the middle Cambrian but their real boom occurred not before the upper Silurian. It should also be noted that the first finds of body-fossils or communities are sometimes preceded by finds of their supposed traces (trace fossils, ichnofossils) or finds of assemblages of traces of their activity (ichnocoenoses). Such finds represent an important source of information even in environments not favorable for the fossilization of calcareous shells (such as the deep-sea bottom or continental detrital sediments). Finally, trace fossils provide information on the quantity and activity of organisms lacking hard shells which, for that reason, are only rarely preserved in the fossil record. Body morphologies and approximate systematic positions of the tracemakers are more difficult to determine from the traces they produce, however.

The evolution of plant life witnessed the dispersal of higher plants and their invasion onto dry land. Starting with the Devonian, we can recognize the presence of more or less continuous plant growth and soil formation under climatically favorable conditions. The boom of sporophytes in the upper Paleozoic determined the world distribution of coal deposits. In the Permian, flora underwent a considerable change. Then, still in the Paleozoic, the typical primitive flora (characterizing the so-called Paleophytic) became Mesozoic-type communities dominated by gymnosperms of the so-called Mesophytic.

PALEOZOIC						
Ma	PERIOD		EPOCH / AGE		Ma	Ma
248	PERMIAN	L	TATARIAN		252	4
	PERMIAN	L	UFIMIAN-KAZANIAN		256	4
260	PERMIAN	E	KUNGURIAN		260	4
	PERMIAN	E	ARTINSKIAN		269	9
280	PERMIAN	E	SAKMARIAN		282	13
	PERMIAN	E	ASSELIAN		290	8
	CARBONIFEROUS	PENNSYLVANIAN	GZELIAN	STEPHAN	296	6
300	CARBONIFEROUS	PENNSYLVANIAN	KASIMOVIAN	STEPHAN	303	7
	CARBONIFEROUS	PENNSYLVANIAN	MOSCOVIAN	WESTPHAL	311	8
320	CARBONIFEROUS	PENNSYLVANIAN	BASHKIRIAN	NAMUR.	323	12
	CARBONIFEROUS	MISSISSIPPIAN	SERPUKHOVIAN	NAMUR.	327	4
340	CARBONIFEROUS	MISSISSIPPIAN	VISEAN		342	15
	CARBONIFEROUS	MISSISSIPPIAN	TOURNAISIAN		354	12
360	DEVONIAN	L	FAMENNIAN		364	10
	DEVONIAN	L	FRASNIAN		370	6
	DEVONIAN	M	GIVETIAN		380	10
380	DEVONIAN	M	EIFELIAN		391	11
	DEVONIAN	E	EMSIAN		400	9
400	DEVONIAN	E	PRAGIAN		412	12
	DEVONIAN	E	LOCHKOVIAN		417	5
	SILURIAN	L	PŘIDOLIAN		419	2
420	SILURIAN	L	LUDLOW		423	4
	SILURIAN	E	WENLOCK		428	5
440	SILURIAN	E	LLANDOVERY		443	15
	ORDOVICIAN	L	ASHGILL		449	6
	ORDOVICIAN	L	CARADOC		458	9
460	ORDOVICIAN	M	LLANDEILO		464	6
	ORDOVICIAN	M	LLANVIRN		470	6
480	ORDOVICIAN	E	ARENIG		485	15
	ORDOVICIAN	E	TREMADOC		495	10
500	CAMBRIAN	L			505	10
	CAMBRIAN	M			518	13
520	CAMBRIAN	E	LENIAN		524	6
	CAMBRIAN	E	ATDABANIAN		530	6
	CAMBRIAN	E	TOMMOTIAN		534	4
540	CAMBRIAN	E	NEMAKIFIAN - DALDYNIAN		545	11

Table 1. Global stratigraphic scale of the Paleozoic
Ma = millions of years.

1.2. Evolution of Principal Ecosystems in the Paleozoic

During the Paleozoic, we may retrace both the formation of a number of evolutionary innovations and the gradual origin of large ecosystems and environments created by organisms. It is evident that the individual steps of these two processes were interconnected.

Open oceans. A dominant microplankton group of the late Precambrian and early Paleozoic is the Acritarcha. The fossil specimens represent resting cysts; their systematic relationships are still debated. The Acritarcha were most diversified in the Ordovician, Silurian, and Devonian. They were probably affected by the late Devonian extinction, as their subsequent fossil record is sparse. The occupation of oceanic ecological niches during the Cambrian and Ordovician enriched the oceanic ecosystems with representatives of cephalopods. They are considered the first group which formed abundant and diverse nekton. In the Silurian, numerous nektonic forms appeared among arthropods, of which eurypterids reached more than 2 m in length. In the late Paleozoic, fish came to dominate in the oceanic nekton. The oldest problematic fish fossils come from the middle Cambrian, but their morphology suggests benthic rather than nektonic life. Sharks and chimeras (Chondrichthyes) and bony (Osteichthyes) fish, which were good swimmers, became abundant in the Devonian and Carboniferous.

Figure 1. Most Paleozoic non-reefal benthic communities were dominated by trilobites and brachiopods
Reconstruction by J. Sovák shows the Silurian locality Kosov at Praha, Czech Republic, with brachiopods *Atrypoidea linguata* and trilobite *Cromus beaumonti*.

Numerous new forms of ichnofossils began to occur shortly before the end of the Proterozoic and at the beginning of the Paleozoic. Each form represents a particular strategy in the search for nourishment (various systems of sediment feeding, burrows of predators and filtrators, gardening). Relatively deep-sea turbidite sequences from those periods show almost no traces of benthos activity. Nevertheless, from the late Cambrian until the Silurian, an expansion of certain types of behavior into the deep sea can be observed. These forms then frequently become extinct in shallow waters. Colonization of deep-sea bottoms seems to be connected with multiple increases in plankton, whose dead substance created in the abyssal ooze a suitable environment for the development of bacterial assemblages. These assemblages served as nutrients for numerous sediment feeders and other organisms taking advantage of endosymbiotic bacteria (mostly polychaetes and lamellibranches).

Epicontinental seas. The development of reef communities is particularly crucial. During the Paleozoic, both the extent of reef environments and the systematic appurtenance of main reef-forming organisms changed several times. See sections 2.1.2 Cambrian life and ecosystems, 2.2.2. Ordovician life, 2.3.2. Silurian Life, 2.4.2 Devonian Life, 2.5.2 Carboniferous Life, and 2.6.2. Permian Life.

Terrestrial settings. Through to the end of the Silurian, plants began to build new biomes in terrestrial settings: soil, swamps, and later also forest growths. In this way, plants gave other organisms the opportunity to occupy the new environments and thus to divaricate their evolutionary lines. Without terrestrial plants, the bloom of insects, amphibians, and reptiles would have been impossible.

1.3. Paleogeographic Characteristics of the Paleozoic

Considering the positions of continental plates, the Paleozoic is characterized by the presence of an extensive continent, Gondwana, comprising the present plates of South America, Africa, Arabia, and India, Australia and Antarctica. In the Paleozoic, Gondwana was located in the Southern Hemisphere and probably also included the southern marginal parts of Europe. Its position was by no means stable. Besides rotational movements, a northerly drift of the northern part of Gondwana can be traced from the Ordovician and Silurian. The changing position of Gondwana may also have been responsible for the extensive glaciations in the Ordovician and Carboniferous, although their causes should be viewed as more complex.

Continental plates lying north of Gondwana (the cores of North America (Canadian Shield), northern Europe (Baltic Shield), Siberia (Siberian Shield), Kazakhstan, and China) were located at low latitudes with warm climates.

1.4. Endogenic Processes in the Paleozoic

Movements of continental plates in the Paleozoic, and the resultant collisions, resulted in the transformation and uplift of mobile regions to form mountain ranges. The earliest Paleozoic times were connected with the waning Cadomian (Assyntian), Baikalian, or Panafrican Orogeny. Processes grouped under the collective term Caledonian Orogeny took place in some mobile regions in the Ordovician, Silurian, and early Devonian. In the late Devonian to Permian period, prominent processes known as the Variscan (Hercynian) Orogeny in the North America Alleghenian Orogeny or Appalachian Orogeny, affected different regions of the world.

The beginning of the Paleozoic is characterized by a predominance of divergent movements of the continental plates: the late Proterozoic supercontinent called Rodinia had broken up and new oceans had formed as a result. By the middle Ordovician, the convergent movements of continents commenced. Subduction of oceanic crust formed volcanic arcs similar to the recent ones, producing mostly basaltic rocks. Till the end of the Paleozoic, collisions of continental plates led to the forming of the Pangea supercontinent. The process led to pulses of orogeny that included the origin of large granite bodies and ore deposits adjacent to them. Certain areas of present continents (northwestern Europe, Appalachian region) arose during these processes.

(For more regional details, see sections in this article on paleography of the Cambrian to the Permian.)

1.5. Extinctions and Recoveries in the Paleozoic

Principles of extinctions and recoveries and their history in Earth's ecosystem are defined and described in *Past Global Crises*. This paragraph provides a brief summary of such events in the Paleozoic.

At the end of the Cambrian, trilobites suffered a considerable extinction. However, the first extinction in oceans classified as a mass extinction occurred at the end of the Ordovician. The primary cause is thought to have been cooling and glaciation of the circumpolar part of Gondwana and a loss of tropical environments on Earth. Once the glaciation was terminated, the benthic assemblages were decimated because lighter water from glaciers covered deep ocean waters, resulting in almost total dysoxia and anoxia of waters and sediments. About 70% of all species of marine animals ceased to exist.

The recovery of assemblages was relatively fast, resulting in fact in the development and reconstruction of reef assemblages, in particular. A further mass extinction occurred in the late Devonian, at the boundary between the Frasnian and Famenian stages. Its cause is not known. Again, a fast recovery took place including development of evolutionarily younger groups of the nekton (fish, cephalopods) and benthos (trilobites).

The largest and most severe mass extinction in Earth's entire history occurred at the end of the Permian when about 95% of all species became extinct. The history of the late Permian is connected with the origin of the Pangea supercontinent, and variations in $^{12}C/^{13}C$ ratio in sediments. This fluctuation argues for variation in the atmospheric content of carbon of biological origin. A possible scenario accounting for partial extinction could have been the fall in sea level in the early Permian, when large areas of the new continent became exposed to weathering and organic carbon in coal beds was oxidized. This process led to a decrease in the oxygen content in the atmosphere (roughly from 30% down to 15%), and simultaneously to an increase in carbon dioxide. The latter gas creates a greenhouse effect that contributed to the warming up and consequent melting of glaciers. The impacts were similar to those at the end of the Ordovician period: stagnancy of abyssal waters resulting in deposition of black shales. Also the role of intensive volcanism (e.g., the Siberian Platform) is considered a possible cause of the extinction.

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Biographical Sketches

Radek Mikuláš (born 1964) is a senior researcher of the Institute of Geology, Academy of Sciences of the Czech Republic, Prague. His professional experience includes a study of trace fossils in a variety of sedimentary environments (deep marine, shallow marine, freshwater, subaerial), aspects of fossil behavior (burrows, borings, plant trace fossils), contexts of geological record (ichnological record of extinctions and recovery, basin analysis) and age (Paleozoic, Mesozoic, modern).

He entered the Institute of Geology, then the Czechoslovak Academy of Science, as an assistant in 1987. He received his Ph.D. study "Trace fossils of the Bohemian Ordovician" from the same institution in 1991. His professional experience outside the Czech Republic includes the study of trace fossils in the Ordovician of Spain (1992), a postdoctoral fellowship at the Department of the Earth Sciences, University of Liverpool (supervised by Dr. T.P. Crimes), and a re-study of trace fossils from the Jurassic of Greenland (1997; University of Copenhagen).

His recent research projects include:

Beginning in 2000, principal investigator for a grant by the Grant Agency of the Czech Republic, "A multidisciplinary research of the locality Dětaň (Oligocene, Doupov Mountains): integration of palaeontology and pedology."

Beginning in 2000, co-investigator for a grant by the Grant Agency of the Czech Republic, "Facies Architecture of the turbidite system of Moravice Formation, Nízký Jeseník Culm Basin, based on sedimentology and ichnofacies analysis."

1998–1999, member of the national working group for UNESCO-IGCP Project #410 "The Great Ordovician Biodiversification Event: Implication for Global Correlation and Resources."

1999, PalSIRP (USA) Grant: “A systematic revision of the ichnotaxa erected in ‘Problematica Silurica’ by A. Fritsch (1908; in J. Barrande et al.: Systeme Silurien...).”

1995–1997, member of the national working group for UNESCO-IGCP Project #335 “Biotic Recoveries from Mass Extinctions.”

1998, PalSIRP (USA) grant “Terrestrial bioerosion and its ichnological consequences.”

Professor Dr. Ivo Chlupáč, born in 1931, published in geology and paleontology while he was still a secondary school student. He studied geology at the Charles University in Prague, then entered the Geological Survey in Prague. Since 1991 he has been a Professor of the Institute of Geology and Paleontology, Charles University, Prague. I. Chlupáč became well known in 1950s for discoveries of Devonian graptolites that were decisive impulses for a renewed interest in solving the Silurian–Devonian boundary problem. I. Chlupáč has been a titled member of the Subcomission on Devonian Stratigraphy since its establishment in 1973. His contribution to solving stratigraphical problems includes a biostratigraphic investigation of the Lower–Middle Devonian boundary beds (1979), detailed characteristics of the Lower Devonian stages, and a detailed study of the Lochkovian–Pragian boundary interval. These works influenced the acceptance of the Lochkovian and Pragian as standard global stages of the Lower Devonian. In systematic paleontology, I. Chlupáč specializes in trilobites and other arthropods. He is an author or co-author of around 300 scientific publications including monographs on phacopid trilobites, geologic field-trip guidebooks, and textbooks.