

## Chapter 1.3. Long History of Life on Earth

Chapter 1.3 provides a brief overview, mostly in chronological order, of the evolution of life on Earth. Although new fascinating paleontological discoveries are made continuously and inferences based on properties of modern organisms become more and more reliable, a number of key facts about past evolution have already been firmly established. These facts provide the basis for studying modern life.

Section 1.3.1 presents data on the first ~6/7 of the chronology of life, from its origin over 3.500 mya to the end of Proterozoic eon 542 mya. A number of crucial events occurred during these ancient times, including the origins of life itself, the first modern-like prokaryotes, photosynthesis, unicellular eukaryotes, multicellular eukaryotes, and a variety of animals. Early fossil record leaves a lot to be desired, and the available fossils are often hard to interpret so that combining direct and indirect data is particularly important for studying these early times.

Section 1.3.2 deals with Phanerozoic eon, from 542 mya to the present. Although all large-scale clades of the Tree of Life were already present at the beginning of this eon, most of the clades of familiar and ecologically important terrestrial living beings evolved later, including land plants, insects, tetrapods, amniotes, mammals, and birds. A rather detailed fossil record of the Phanerozoic eon revealed a number of fascinating transitory forms and many episodes of diversification and extinction.

Section 1.3.3 considers extant life from the perspective of its evolutionary history. Phylogenetic relationships of modern organisms, the origin of their spatial distributions, the recent changes in the environment, and the ongoing mass extinction are reviewed. It is impossible to understand diversity and complexity of modern life and to try to preserve what is still left of it without taking into account its evolutionary origin.

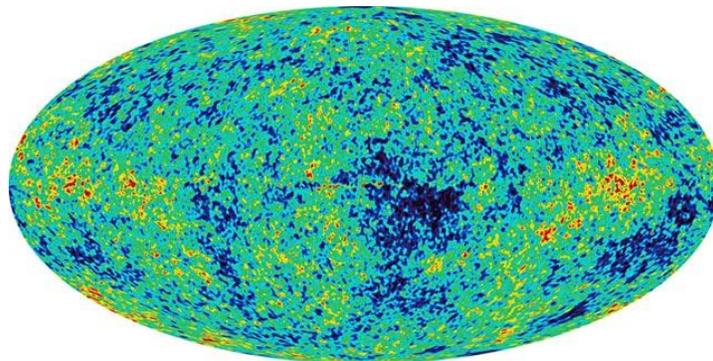
Chapter 1.3 relies on indirect and direct evidence, introduced in Chapters 1.1. and 1.2, respectively. Chapter 1.4 continues the chronological approach of Chapter 1.3, dealing in detail with the recent history of the *Homo sapiens* clade. Chapter 1.5 treats past evolution from a complementary perspective and presents timeless generalizations emerging from it.

### Section 1.3.1. The first 3 billion years of life

The Earth cooled down and became habitable around 4,200 mya and life originated in less than 700My afterward. The origin of life remains a mystery as we have no direct data and no reliable theory on this process. Fossils indicate that prokaryotes and their communities already thrived 3,500 mya, and major clades of modern Bacteria and Archaea diverged well before ~2,500 mya. Oxygenic photosynthesis evolved ~2,800 mya, triggering radical changes in the composition of oceanic waters and slow accumulation of free oxygen in the atmosphere. Eukaryotes appeared at least 1,800 mya and their major clades, including multicellular red, brown and green algae, fungi, and animals, diverged before 1,000 mya. Diversification of metazoans occurred during Cryogenian and Ediacaran periods, and oxygenation of middle oceanic waters 575 mya was followed by the evolution of Ediacaran biota of large soft-bodies animals. Extinction of this biota, perhaps due to an episode of global anoxia in surface oceanic waters, marked the end of the Proterozoic eon 542 mya.

#### *1.3.1.1. Origin of habitable Earth and of life*

The Universe we live in appeared 13.7 billion years ago as the result of the Big Bang. Initially, the Universe was very hot, but as the space expanded the temperature dropped rapidly, allowing the formation of stars and galaxies several hundreds of millions of years later (Fig. 1.3.1.1a). Only hydrogen, helium, and lithium were produced by the Big Bang in significant amounts, and heavier elements were synthesized later in the first generation of stars and were released into space by those of them that exploded as supernovae. The Sun, formed ~4,600 mya, is a typical second-generation star.



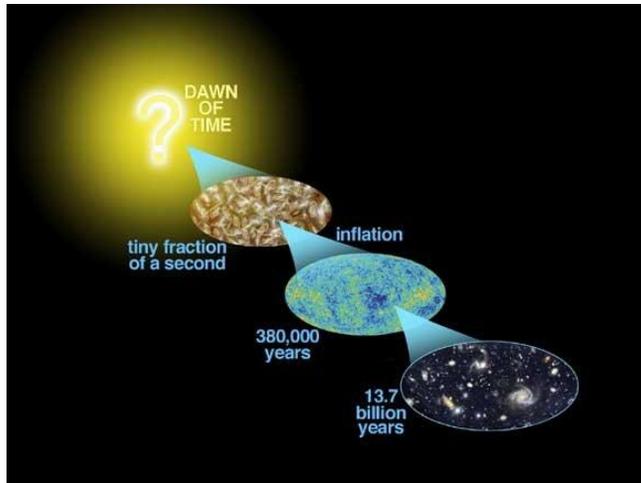


Fig. 1.3.1.1a. A full-sky map of the oldest light in the universe. Colors indicate warmer (red) and cooler (blue) spots. Patterns in the Big Bang afterglow were frozen in place ~380,000 years after the Big Bang. These patterns are tiny temperature differences within this microwave light bathing the universe, which now averages a frigid 2.73K. (top, [science.nasa.gov/headlines/y2003/11feb\\_map.htm](http://science.nasa.gov/headlines/y2003/11feb_map.htm)). The scheme of the early history of the universe, derived from these and other data. Various periodic processes make it possible to talk about years before the origin of the Solar system (bottom).

As it is the case for a substantial fraction of stars, the Sun is surrounded by planets that appeared together with it. Planets that constitute the Solar system were formed ~4,600 mya by accretion of smaller objects and were very hot initially, due to release of energy in collisions between these objects (Fig. 1.3.1.1b). As the result, the molted Earth differentiated into core and mantle. Around 4,500 mya a collision of young Earth with a huge object led to formation of the Moon. The collision was tangential, because the light, iron-poor Moon is made only of the mantle material (Fig. 1.3.1.1.c).



Fig. 1.3.1.1b. Formation of the solar system from a large cloud of gas and dust known as the solar nebula that swirled around the developing Sun. Within this cloud, countless small objects collided and stuck together, gradually forming larger and larger bodies (<http://www.amnh.org/education/resources/rfl/web/meteoriteguide/key.html>).

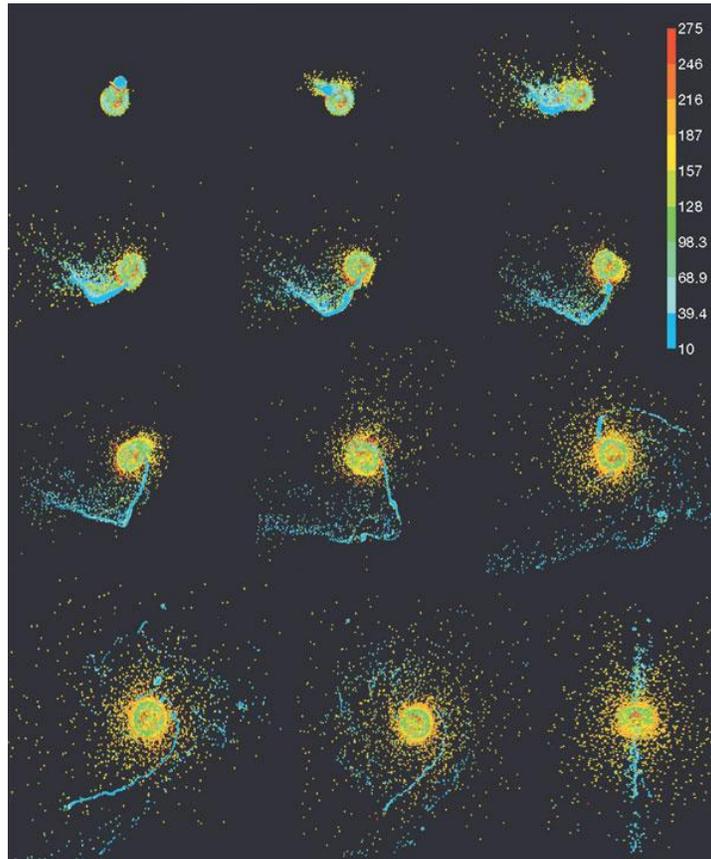


Fig. 1.3.1.1c. The orientation and size of the gigantic impact that created the Moon can be inferred from the angular momentum contained in the Earth's spin and the Moon's orbit, a quantity that has been nearly conserved over the past 4,500My. Simulations show that there is a class of impacts that yield an iron-poor Moon, as well as the current masses and the angular momentum of the Earth-Moon system (*Nature* 412, 708, 2001).

After formation of the Moon, the Earth was very hot again, but most of the heat was quickly lost into space. As it cooled, the Earth's surface passed through every temperature regime between silicate vapor to liquid water and perhaps even to ice, eventually reaching an equilibrium with sunlight. Inevitably the surface passed through a

time when the temperature was  $\sim 100^{\circ}\text{C}$ , which was optimal for prebiotic synthesis of complex organic compounds (Fig. 1.3.1.1d). This potentially evolutionarily significant warm period lasted for  $10^5 - 10^7$  years.



Fig. 1.3.1.1d. Initiation of clement surface conditions on the earliest Earth (*PNAS* 98, 3666, 2001).

The Earth certainly cooled down by 4,280 mya, which is the age of the earliest known rocks, determined using  $^{146}\text{Sm}/^{142}\text{Nd}$  radiometric dating. These rocks have been found in Nuvvuagittuq greenstone belt (Fig. 1.3.1.1e) and may represent the oldest preserved crustal section on Earth.



Fig. 1.3.1.1e. The oldest known rocks, Nuvvuagittuq greenstone belt, Quebec, Canada (*Science* 321, 1828, 2008).

Life appeared on Earth between  $\sim 4,300$  mya (when the Earth became habitable) and  $\sim 3,500$  mya (the age of first unambiguous fossils). There are no direct data on how this happened, and no comprehensive theory (Chapter 3.2). Reduced  $\delta^{13}\text{C}$  in certain  $\sim 3,800$  Ma old rocks could be a trace of life, but this interpretation remains controversial.

Still, because 3,500 Ma old prokaryotes were already quite diverse (Section 1.3.1.2), LUCA probably lived at least 3,700-3,600 mya. It is very unlikely that life which we see today originated outside the Earth. Life can hardly survive in space for a long time, and this hypothesis does not abolish the problem of the origin of life, because the whole Universe had a beginning in time. Because all modern life evolved from the same LUCA, even if there were multiple origins of life all but one of them left no living descendants.

LUCA already was a rather advanced organism, definitely possessing RNA and proteins, and the mechanism of translation. It is less clear whether LUCA also possessed DNA, or used RNA as its hereditary material. LUCAs genome almost certainly encoded at least several hundred proteins. Phylogenetic analysis of the catalytic domains of class I aminoacyl-tRNA synthetases, the key enzymes of translation, indicates that extensive protein evolution occurred before LUCA (Fig. 1.3.1.1f). Still, we have no clear idea on how much time it took for LUCA to evolve from the very first living beings.

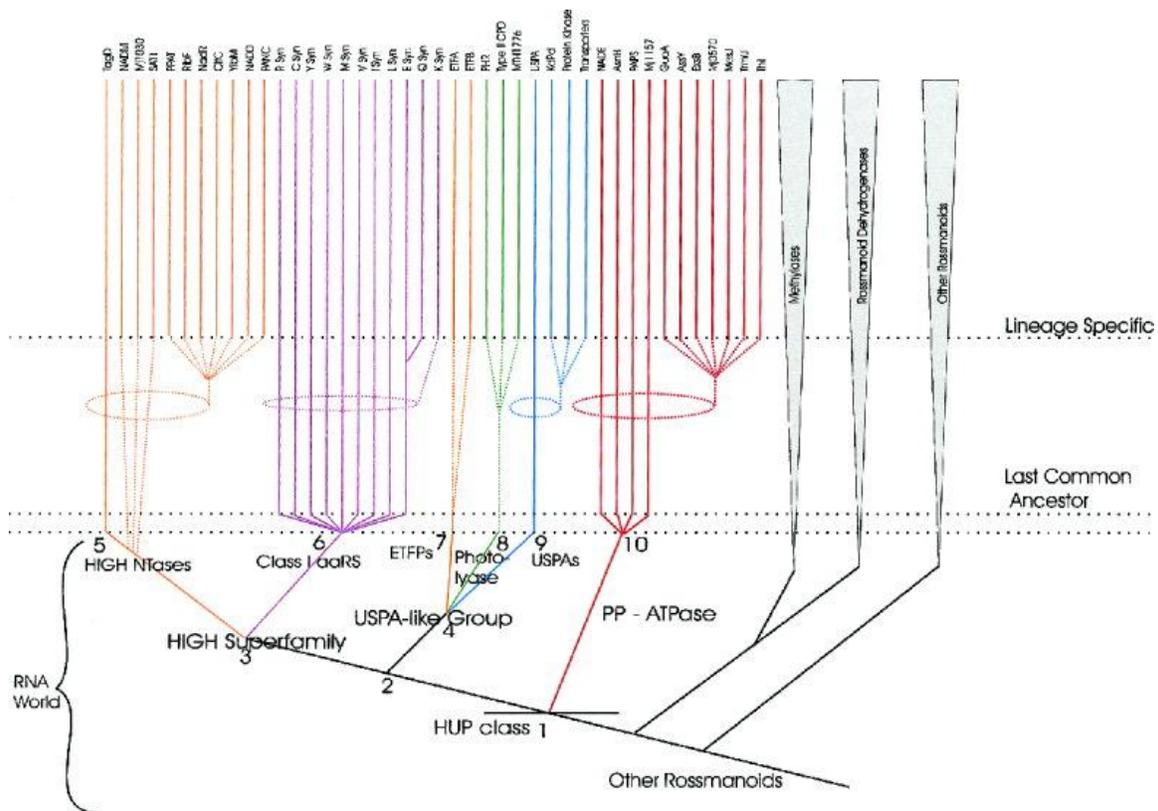


Fig. 1.3.1.1f. Phylogenetic tree of a large superfamily of proteins, which includes class I aminoacyl-tRNA synthetases that were certainly present in LUCA. These aminoacyl-tRNA synthetases form only one clade on this tree (purple), together with several other clades, comprising HIGH nucleotide transferases (yellow), Electron-transfer flavoproteins (orange), Photolyases (green), USPA-domain proteins (blue), and PP-loop ATPases (red) (*Proteins* 48, 1, 2002).

### 1.3.1.2. Prokaryotes

The earliest unambiguous fossils are ~3,500 Ma old. They have been found in the only two known areas of 3,600-2,700 Ma old Earth's crust, the Pilbara craton (geological province) in Western Australia and the Kaapvaal craton in South Africa. Similarities between Pilbara and Kaapvaal cratons suggest that they were parts of the same ancient continent, called Vaalbara.

The earliest life we know directly was already quite diverse, despite being represented only by prokaryotes. Prokaryotic microfossils can be recognized by small sizes of the cells. In addition to individual cells, the earliest fossils are also represented by macroscopic communities of prokaryotes, microbial mats and stromatolites. A microbial mat is a multi-layered sheet of micro-organisms, usually consisting of many distinct species that form an ecosystem (Fig. 1.3.1.2a).



Fig. 1.3.1.2a. Modern microbial mats are quite common.

A stromatolite is a thick build-up of microbial mats. Stromatolites are rare today, because macroscopic eukaryote predators prevent their formation. Still, they grow where these predators are absent due to anomalously high salinity, *e. g.*, in the Bay of Sharks on the Australian coast and in tidal pools in the Red Sea (Fig. 1.3.1.2b).



Fig. 1.3.1.2b. Contemporary stromatolites in the Bay of Sharks (Doug Futuyma).

Two sites that harbor fossils of ages slightly below 3,500 Ma have been carefully investigated in the Pilbara Craton. Kitty's Gap Chert (chert is a fine-grained silica-rich sedimentary rock) contains microbial fossils that are 3,466 Ma old (Fig. 1.3.1.2c), mostly represented by colonies of coccoidal microorganisms that occur in two size ranges, 0.4-0.5 mm and 0.75-0.8 mm. These colonies coat the surfaces of the volcanic particles and often form either dense, carpetlike associations up to tens of micrometers in diameter comprising hundreds of individuals. All colonies are associated with a polymer film that coats both the organisms and their substrate. Multispecies microbial mats, formed at a boundary representing a short period of nondeposition, consisted predominantly of coccoids and also included small filaments tens of micrometers in length and rare, short rods 1 mm in length. The interactions between the microbes, their colonies and biofilms, and their environment were obviously intimate and complex.



Fig. 1.3.1.2c. Kitty's Gap Chert and its microfossils (*Processes on the Early Earth* 405, 105, 2006; *Nature* 455, 1101, 2008). The microorganisms were preserved by rapid silicification.

Strelley Pool Chert is a 3,430 Ma old sedimentary rock formation containing laminated structures which almost certainly are fossil stromatolites (Fig. 1.3.1.2d). Interpretation of these fossils is facilitated by their excellent preservation and morphological variety. A multi-kilometre-scale study of the Strelley Pool Chert identified seven stromatolite morphotypes in different parts of a peritidal platform. Morphotype-specific analysis of the structures within their palaeoenvironment suggests that the diversity, complexity and environmental associations of the stromatolites describe patterns that reflect the presence of organisms. In particular, structures called the Large Complex Cones have geometric, textural and chemical attributes that provide strong evidence for biogenesis, and have no natural or experimental abiological analogue. They are plausibly explained as biosedimentary structures that resemble younger conical stromatolites of widely accepted biogenicity. The other six stromatolite facies also display attributes that indicate probable biogenesis. Moreover, signatures of life in the Strelley Pool Formation are also observed at the microscopic scale, as biosedimentary fabrics and organic layers. Thus, 3,430 mya prokaryotes flourished on a broad peritidal platform, creating a reef-like build-up in shallow waters as surfaces became submerged.

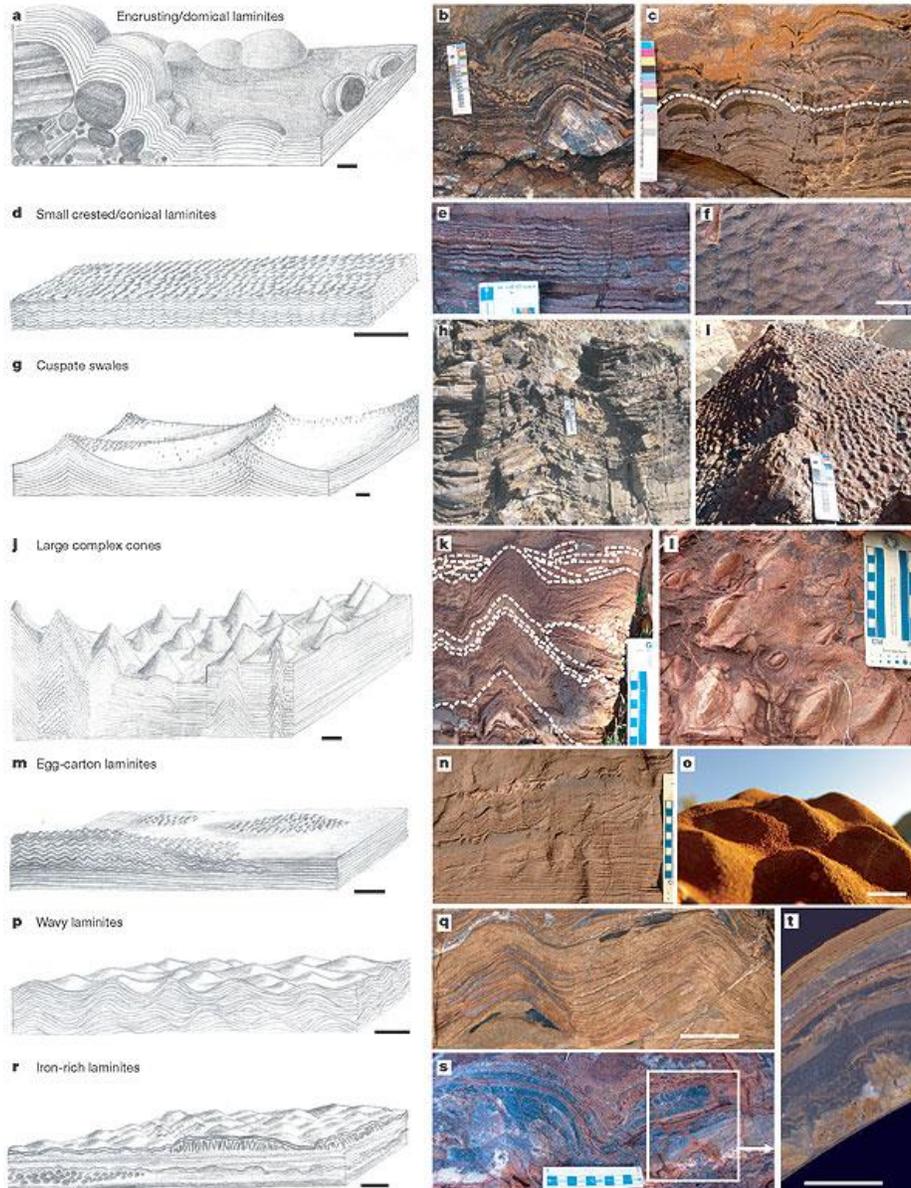


Fig. 1.3.1.2d. Strelley Pool Chert, general view (top) and stromatolite facies, including reconstructed three-dimensional views and outcrop photographs (*Nature* 441, 714, 2006; *PNAS* 106, 9548, 2009).

The first very likely record of photosynthesis, apparently anoxygenic, is provided by Buck Reef Chert (Kaapvaal Craton), where 3,416 Ma old marine photosynthetic microbial mats were found (Fig. 1.3.1.2e). From sedimentary structures and distributions of sand and mud, it seems that deposition occurred in open shallow to deep marine environments. Most carbonaceous matter was formed by photosynthetic mats within the euphotic zone and distributed as detrital matter by waves and currents to surrounding environments. The carbon isotopic composition of carbonaceous matter, the presence of siderite and lack of primary ferric oxides, and the restriction of microbial mats to shallow water indicate the presence of photosynthetic, probably anoxygenic, microbes.



Fig. 1.3.1.2e. Buck Reef Chert, general view and remains of marine photosynthetic microbial mats. The black gob at lower left is an old grain of organic carbon in the Buck Reef Chert, which became a framework for the newer mat (dark lines in lighter areas). Bar = 1 millimeter (*Nature* 431, 549, 2004).

Altogether, 48 Archean deposits containing biogenic stromatolites have been found so far. Among them, 14 deposits contain 40 morphotypes of putative microfossils, and 13 are particularly ancient, being 3200-3500 Ma old (Fig. 1.3.1.2f).

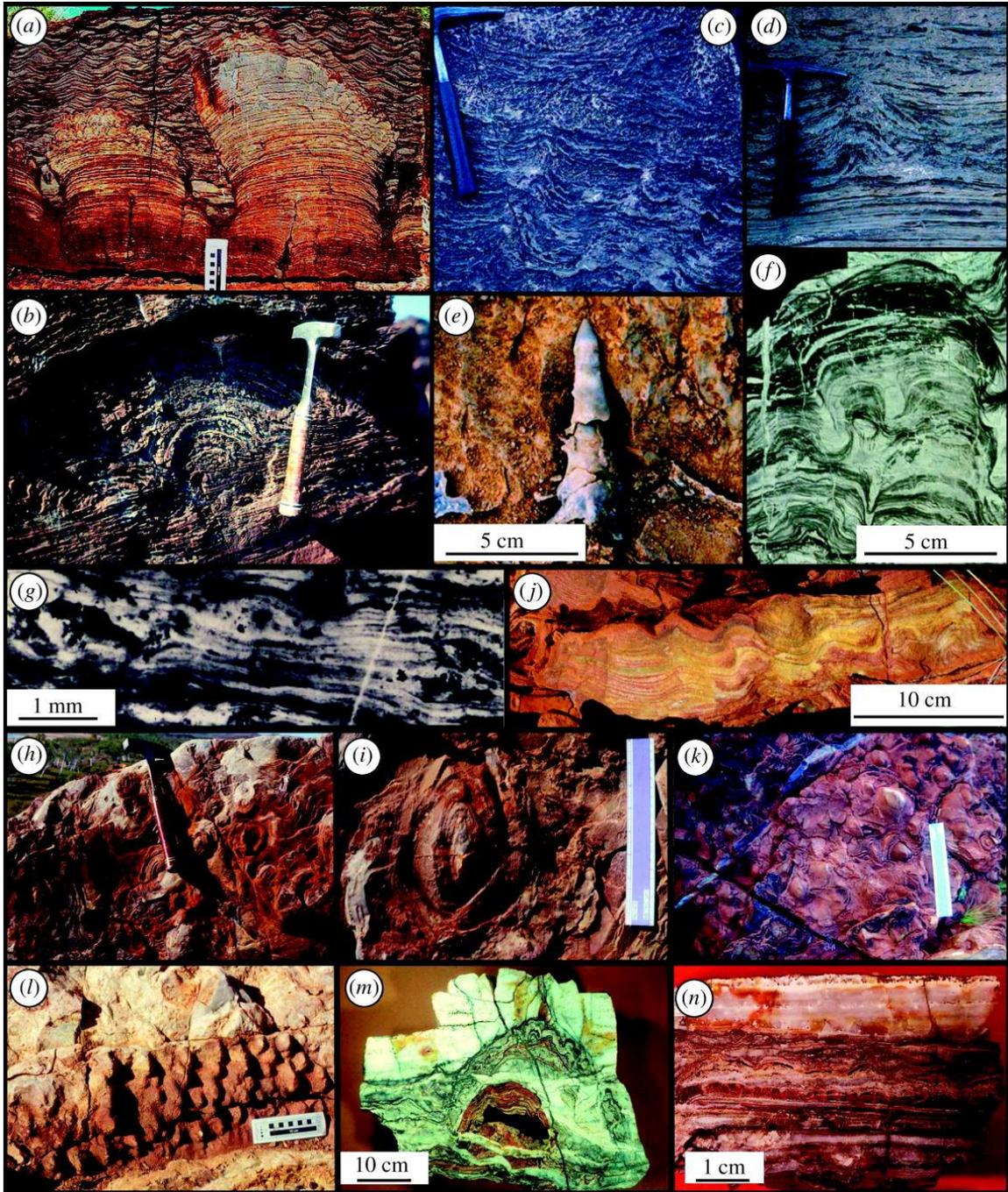


Fig. 1.3.1.2f. Archaean stromatolites/microbial mats (*Phil. Trans. Roy. Soc. B* 361, 869, 2006).

Photosynthesis carried by some of the earliest known forms of life was almost certainly anoxygenic, apparently with  $H_2$  and  $H_2S$  used as reductants. After this, protocyanobacteria probably evolved the ability to use ferrous iron as reductant not later

than 3,000Mya. Finally, microfossils, stromatolites, and chemical biomarkers in Australia and South Africa indicates that modern-looking cyanobacteria containing chlorophyll a and capable of oxygenic photosynthesis appeared by 2,900Mya (Fig. 1.3.1.2g).



Fig. 1.3.1.2g. (top) An early cyanobacteria microfossil (*Photosynthesis Research* 88, 109, 2006). (bottom) Fossils of 2,900My old microbial mats from the Pongola in South Africa (left) and contemporary microbial mats in intertidal zones (right). Such contemporary

mats contain a lot of cyanobacteria, and their presence in these fossils is very likely but not proven (*Nature* 452, 40, 2008).

Fossil conical stromatolites, likely formed by photosynthetic and phototactic microbes, sometime contain small bubbles, which were probably filled with O<sub>2</sub> released in the course of oxygenic photosynthesis. Comparison of these fossils with conical aggregates formed by modern cyanobacteria support this interpretation (Fig. 1.3.1.2h). Apparently, fossil bubbles are present only in stromatolites that are 2,700 Ma old or younger, indicating that oxygenic photosynthesis became common only by that time. This is consistent with the record of accumulation of O<sub>2</sub> in the oceans and atmosphere (Chapter 1.2).

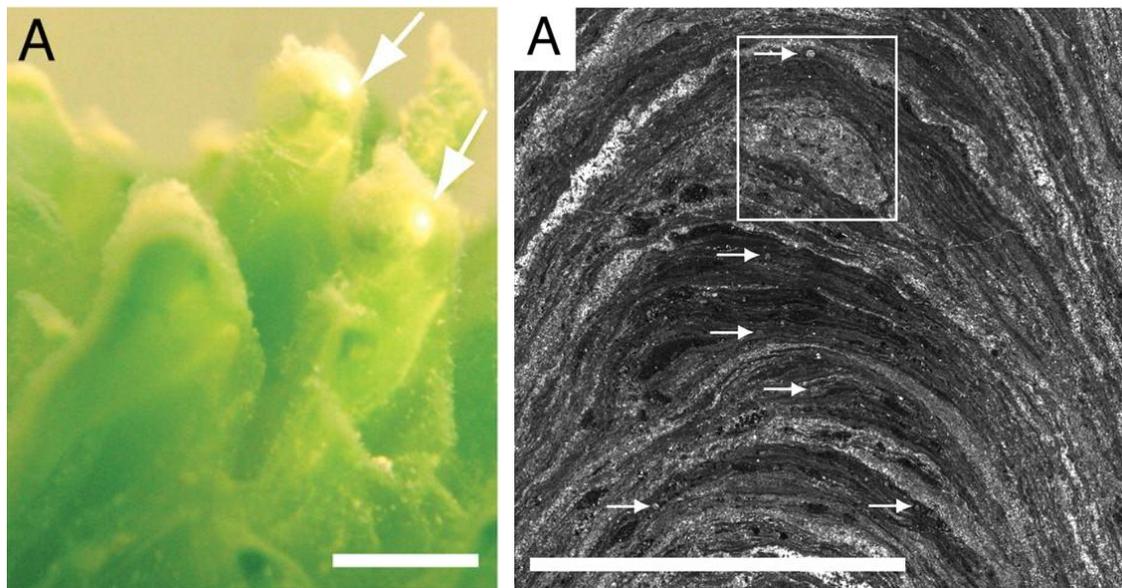


Fig. 1.3.1.2h. Oxygen and bubble production in modern conical aggregates dominated by cyanobacteria. Bubbles often form at the tips of cones and are partly or completely covered by biofilm (Scale bar 5mm, left). Center of a conical Proterozoic stromatolite. The arrows point to fossil bubbles. (Scale bar 1 cm, right) (*PNAS* 106, 10939, 2009).

The earliest known prokaryotes that lived on dry land are ~2,600 Ma old. Unusually carbonaceous ancient soils, palaeosols, have been found in the Barberon Greenstone Belt in South Africa. The elemental ratios (C, H, N, P) and isotopic

compositions of their organic matter and its host rocks show that the organic matter very probably represents remnants of microbial mats that developed on the soil surface (Fig. 1.3.1.2i).

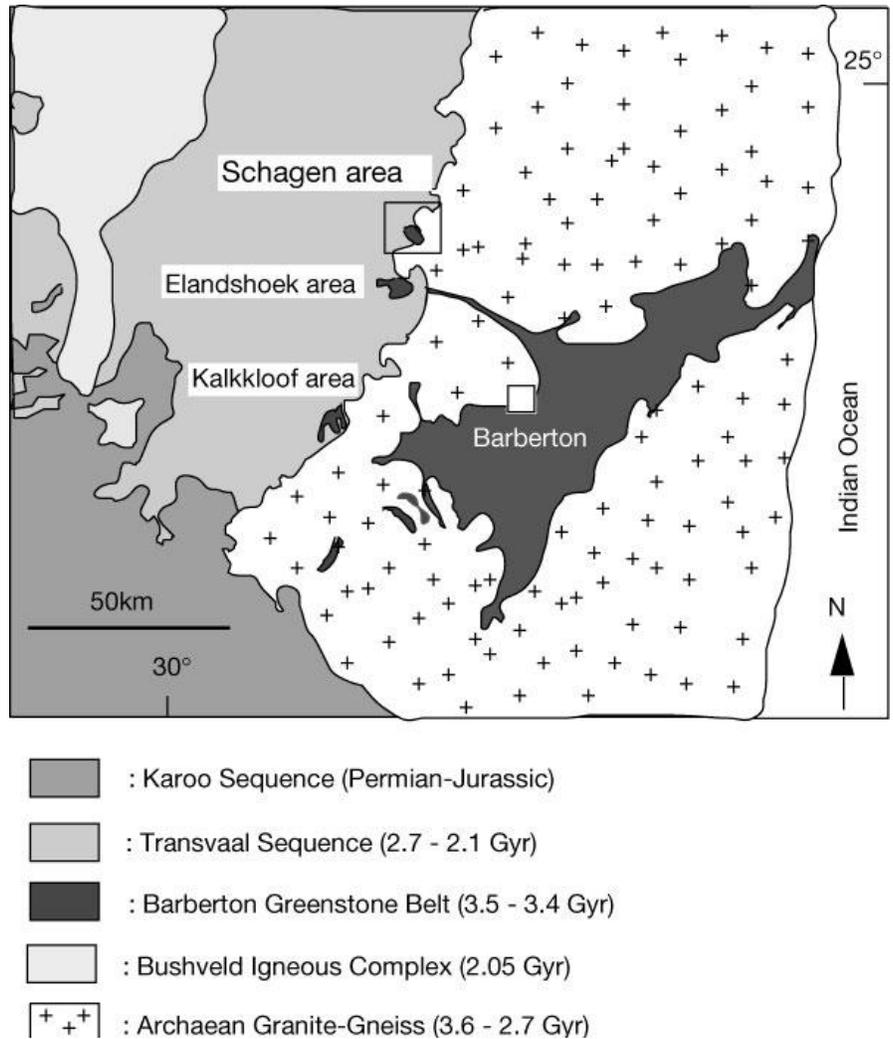


Fig. 1.3.1.2i. Barberton Greenstone Belt (*Nature* 408, 574, 2000).

Naturally, evolution of prokaryotes did not stop in Archean or Proterozoic eon, and continues to this day (Chapter 1.6). We can shed some light on the dynamics of this process by combining fossil evidence with phylogenetic reconstructions based on genomes of extant prokaryotes (Fig. 1.3.1.2j). Because photosynthetic Cyanobacteria probably originated before 2,900 mya and, almost certainly, before 2,700 mya (Section 1.3.1.3), major groups of Bacteria had to diverge very early.

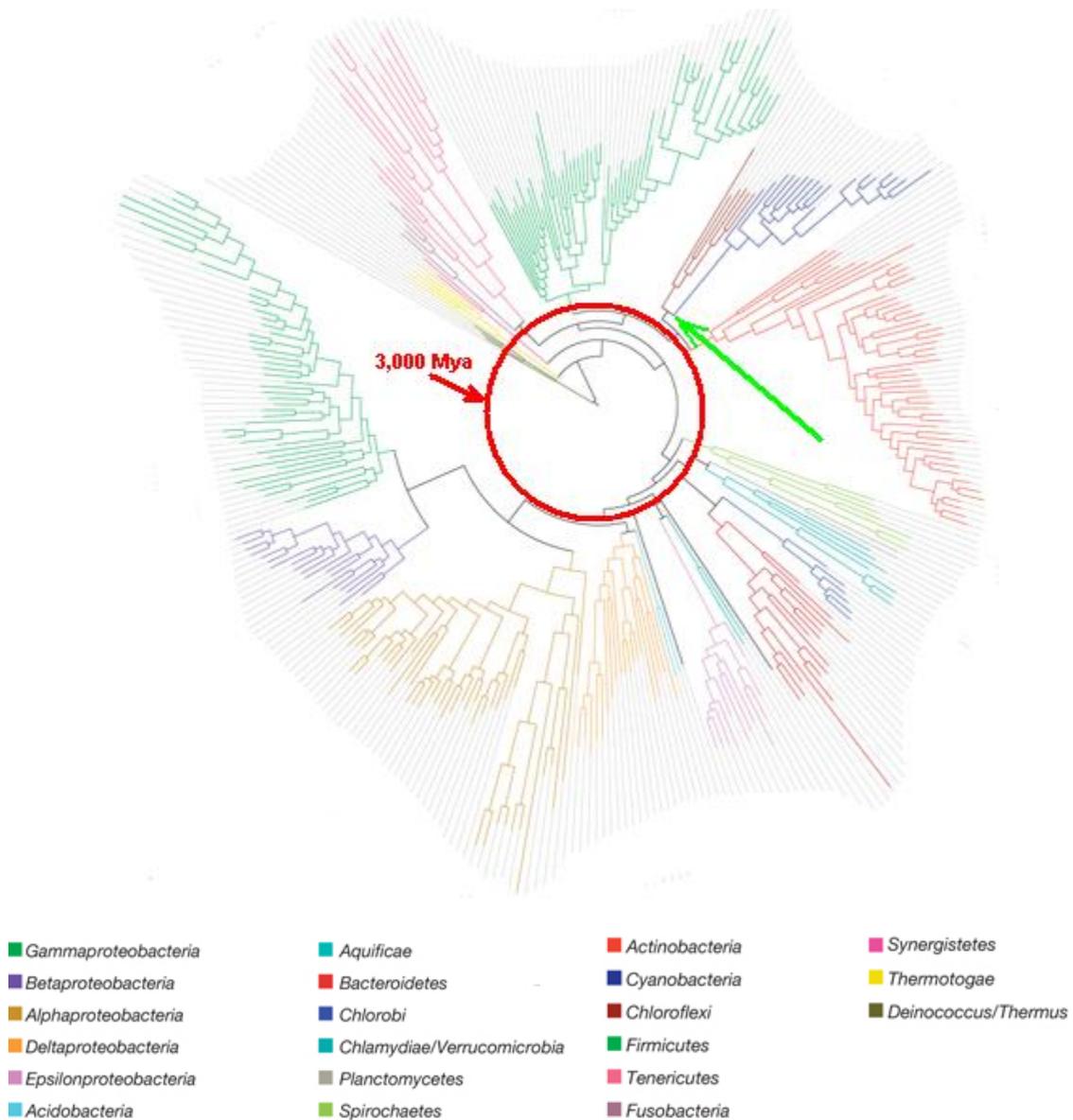


Fig. 1.3.1.2j. Phylogeny of major groups of Bacteria. The origin of Cyanobacteria is shown by a green arrow, and the stage of bacterial divergence roughly 3,000 mya is shown by a red circle (*Nature* 462, 1056, 2009).

The most basal cladogenesis within extant prokaryotes, and within the Universal Tree of Life, the one which produced Bacteria (or Eubacteria) and Archaea (or Archaeobacteria), probably occurred well before 3,500Mya (Fig. 1.3.1.2k). Some discrepancies between phylogenies of Bacteria shown in Fig. 1.3.1.2j and Fig. 1.3.1.2k reflect our yet incomplete understanding of this phylogeny. In fact, widespread LGT

makes representing it by a tree only an approximation (Section 1.1.3), although, apparently, still a useful one.

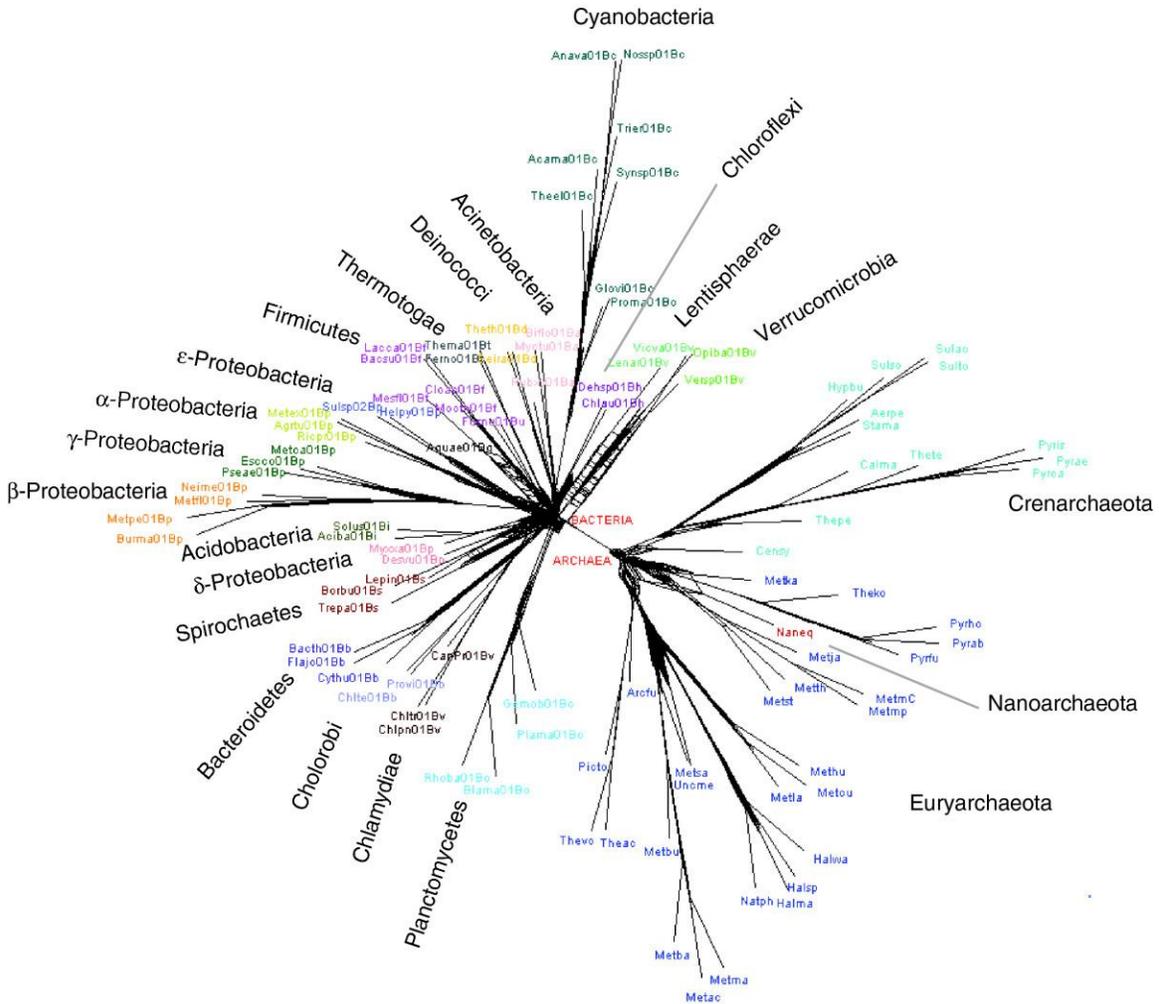


Fig. 1.3.1.2k. Phylogeny of Bacteria and Archaea (*Journal of Biology* 8, 59, 2009).

There are no definite direct data on temperatures under which the earliest life evolved. However, temperature may leave impacts on proteins of ancient organisms that may be reconstructed by phylogenetic analysis of extant genomes. This analysis suggests that there probably were two environmental temperature-related phases during the early evolution. In the first phase, thermotolerance increased from a mesophilic LUCA to thermophilic ancestors of Bacteria and of Archaea–Eukaryota; and in the second phase it decreased (Fig. 1.3.1.2l). If this conclusion is correct, the two lineages descending from

the LUCA adapted in parallel to high temperatures, possibly in response to a climate change of the early Earth, and/or aided by the transition from an RNA genome in the LUCA to organisms with more thermostable DNA genomes.

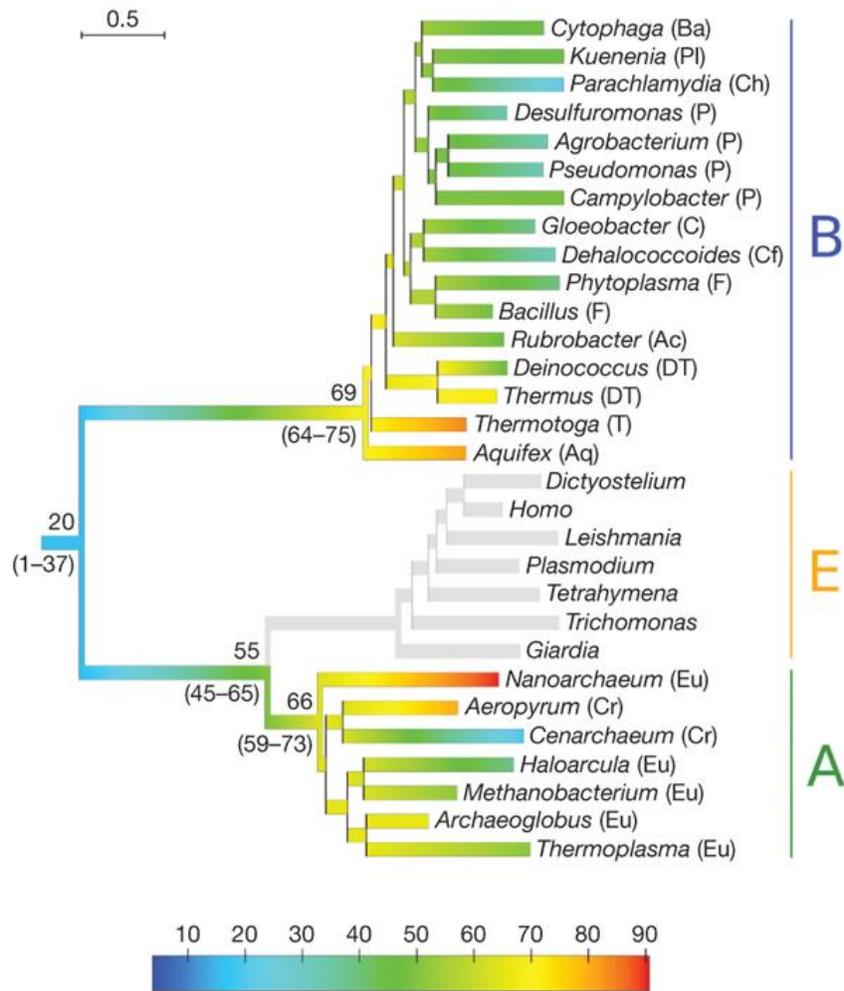


Fig. 1.3.1.2I. Reconstructed optimal growth temperatures of ancestral organisms. B, E, and A stands for Bacteria, Eukaryota, and Archaea. The tree root represents LUCA (*Nature* 456, 942, 2008). The clade of Eukaryotes (grey), which diverged from Archaea, was not analyzed.

### 1.3.1.3. Eukaryotes

Chemical biomarkers suggest that eukaryotes originated from Archaea (Fig. 1.3.1.2I) at least 2,700 mya. Eukaryote cells are characterized by nuclear membrane, separating the nucleus from cytoplasm, by mitochondria, originated from endosymbiotic

alpha-proteobacterium, and by the endoplasmic reticulum. We do not know in which order these traits appeared, because of the lack of information about intermediate forms possessing only some of them. Some modern eukaryotes lack mitochondria, but nuclear genomes of all such eukaryotes studied so far carry genes that were transferred from mitochondria, indicating their origin from mitochondrial ancestors. The genome of LECA, Last Eukaryotic Common Ancestor, probably already contained a fair number of introns (*Nature* 440, 623, 2006). Fig. 1.3.1.3a summarizes the known record of body fossils of all early eukaryotes, except animals.

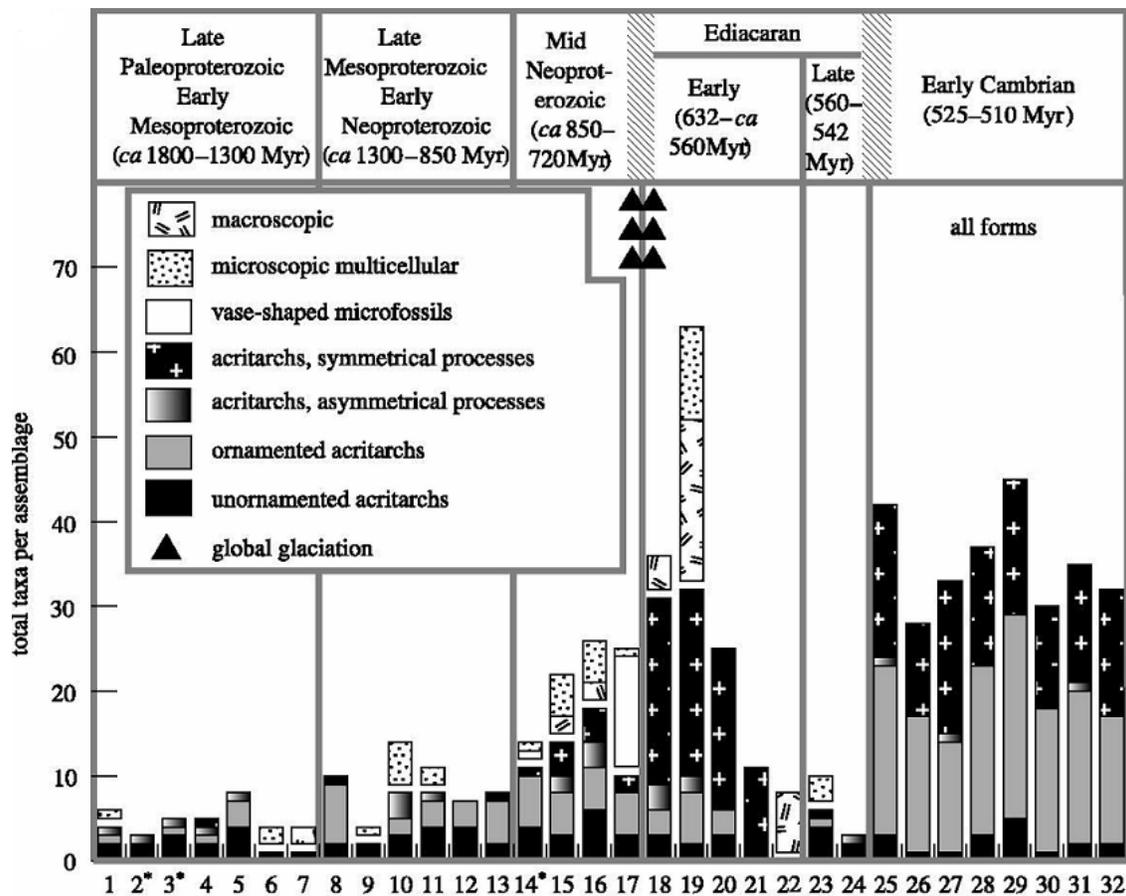


Fig. 1.3.1.3a. The composition and taxonomic richness of non-metazoan eukaryotes in Proterozoic to Early Cambrian (*Phil. Trans. Royal Soc. B* 361, 1023, 2006).

The earliest reliable eukaryote microfossils are remnants of *Valeria lophostriata*, which appeared 1,800 mya and existed, without noticeable morphological changes, until 745 mya (Fig. 1.3.1.3b). A variety of eukaryotes of substantial cytological complexity

lived 1,500-1,300 mya (Fig. 1.3.1.3c). Still, fossils from this period are mostly hard to interpret.

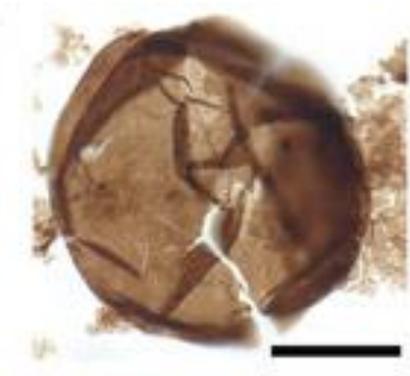


Fig. 1.3.1.3b. *Valeria lophostriata* (bar = 30 mkm) (*Nature Geoscience* 2, 415, 2009).

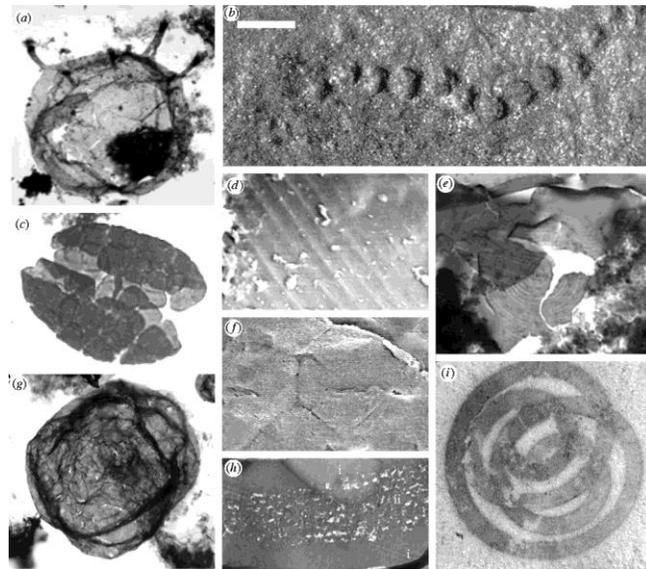


Fig. 1.3.1.3c. Diversity of Late Palaeoproterozoic to Early Mesoproterozoic (1,800 - 1,300 Ma) eukaryotic microfossils (*Phil. Trans. Royal Soc. B* 361, 1023, 2006).

Multicellular eukaryotes appeared by the end of the Mesoproterozoic 1,200 mya. A variety of fossils from these and later times, both uni- and multicellular, can be attributed to several extant clades, including red algae, green algae, xanthophytes, and possibly fungi (Fig. 1.3.1.3d). Thus, major clades of eukaryotes diverged during Mesoproterozoic or even Paleoproterozoic eras.

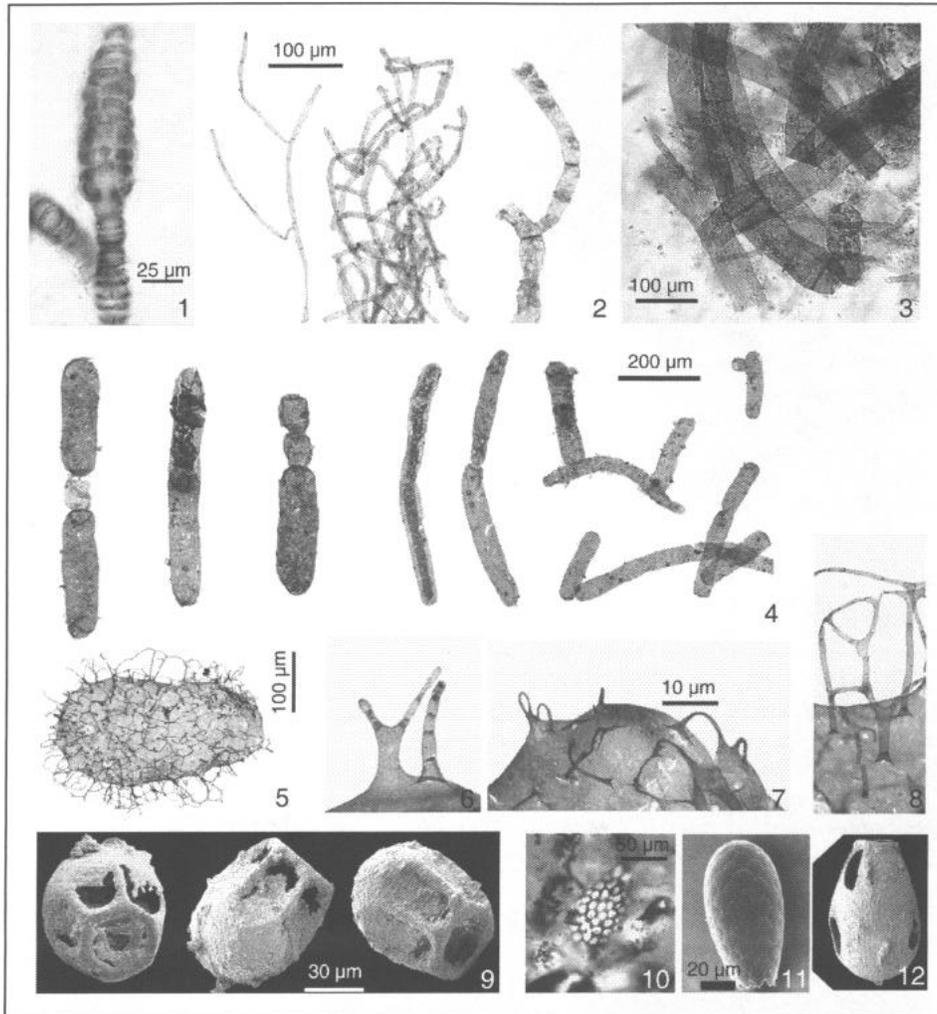


Fig. 1.3.1.3d. Mesoproterozoic and Neoproterozoic eukaryotic fossils probably belonging to total groups of extant clades. (1) *Bangiomorpha pubescens*, ~1,200 Ma, showing radial division of cells within uniseriate filaments, interpreted as Bangiophyte red alga; (2) *Proterocladus sp.*, ~750 Ma, interpreted as Cladophorale green alga; 3-4) *Paleovaucheria clavata*, ~1,000 Ma and ~750 Ma interpreted as a vaucheriacean yellow-green alga; 5-8) *Tappania plana*, ~800 Ma, a complex multicellular form with septate (6), anastomosing processes (8) interpreted as a possible fungus; 9, 10, 12) vase-shaped microfossils from the ~750 Ma Chuar Group, Arizona, representing testate amoebae, 9) *Melanocyrrilliurn hexodiadema*, interpreted as a lobose testate amoeba, 10) *Melicerion poikilon* interpreted as a euglyphid testate amoeba; 11) modern analog *Euglypha tuberculata*; 12) vase-shaped microfossil with holes in the test, possibly due to predation (*Advances in Experimental Medicine and Biology* 607, 1, 2007).

Elucidating early evolution of eukaryotes remains one of the major unsolved problems in phylogenetics. The difficulty of this problem to a large extent is due to a rapid succession of ancient cladogeneses that produced the principal eukaryotic clades. Also, the fossil record known so far sheds no light on this process. To complicate things further, early evolution of eukaryotes involved not only cladogeneses but also a number of symbioses that produced primary, secondary, and even tertiary plastids.

Most of extant eukaryotes can be attributed to one of following six "superclades", although some groups apparently do not belong to any of them:

1) Unikonta, a large clade of diverse heterotrophic eukaryotes that can be both unicellular and multicellular. Unikonts consist of two clades, Amoebozoa and Opisthokonta. Amoebozoa are mostly amoeboid protists with blunt pseudopodia, as well as multinucleate or multicellular slime moulds (Fig. 1.3.1.3e; phyla names are given in parentheses). Opisthokonta (having rear flagellum) comprise unicellular choanoflagellates, unicellular and multicellular fungi, and multicellular animals, or metazoans (Fig. 1.3.1.3f).

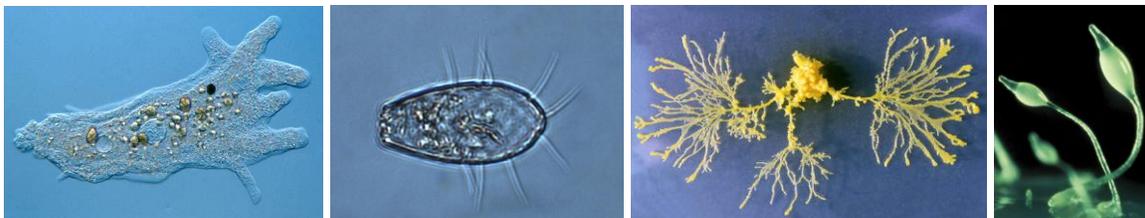


Fig. 1.3.1.3e. Unikonta, Amoebozoa (left to right): naked lobose amoeba (Archamoebae) *Amoeba proteus*, testate amoeba (Archamoebae) *Euglypha tuberculata* (see also Fig. 1.3.1.3d-11), plasmodial slime mold (Myxogastria) *Physarum polycephalum*, cellular slime mold (Dictyostelia) *Dictyostelium discoideum*.



Fig. 1.3.1.3f. Unikonta, Opisthokonta (left to right): choanoflagellate (Choanoflagellata) *Salpingoeca sp.*, chytrid fungus (Fungi) *Cladochytrium sp.*, basidiomycete (Fungi) *Russula rhodopus*, animal (Animalia) *Homo sapiens*.

2) Excavata, a clade of mostly flagellate protists, some of which lost mitochondria (Fig. 1.3.1.3g).

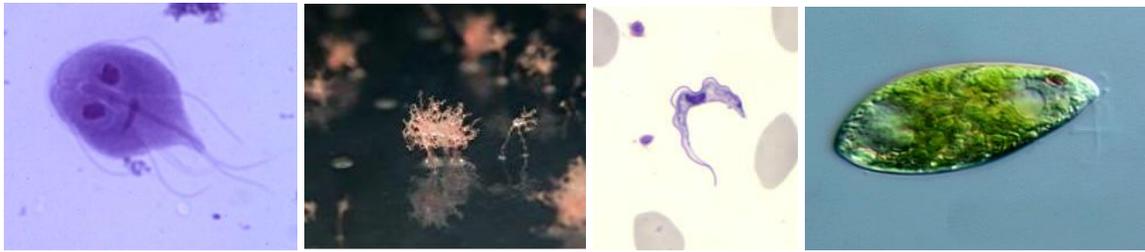


Fig. 1.3.1.3g. Excavata (left to right): human diplomonad pathogen (Metamonada) *Giardia lamblia*, cellular slime mold (Acrasia) *Acrasis sp.*, human kinetoplastid pathogen (Kinetoplastida) *Trypanosoma brucei*, photosynthetic euglena (Euglenozoa) *Euglena viridis*.

3) Rhizaria, a clade of mostly ameboid protists with filose, reticulose, or microtubule-supported pseudopods (Fig. 1.3.1.3h).

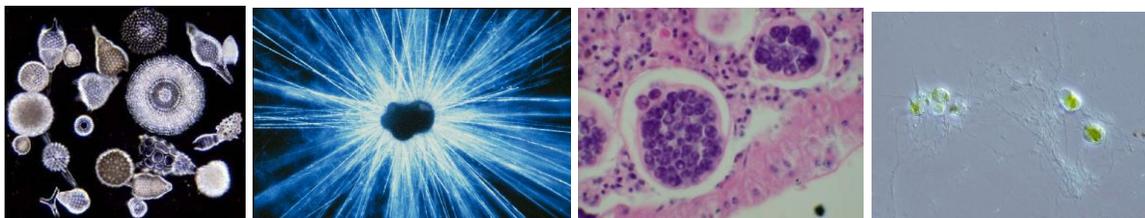


Fig. 1.3.1.3h. Rhizaria (left to right): various radiolaria (Radiolaria), planktonic foraminifera (Foraminifera) *Globigerinella aequilateralis*, marine parasitic haplosporidian (Haplosporidia) *Perkinsus chesapeaki*, photosynthetic chlorarachniophyte (Chlorarachniophyta) *Chlorarachnion reptans*.

4) Haptophyta+allies, a clade of mostly flagellate protists, autotrophic and heterotrophic (Fig. 1.3.1.3i).



Fig. 1.3.1.3i. Haptophyta+allies (left to right): autotrophic haptophyte (Haptophyta) *Prymnesium parvum*, heterotrophic kathablepharid (Cryptophyta) *Leucocryptos sp.*, autotrophic cryptomonad (Cryptophyta) *Cryptomonas ovata*.

5) Chromalveolata, a large clade of diverse eukaryotes that can be both unicellular and multicellular and autotrophic and heterotrophic. Chromalveolata consists of two separate clades: Alveolata and Heterokonta (or Stamenopila). Alveolata are protists and comprises three phyla, Ciliata, Apicomplexa, and Dinophyta. Heterokonts vary from unicellular flagellates to large sea weeds, all of which, however, pass in their life cycles through a motile stage, in which cells possess two flagella of different shapes (Fig. 1.3.1.3k, l).

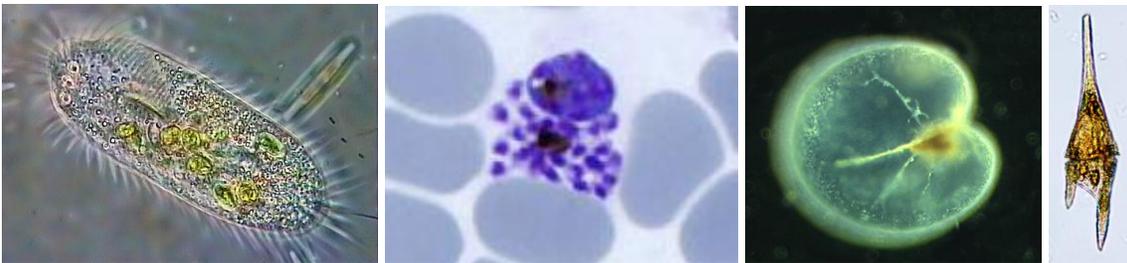


Fig. 1.3.1.3k. Chromalveolata, Alveolata (left to right): ciliate (Ciliata) *Stylonychia sp.*, apicomplexan human pathogen (Apicomplexa) *Plasmodium falciparum*, heterotrophic dinoflagellate (Dinophyta) *Noctiluca scintillans*, autotrophic dinoflagellate (Dinophyta) *Ceratium furca*.



Fig. 1.3.1.3l. Chromalveolata, Heterokonta (left to right): heterotrophic water mold (Oomycetes) *Phytophthora infestans* (plant pathogen), diatom (Bacillariophyta) *Thalassiosira pseudonana*, golden alga (Chrysophyta) *Dinobryon sp.*, yellow-green alga (Xanthophyta) *Vaucheria sp.* (Fig. 1.3.1.3d-3,4), brown alga (Phaeophyta) *Fucus vesiculosus*.

6) Archaeplastida (carrying ancient plastids), a clade of mostly autotrophic eukaryotes with primary plastids, comprising glaucophyte algae, red algae, and green plants (Fig. 1.3.1.3m).



Fig. 1.3.1.3m. Archaeplastida (left to right): glaucophyte (Glaucophyta) *Glaucocystis nostochinearum*, red alga (Rhodophyta) *Porphyra purpurea* from the family Bangiophyceae (compare to Fig. 1.3.1.3d-1), green alga (Viridiplantae) *Cladophora glomerata* from the order Cladophorales (compare to Fig. 1.3.1.3d-2), a land plant (Viridiplantae) *Rosa rugosa*.

Still, the tree of eukaryotes remains uncertain. First, the relationships between the six superclades have not yet been resolved unambiguously. Second, it is not even certain that these superclades are real clades. Although phylogenetic affinity between organisms attributed to a superclade is not in doubt, monophyly of some of the superclades is

uncertain: they might include only some, but not all descendants of a particular common ancestor. As far as acquisition of plastids is concerned, we know the following:

1) There was a single origin of primary chloroplasts, from an endosymbiotic cyanobacterium, by the common ancestor or Archaeplastida, after which chloroplasts diverged substantially between the red and green algae (Fig. 1.3.1.3n).

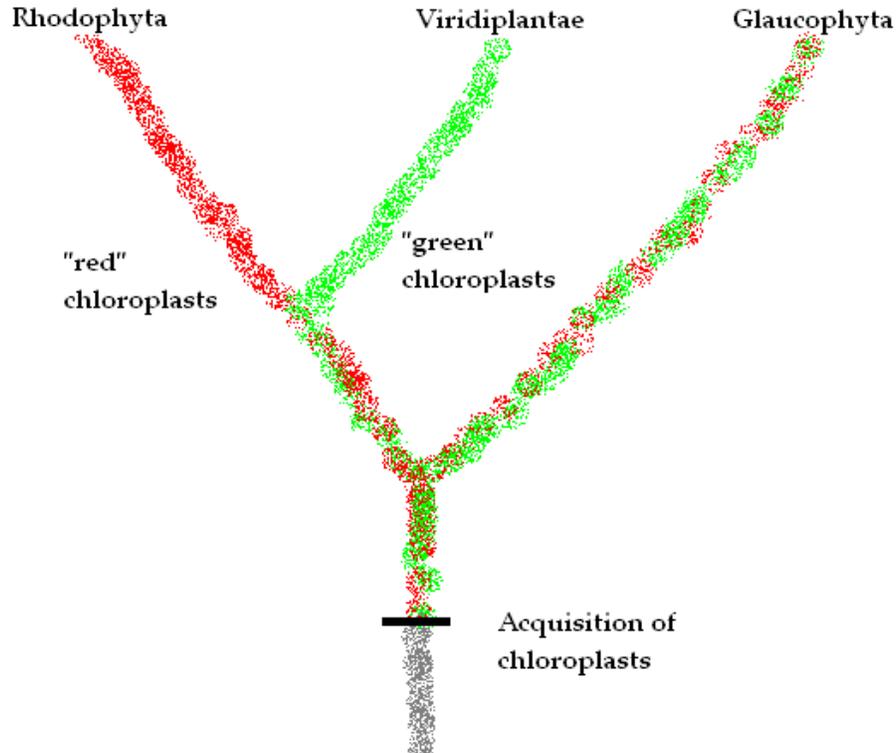


Fig. 1.3.1.3n. Phylogeny of Archaeplastida. Glaucophyta probably is an outgroup, but this is not certain.

2) Secondary plastids originated from endosymbiotic green algae were independently acquired by Chlorarachniophyta (superclade Rhizaria) and Euglenophyta (superclade Excavata), which otherwise consist of primitively heterotrophic organisms.

3) Many groups within Haptophyta+allies (Haptophyta and Cryptophyta) and Chromalveolata (most of Dinophyta among Alveolata, and several phyla of Heterokonta, including Bacillariophyta, Chrysophyta, Xanthophyta, and Phaeophyta) carry plastids which originated from endosymbiotic red algae. It is not clear if their plastids are

secondary, originating directly from endosymbiotic red algae, or tertiary, originating from some other eukaryote that already acquired a red alga-derived plastid.

4) Some Dinophyta possess unique tertiary plastids, taken from cryptophytes, haptophytes, and heterokonts. Still others possess plastids of both red algae and green algae ancestry.

The key uncertainty is concerned with 3), the origin of red algae-derived plastids in Haptophyta+allies and Chromalveolata. The possible scenarios depend on the phylogenetic relationships between the eukaryotic superclades (Fig. 1.3.1.3o). As long as Archaeplastidae is an outgroup to Haptophyta+allies and Chromalveolata, it is possible that there was only a single acquisition of red-algae-derived plastid, followed by their multiple losses. If, however, Chromalveolata is an outgroup to Haptophyta+allies and Archaeplastidae, this scenario is impossible, and there must be at least two acquisitions.

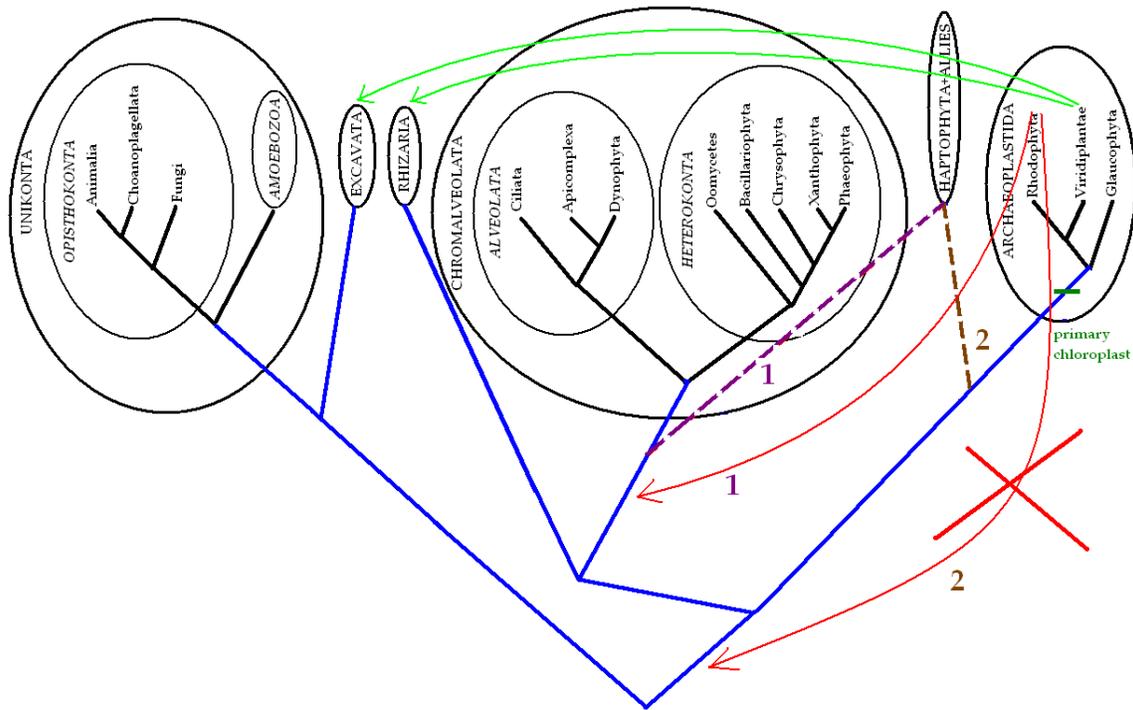


Fig. 1.3.1.3o. Interrelation between possible phylogeny of eukaryotes and the scenario of acquisition of red algae-derived plastids. Depending on the phylogenetic affinity of Haptophyta+Allies, a single origin of such plastids is either possible (hypothesis 1) or impossible (hypothesis 2), because endosymbiosis involving red algae could not occur

before their origin. Green arrows show acquisition of green algae-derived palstids by Euglenozoa and Chlorarachniophyta. Multiple acquisitions of extra plastids by Dinophyta are not shown (see *Current Biology* 19, R81, 2009; *BioScience* 59, 471, 2009; *Journal of Eukaryotic Microbiology* 56, 1, 2009; *Molecular Biology and Evolution* 26, 2745, 2009).

If "superclades" are not monophyletic, more possibilities emerge. For example, one analysis concluded that Archaeplastida are paraphyletic (Section 1.1.3), with as many as four other superclades (Excavata, Rhizaria, Chromalveolata, and Haptophyta+Allies) nested within it. If this is the case, there must have been many ancient losses of primary plastids, sometimes followed by acquisitions of secondary or tertiary plastids (Fig. 1.3.1.3p). Clearly, key facts about early diversification of eukaryotes remain obscure.

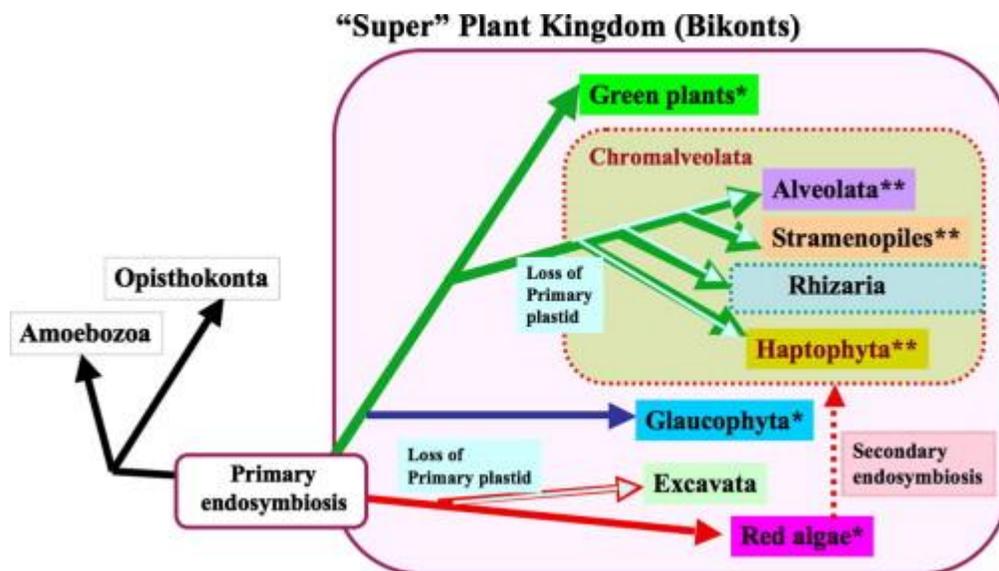


Fig. 1.3.1.3p. A possible scenario of eukaryote evolution assuming that Excavata, Rhizaria, Chromalveolata, and Haptophyta+Allies are all nested, in different places, within Archaeplastids, forming a giant clade Bikonts (*Molecular Phylogenetics and Evolution* 53, 872, 2009).

Large multicellular organisms independently evolved at least six times, in red algae, green plants (twice), and brown algae (Fig. 1.3.1.3q), as well as in fungi (Fig. 1.3.1.3r) and animals. This evolution certainly began in the Proterozoic eon. Fig. 1.3.1.3s

shows the phylogeny of aquatic green plants; their evolution in the Phanerozoic eon, involving adaptation to terrestrial life, will be treated later (Section 1.3.2.3).

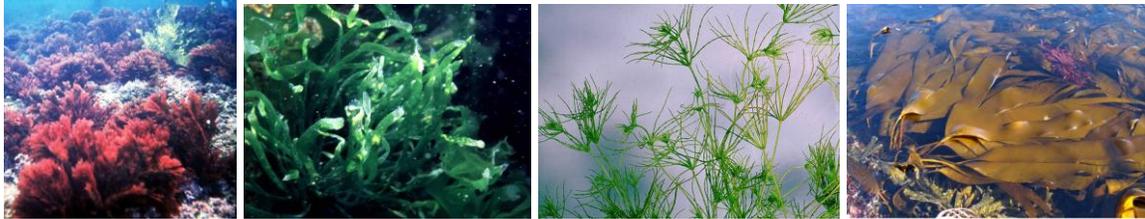


Fig. 1.3.1.3q. Large extant eukaryotic algae: *Delisea pulchra* (Rhodophyta), *Ulva intestinalis* (Viridiplantae, Chlorophyta), *Chara sp.* (Viridiplanta, Streptophyta), *Laminaria digitata* (Phaeophyta).

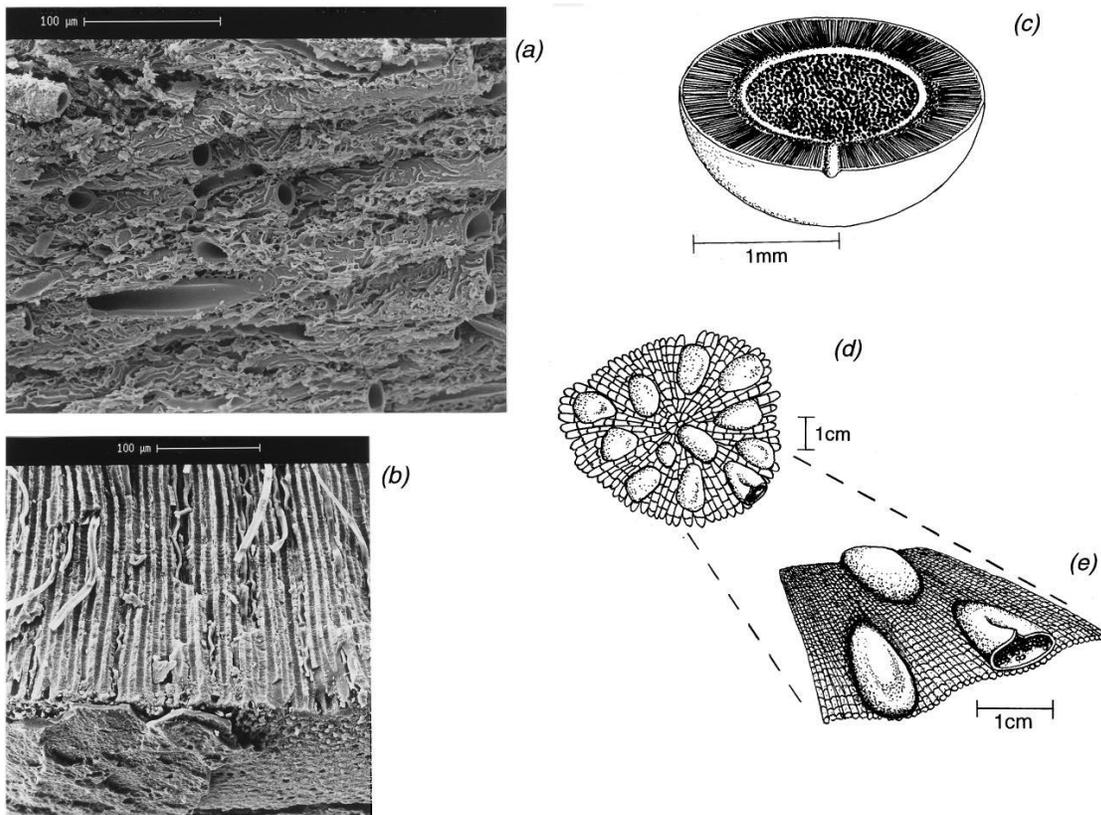


Fig. 1.3.1.3s. A fossil fungus *Prototaxites*, which appeared in the fossil record 420 mya and for 50 Ma, until the evolution of large trees, remained the largest known organism that lived on land. *Prototaxites*, produced unbranched trunks as long as 8 m and 1 m in diameter, constructed of a relatively homogenous tissue of interwoven tubes (*Geology* 35, 399, 2007).

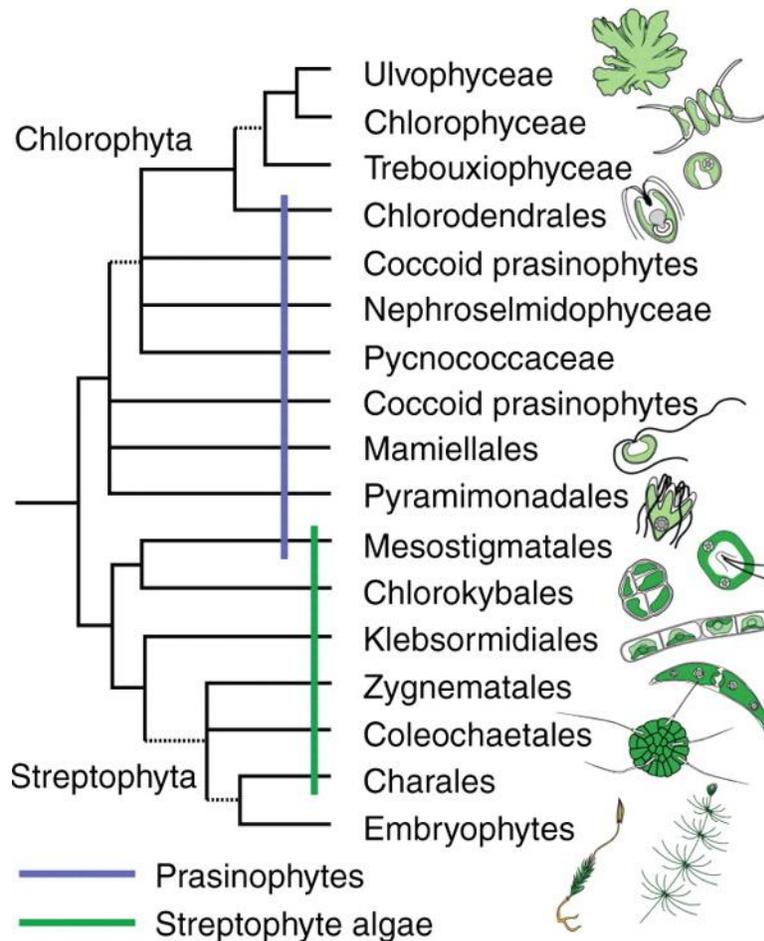


Fig. 1.3.1.3s. A plausible phylogenetic tree of the Viridiplantae, consisting of two clades, Chlorophyta and Streptophyta (Charophyta). The term "prasinophytes" is used for scaly green flagellates (Mesostigmatales and basal Chlorophyta) (*Annals of Botany* 103, 999, 2009).

#### 1.3.1.4. Animals

The closest living relatives of multicellular animals (or metazoans) are choanoflagellates, and the closest clade that independently evolved multicellularity, mostly in the course of adaptation to terrestrial habitats in the Paleozoic era, is Fungi (Fig. 1.3.1.3o; Fig 1.3.1.4a). Choanoflagellate cells bear a single apical flagellum (Fig. 1.3.1.3f) and the genome of a choanoflagellate *Monosiga brevicollis* contains ~9,200 intron-rich genes (*Nature* 451, 783, 2008). Presumably, multicellularity of animals evolved less than 1,000 mya.

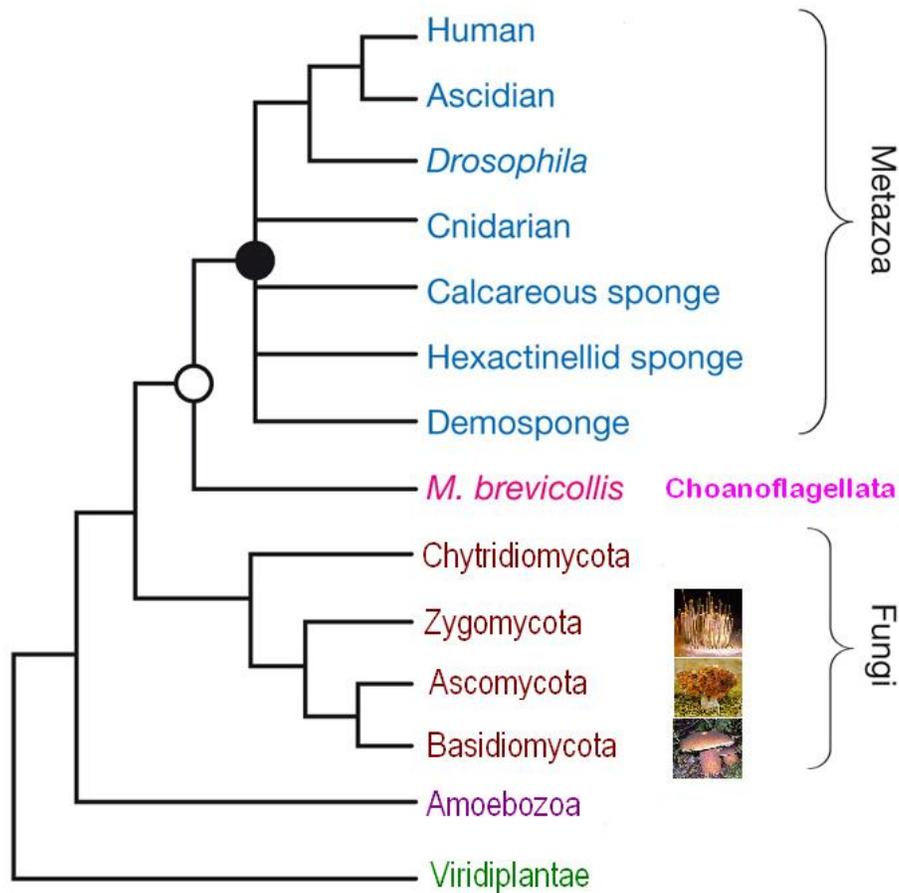


Fig. 1.3.1.4a. Phylogenetic position of animals and fungi, among other eukaryotes (Nature 443, 818, 2006). *Phycomyces blakesleeanus* (Zygomycota), *Gyromitra esculenta* (Ascomycota), and *Boletus edulis* (Basidiomycota) are terrestrial fungi; see Fig. 1.3.1.3f for picture of a fungus from Chytridiomycota.

Phylogenetic analyses based on modern genomes suggest that diversification of metazoans began in the Cryogenian (Fig. 1.3.1.4b). Extant representatives of the major clades produced by the first cladogeneses of animals, sponges (calcisponges and demosponges), cnydarians, and bilaterian animals (protostomes and deuterostomes) are shown in Fig. 1.3.1.4c. The earliest known animal fossils are biomarkers, the hydrocarbon remains of C30 sterols produced by demosponges, which appeared in marine sediments from late Cryogenian, > 635 mya (Fig. 1.3.1.4d), in excellent agreement with indirect evidence (Fig. 1.3.1.4b). Stromatolites also disappeared from the fossil record

approximately at that time, probably because of the appearance of macroscopic predators. The earliest body fossils that may represent animals are ~600 Ma.

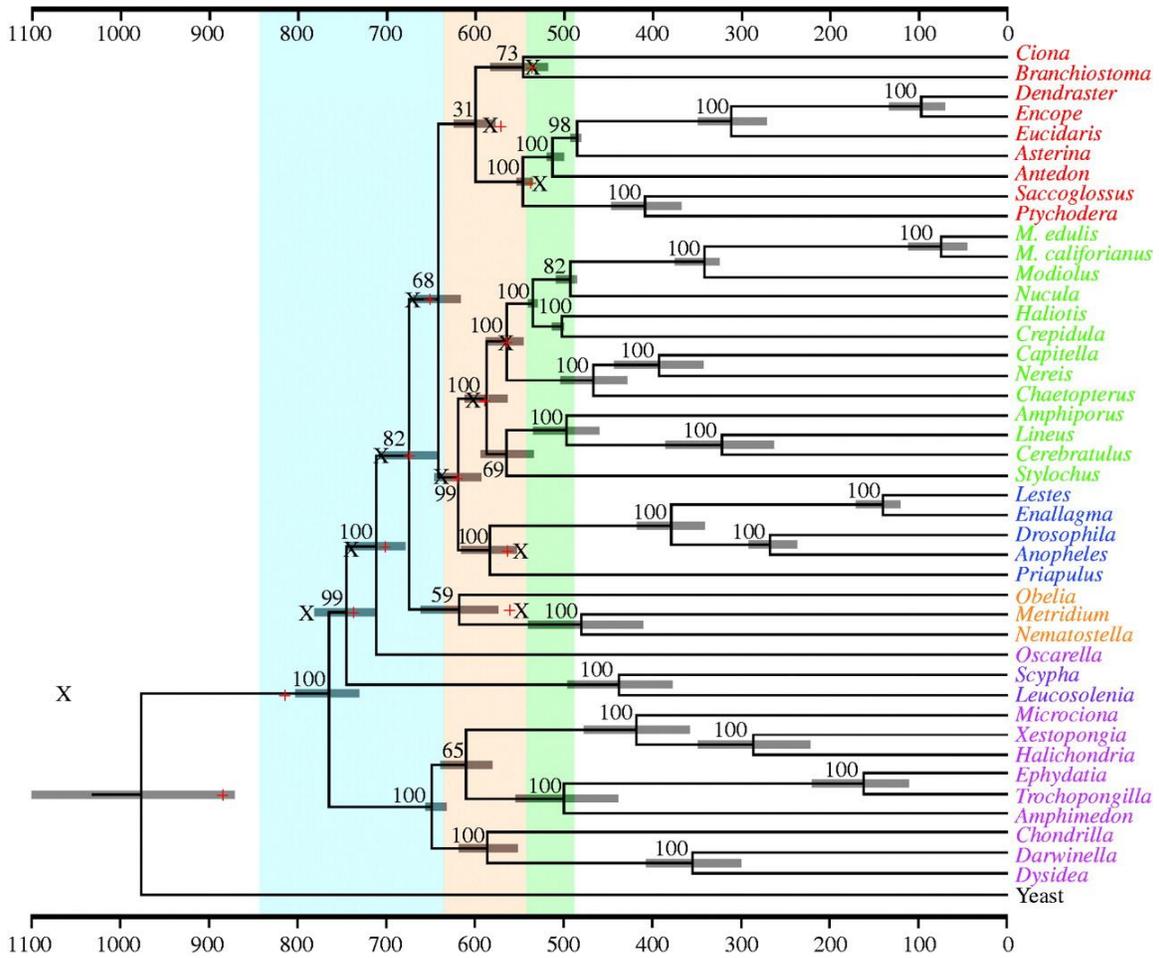


Fig. 1.3.1.4b. The inferred timing of the metazoan radiation. The phylogenetic tree for 41 metazoan taxa rooted on the yeast *Saccharomyces cerevisiae* is shown. Among metazoans, the deuterostomes are shown in red, spiralian protostomes in green, ecdysozoan protostomes in blue, cnidarians in orange, the homoscleromorph *Oscarella* in salmon pink, calcisponges in purple and demosponges in magenta. Note that much of the metazoan diversification occurs during the Ediacaran (brown), which lies between the Cryogenian (ice blue) and the Cambrian (green). (*Phil. Trans. R. Soc. B* 363, 1435, 2008).



Fig. 1.3.1.4c. Representatives of major extant clades of animals: syconoid sponge *Sycon ciliatum* (calcisponge, Calcarea), fire sponge *Latrunculia corticata* (demosponge, Demospongiae), sea anemone *Pachycerianthus fimbriatus* (cnidaria, Cnidaria), nematode *Caenorhabditis elegans* (ectdysozoan protostome, Ecdysozoa), polychaete *Nereis succinea* (spiralian protostome, Lophotrochozoa), starfish *Solaster endeca* (deuterostome, Echinodermata).

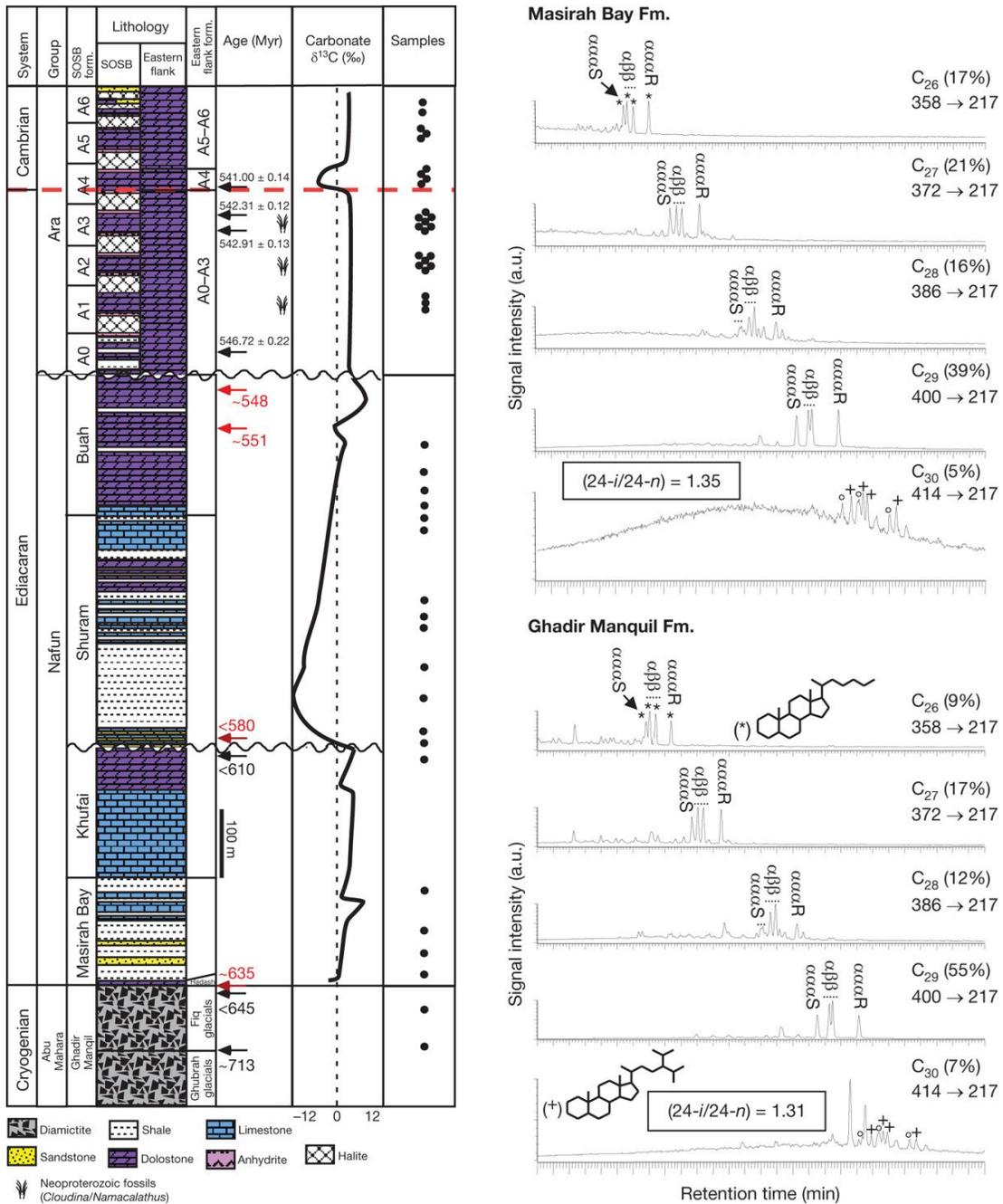


Fig. 1.3.1.4d. (left) Stratigraphic distribution of samples where biomarkers from demosponges, desmethylsteranes, were found in sediments of Huqf Supergroup, South Oman. Absolute dates in red are from correlation with other dated sediments worldwide (Namibia, South China) using comparisons of  $\delta^{13}\text{C}$  stratigraphic features. Absolute dates in black are from direct U–Pb zircon age measurements on Huqf detrital zircons and ash beds. (right) Chromatograms of C<sub>26</sub>–C<sub>30</sub> desmethylsteranes found in these sediments (*Nature* 457, 718, 2009).

Ediacaran period begun at the end of the Marinoan glaciation 635 mya, but fossils of diverse macroscopic animals, known as Ediacaran biota, appeared only 575 mya, shortly after the Gaskiers glaciation (Fig. 1.2.2.4a). It seems plausible that evolution of Ediacaran biota was triggered by persistent oxygenation of water masses, perhaps with the exception of deep water, throughout the oceans (Fig. 1.2.4.3d). Indeed, the iron content of deep-sea sediments shows that ocean was anoxic before and during the Gaskiers glaciation and became oxic afterward (*Nature* 444, 744, 2006; *Science* 315, 92, 2007). The Ediacara biota, first recognized in Australia (Fig. 1.3.1.4e) but now known from many sites around the globe, included a mixture of stem- and crown-group radial animals (Section 1.2.3.4), stem-group bilaterian animals, and perhaps species of other eukaryotic kingdoms. These soft-bodied organisms were preserved under beds of sand or volcanic ash, and four distinct preservational styles (Flinders, Fermeuse, Conception, and Nama) affected the types of organisms and features that could be preserved.



Fig. 1.3.1.4e. Ediacara Hills.

Even the earliest Ediacaran communities (575–565 Ma) show vertical and lateral niche subdivision of the sessile, benthic, filter-feeding organisms, which is strikingly like that of Phanerozoic and modern communities (Fig. 1.3.1.4f). Later biological and ecological innovations include mobility (>555 Ma), calcification (550 Ma), and predation (<549 Ma) (Fig. 1.3.1.4g). The Ediacara biota disappeared abruptly 542 mya (*Ann. Rev. Earth and Planetary Sci.* 33, 421, 2005). The extinction of Ediacara biota, apparently triggered by a global anoxia or some other drastic change of the environment (Figs.

1.2.2.4a,b) was one of the most dramatic events in the history of life, and is regarded as the end of the Proterozoic eon.

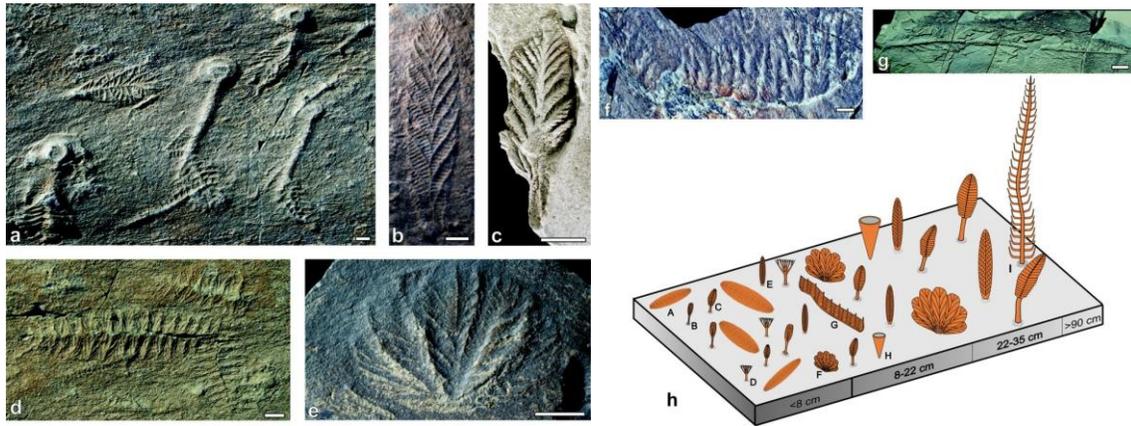


Fig. 1.3.1.4f. Representatives of early Ediacara biota. Avalon Assemblage on upper bedding surfaces from Newfoundland (a, c–h) and Charnwood, England (575–560Mya).



Fig. 1.3.1.4g. Later Ediacaran biota. (left). White Sea assemblage preserved on bed soles from Australia (a–e, h–i), northern Russia (f–g), and northwestern Canada (j). The oldest occurrences are <math>< 560\text{My}</math> old and the youngest may range to near the base of the

Cambrian. (right). Nama Assemblage fossils from Namibia. Scale bar represents 2 cm. The type assemblage is of shallow-water origin and has been dated at >549–542Mya.

Because cladogeneses that produced major extant clades of animals apparently occurred in the Cryogenian, interpretation of at least some Ediacaran fossils as members of total groups of these clades is plausible. However, these interpretations are usually difficult. One of exceptions is *Kimberella quadrata*, an Ediacaran fossil that almost certainly was a bilaterian, likely a protostome, and perhaps a mollusc (Fig. 1.3.1.4h). Another are two quite different 580-600 Ma old embryos of bilaterian animals (Fig. 1.3.1.4i), which imply that the last common ancestor of bilaterians lived much earlier, in agreement with conclusions from molecular phylogenetics (Fig. 1.3.1.4b). Still, it seems that the known fossil record of Ediacara biota remains rather incomplete.

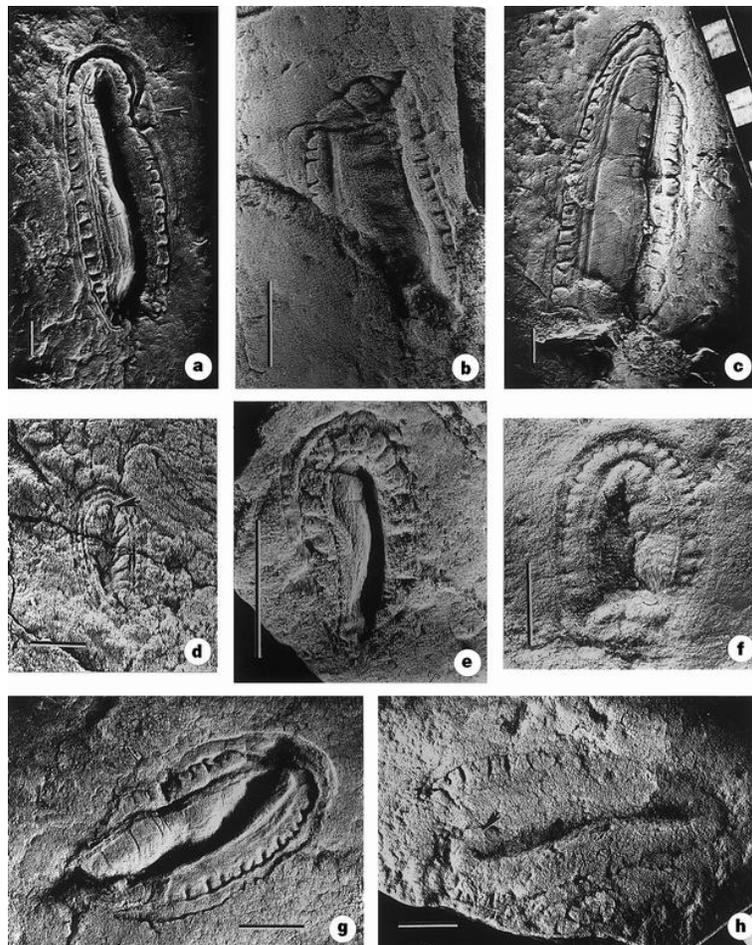


Fig. 1.3.1.4h. Specimens of a possible Ediacaran mollusc *Kimberella quadrata* from Ust'-Pinega Formation, Winter Coast of White Sea, Russia (*Nature* 388, 868, 1997).

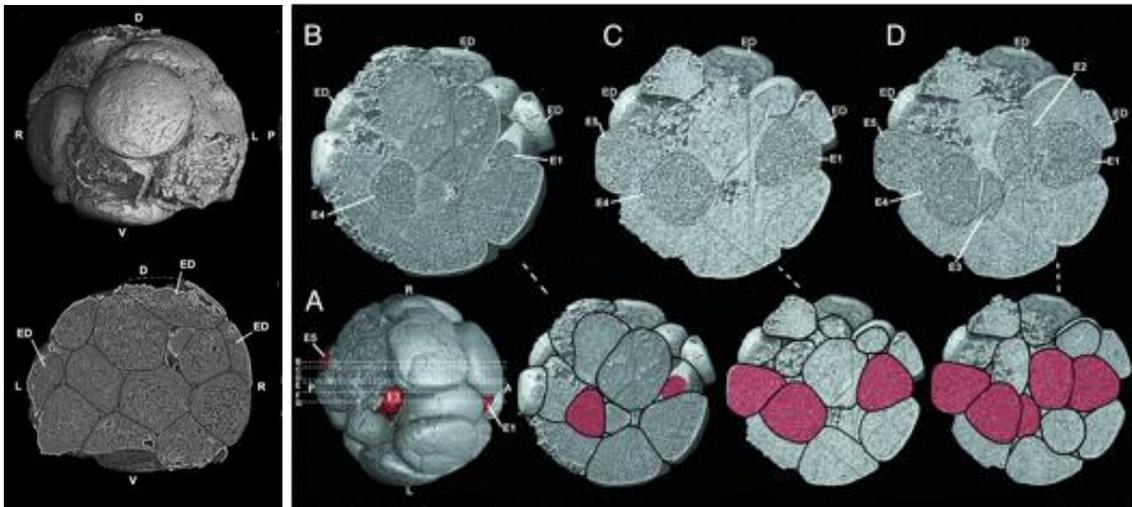


Fig. 1.3.1.4i. Two different fossil embryos of bilaterian animals (left and right) from Doushantuo phosphate deposits, China, investigated by synchrotron radiation microtomography (*PNAS* 106, 19056, 2009).

Remarkably, transition to multicellularity in metazoans was not accompanied by a large increase in the number of protein-coding genes. *Drosophila melanogaster* genome contains ~14,000 genes and genomes of mammals contain ~20,000 genes, or ~2 times more than choanoflagellates. Apparently, at the DNA level complexity of multicellular organisms is mostly due to regulatory intergenic DNA (Chapter 1.5). Still, there are a number of genes, called homeotic genes, which individually play major roles in the development and evolution of body plans of metazoans.

In particular, a family of paralogous genes, known as Hox genes, specifies the anterior-posterior axis and segment identity of animals. Hox genes contain a DNA region called homeobox that encodes protein DNA-binding domain known as homeodomain. The proteins encoded by Hox genes work as regulators of transcription. Their mutations can have drastic effects on the whole organization of the body (Fig. 1.3.1.4j). Usually, Hox genes within the genome form several clusters, each containing from two to >10 adjacent genes. The order of the Hox genes within such clusters is often the same as the order of the regions they affect along the main (anterior-posterior) axis of the body.

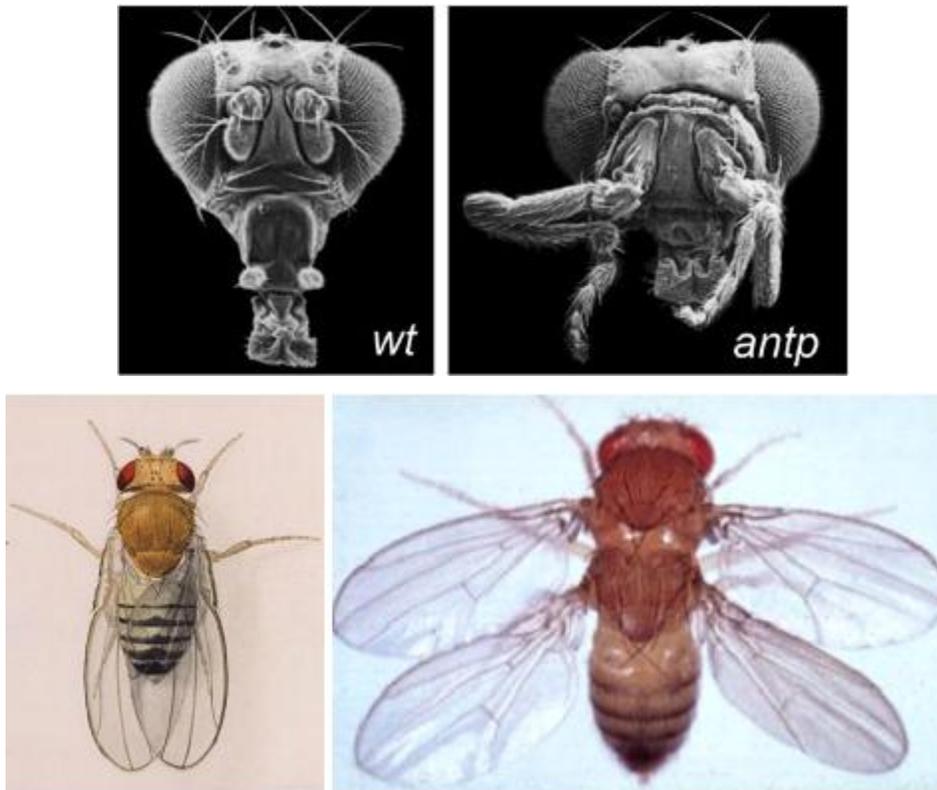


Fig. 1.3.1.4j. (top) Antennapedia is a Hox gene which controls the placement of legs. In *Drosophila*, some mutant alleles of Antennapedia convert antenna into ectopic legs. Left: wild-type phenotype; right: an Antennapedia mutation. (bottom) Ultrabithorax is another Hox gene. In *Drosophila*, it represses the formation of wings on the 3rd thoracic segment. Left: wild-type phenotype, right: abd Ultrabithorax mutation.

Evolution of animals with more complex body plans was accompanied by diversification, by gene duplication, of their repertoire of homeobox genes. Bilaterian animals have a Hox gene cluster essential for patterning the main body axis, and a ParaHox gene cluster. Comparison of Hox genes in genomes of bilaterians and cnidarians suggest that both Hox and ParaHox gene clusters evolved from a simple ProtoHox cluster (Fig. 1.3.1.4k). Still, progressive increase of complexity of regulatory regions of already existing genes was also crucial for the evolution of complex metazoans (Chapter 1.5).

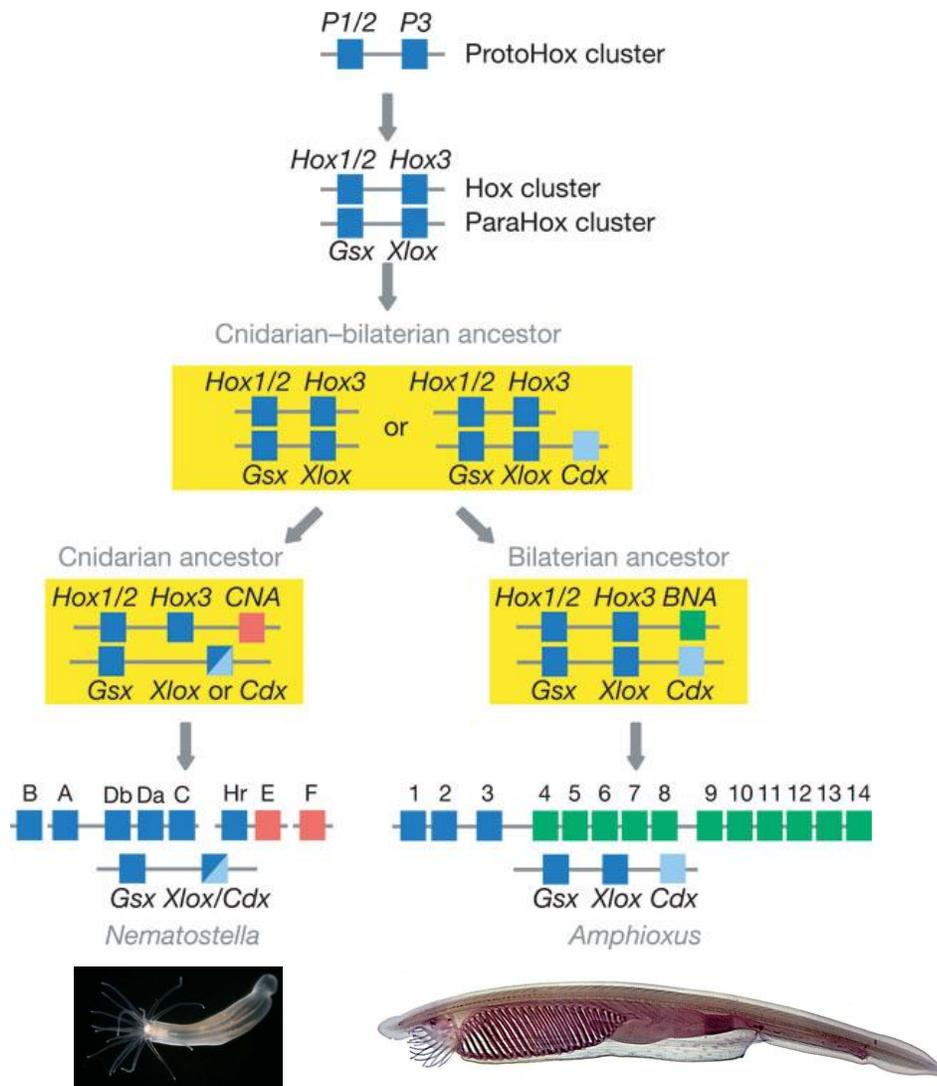


Fig. 1.3.1.4k. A plausible scenario of evolution of Hox genes in animals. The ProtoHox cluster may have contained only two anterior genes and its duplication generated two equally simple Hox and ParaHox clusters. The ancestral bilaterian Hox cluster may have contained an extra non-anterior Hox gene (BNA), a precursor of future central and posterior genes. An independent duplication in the Hox cluster would have generated the precursor of cnidarian non-anterior Hox genes (CNA), which later on became HoxE and HoxF of *Nematostella*. The third ParaHox gene Cdx might have appeared through a duplication in the ParaHox cluster in early bilaterians. Later, genes in Hox cluster independently proliferated, by tandem duplications, in cnidarians and bilaterians (*Nature* 442, 684, 2006).

### Section 1.3.2. Phanerozoic eon

Fossil record of the Phanerozoic eon is much more complete than that of the earlier eons, to some extent due to the origin of large organisms with hard skeletons. Although all major clades of the Tree of Life were already present by the start of the Paleozoic era 542 mya, Cambrian biota was very different from the modern one. Phanerozoic life kept evolving in the sea, in particular, fishes evolved jaws and bones 450 and 420 mya. Still, the most dramatic events were adaptation of green algae (~450 mya), arthropods (~420 mya), and vertebrates (370 mya) to terrestrial habitats, and the subsequent evolution of land plants, insects, and tetrapods. There were several mass extinctions in Phanerozoic eon, including end-Permian, which marked the end of the Paleozoic era, and KT (end-Cretaceous), which marked the end of the Mesozoic era.

#### *1.3.2.1. Cambrian biota*

Phanerozoic eon, Paleozoic era, and Cambrian period began 542 mya, at the time of a global, although short-term, decline of  $\delta^{13}\text{C}$  and of extinction of the Ediacaran biota. (Figs. 1.2.2.4a, b). This extinction and the subsequent advent of the Cambrian biota may have been triggered by a major change in ocean circulation, which oxygenated deep water and terminated a long period during which the Neoproterozoic ocean was stratified, with sulphidic deep water. Several million years after this, multiple new animals, some of which clearly belong to groups of extant clades, began to appear in the fossil record. This phenomenon is often called the "Cambrian explosion", although it mostly reflects better preservation of Cambrian organisms, compared to the Ediacaran biota, partially due to evolution of hard skeletons and shells, instead of the origin of new major clades (Section 1.3.1.4). Fossil record of other marine organisms, including phytoplankton, also became richer in Cambrian, apparently reflecting both their diversification and better preservation. The Cambrian is marked by a very high number of exceptionally well-preserved faunas, including the Lower (early) Cambrian Yunnan (China) and Sirius Passet (Greenland) faunas, the Middle Cambrian Burgess Shale (British Columbia, Canada, Fig. 1.3.2.1a) fauna, and the Upper (late) Cambrian Orsten (Sweden) fauna.

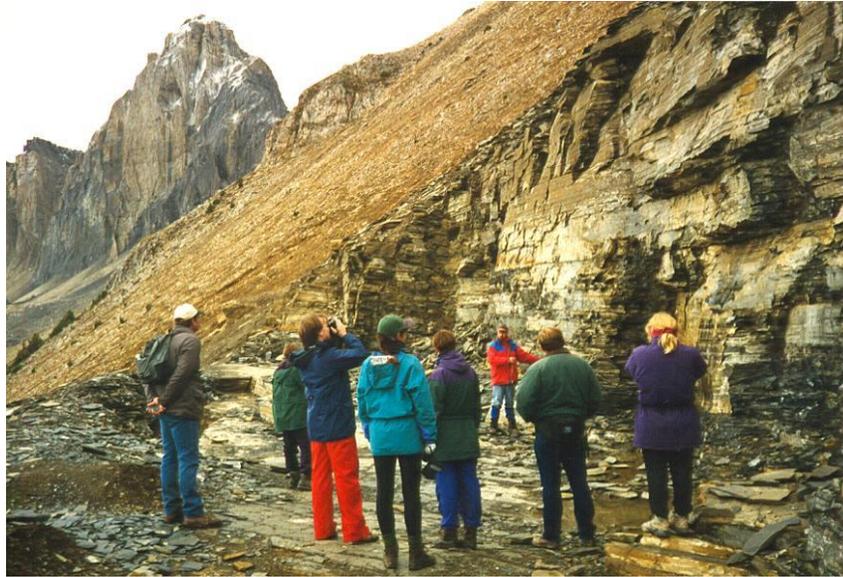


Fig. 1.3.2.1a. The Burgess Shale is a black shale Lagerstätte high up in the Canadian Rockies in Yoho National Park near the town of Field, British Columbia.

A relatively rich fossil record of the Cambrian made it possible to reconstruct the course of diversification of animals at that time. Mineralized fossils, mostly less than 1cm in size, known as "small shelly fauna", appear from almost the very beginning of the Cambrian. They diversified ~537 mya, about 5 Ma into the Cambrian period, and mostly disappeared 10 Ma later. Molluscs, arthropods, and brachiopods also appear in the first 10 Ma of the Cambrian. In fact, there is only one extant phylum of animals, Bryozoa, whose known fossil record does not extend back into the Cambrian period, and starts instead in the Early Ordovician period, about 480 mya, although wide diversity of Ordovician bryozoans leaves no doubt that they originated much earlier. Many hundreds of different fossil genera have been described from the first 20 Ma of the Cambrian. After this, diversity of known fossils declined substantially 520-510 mya.

Lower Cambrian Maotianshan Shale (central Yunnan, China), which is 530 Ma old, already contains metazoan fossils with diverse body plans, some of which may turn out to be short-lived (Fig. 1.3.2.1b) but many others survived until the present, in several cases without changing too much (Fig. 1.3.2.1c). Other fossils from these deposits do not match closely any extant organisms but are likely to be similar to the common ancestors of large modern clades, in particular, of arthropods (Fig. 1.3.2.1d) and vertebrates (see Section 1.3.2.2).

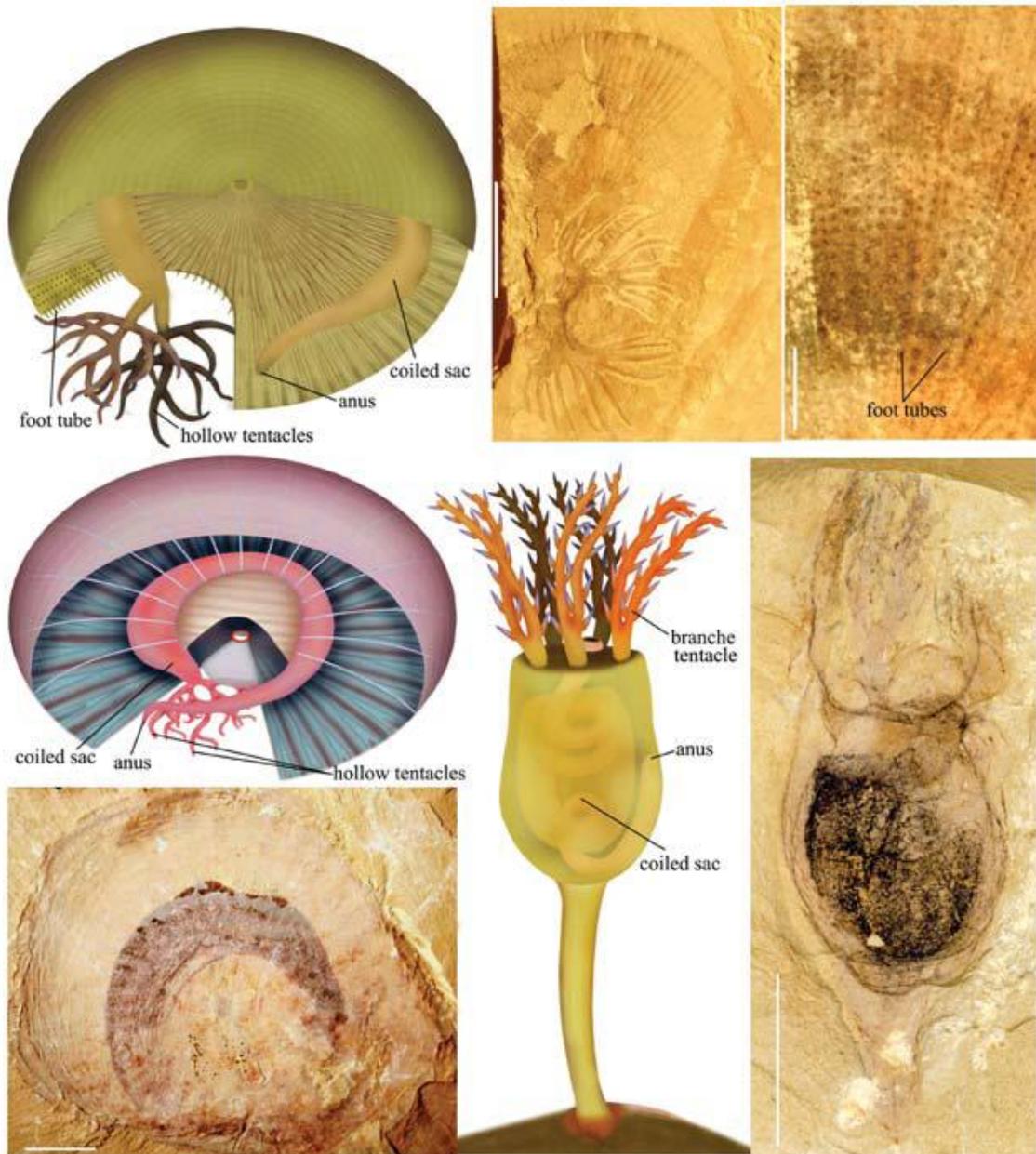


Fig. 1.3.2.1b. Early Cambrian lophophore-bearing animals. (A-E) The pelagic medusiform lophophore-bearing animals, *Rotadiscus* (A-C) and *Eldonia* (D-E). (F,G) Solitary sessile lophophore-bearing animals, *Phlogetes* (= *Chenungkongella*). Scale bars all are 1 cm. These animals may be deuterostomes, perhaps related to extant echinoderms, but this is uncertain.

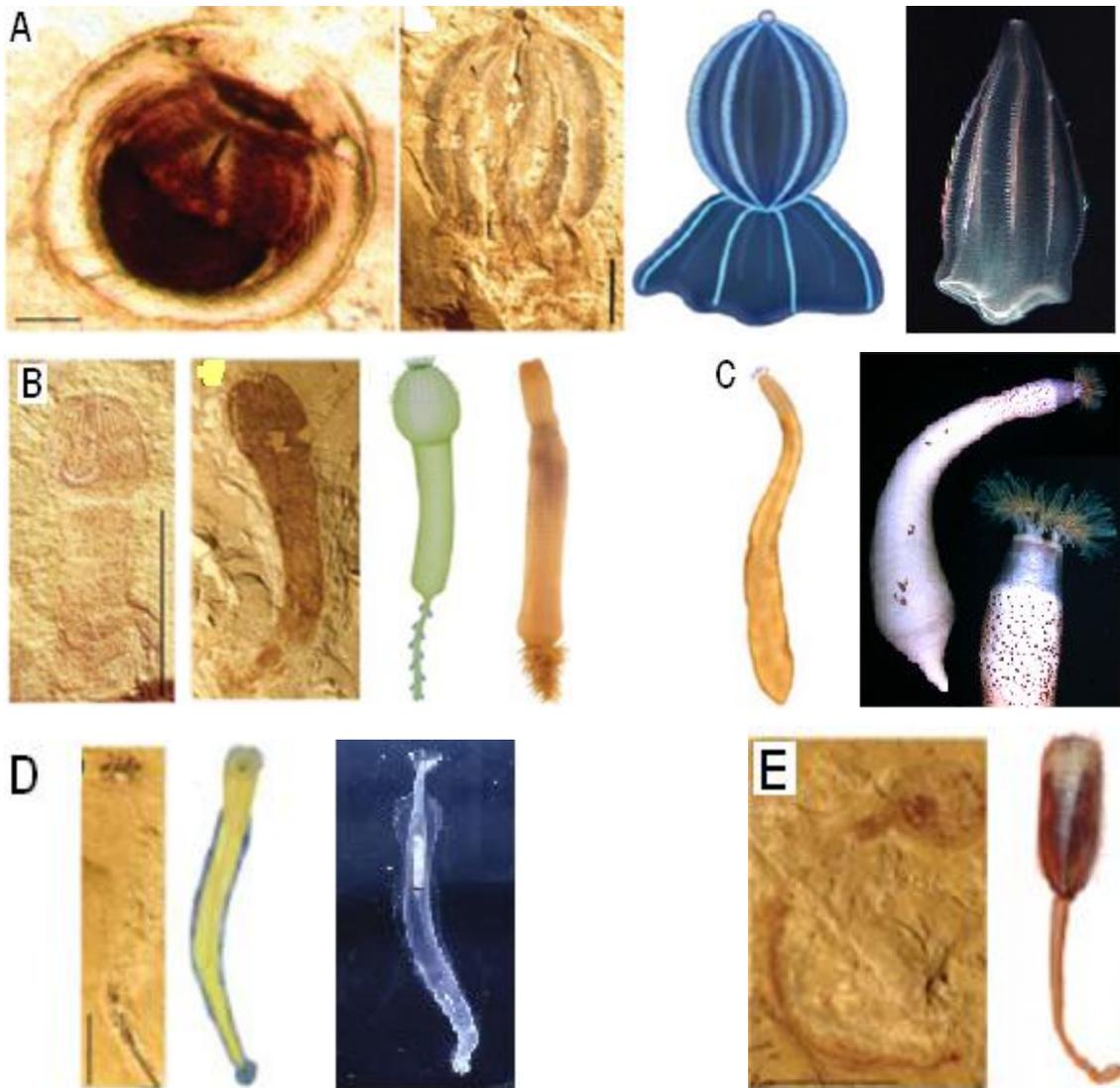


Fig. 1.3.2.1c. Several Early Cambrian fossils of animals from groups with conserved body plans. Ctenophora (A, left to right): embryo, photograph, and restoration of an adult ctenophore *Maotianoascus octonarius*, an extant ctenophore *Beroë ovata*; Priapulida (B): two fossils and a restoration of *Xiaohaiqingella* and an extant priapulid *Priapulid caudatus*; Sipunculida (C): restoration of fossil *Cambrosipunculus tentaculatus* and a living sipunculan; Chaetognatha (D): fossil and restoration of *Eognathacantha ercainella* and a living chaetognath *Sagitta gazellae*; Brachiopoda (E): fossil and living *Lingula spp* (*International Journal of Developmental Biology* 53, 733, 2009).

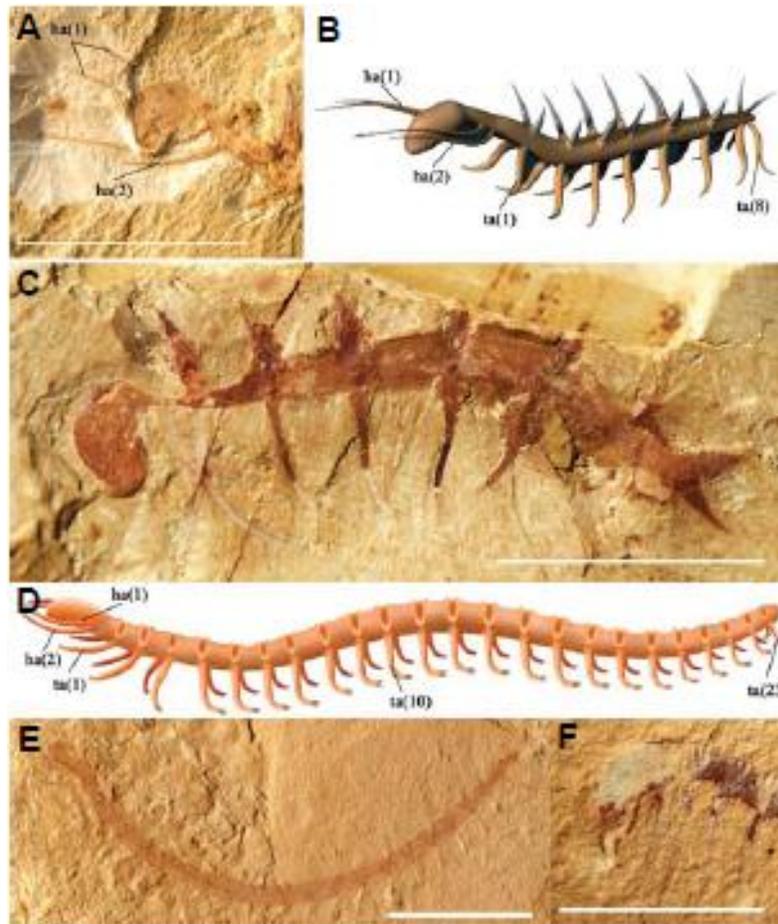


Fig. 1.3.2.1d. The two-segmental head worm-like organisms, perhaps resembling the common ancestor of extant arthropods. Photographs (A, C) and restoration (B) of *Hallucigenia fortis*. Restoration (D) and photographs (E, F) of *Cardiodictyon catenulum*. Abbreviations: ha, head appendage; ta, trunk appendage. Scale bars are 1 cm in (A,C,E); 0.5 cm in (F) (*International Journal of Developmental Biology* 53, 733, 2009).

Middle-Cambrian Burgess Shale fauna is 505 Ma old and contains, among others, a number of stem-group arthropod fossils (Fig. 1.3.2.1e). Moreover, there are Cambrian fossils of stem-group and even crown-group crustaceans (Fig. 1.3.2.1f). These findings strongly suggests that diversification of arthropods occurred in the Neoproterozoic.

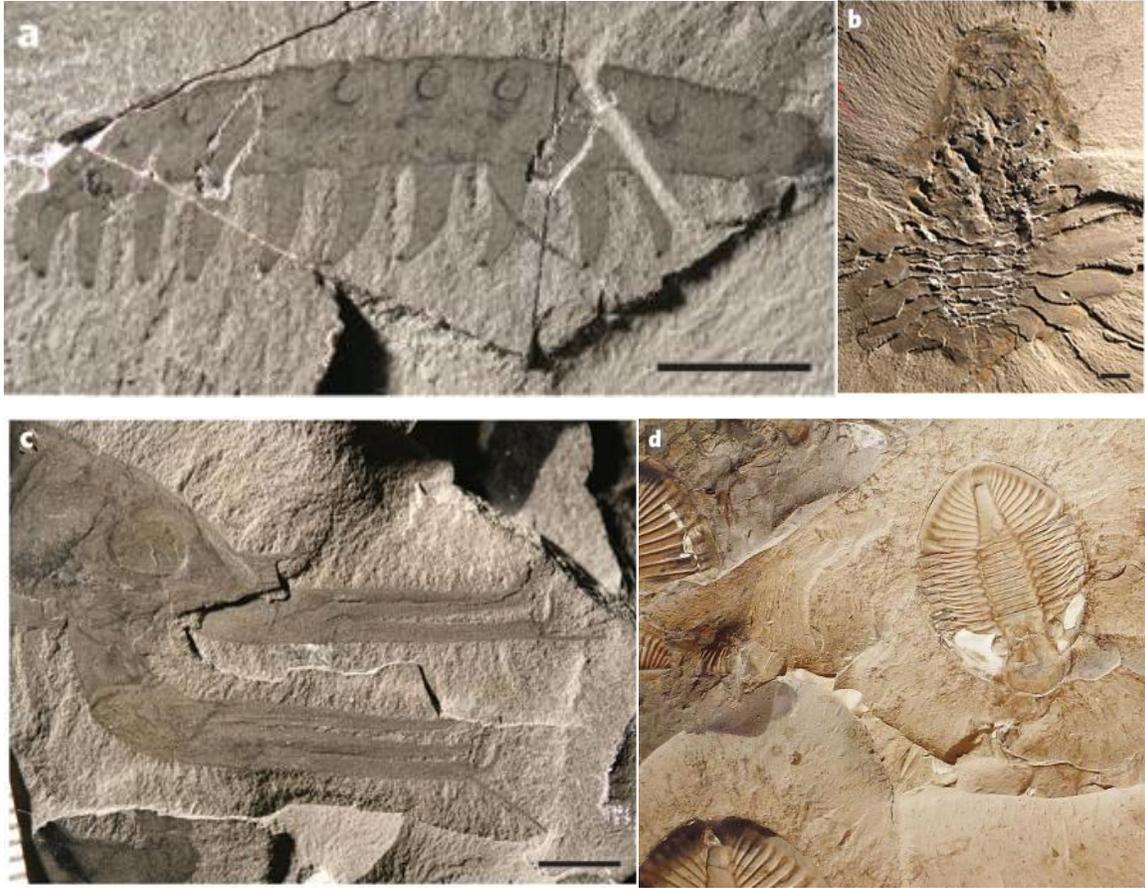
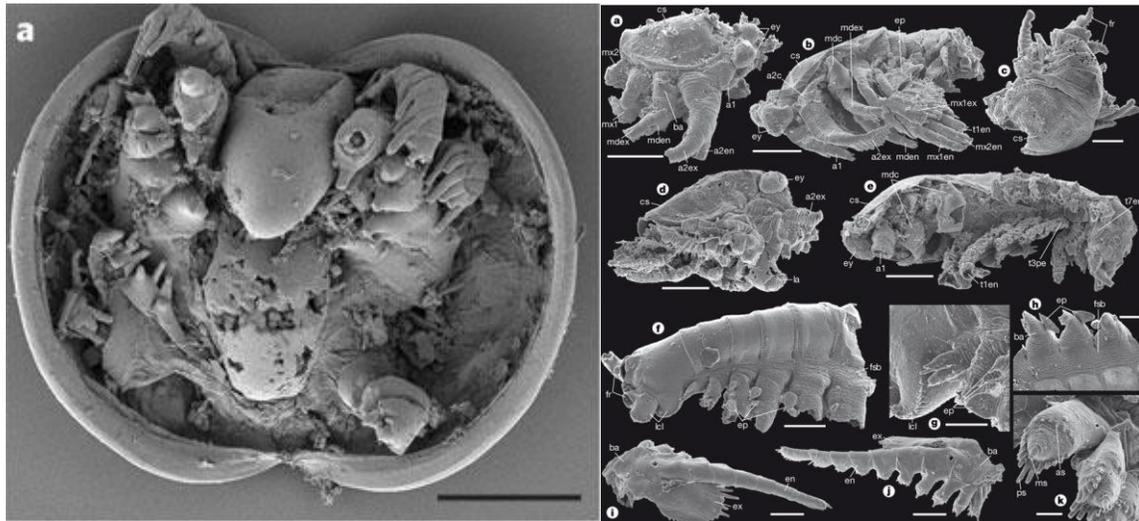


Fig. 1.3.2.1e. Stem group arthropods from the Burgess Shale fauna. (a) *Ayshezia pedunculata*. (b) *Laggania cambria*, an anomalocaridid. (c) The great appendages of the megacheiran *Leanchoilia superlata*. (d) Trilobites (*Nature* 457, 812, 2009).



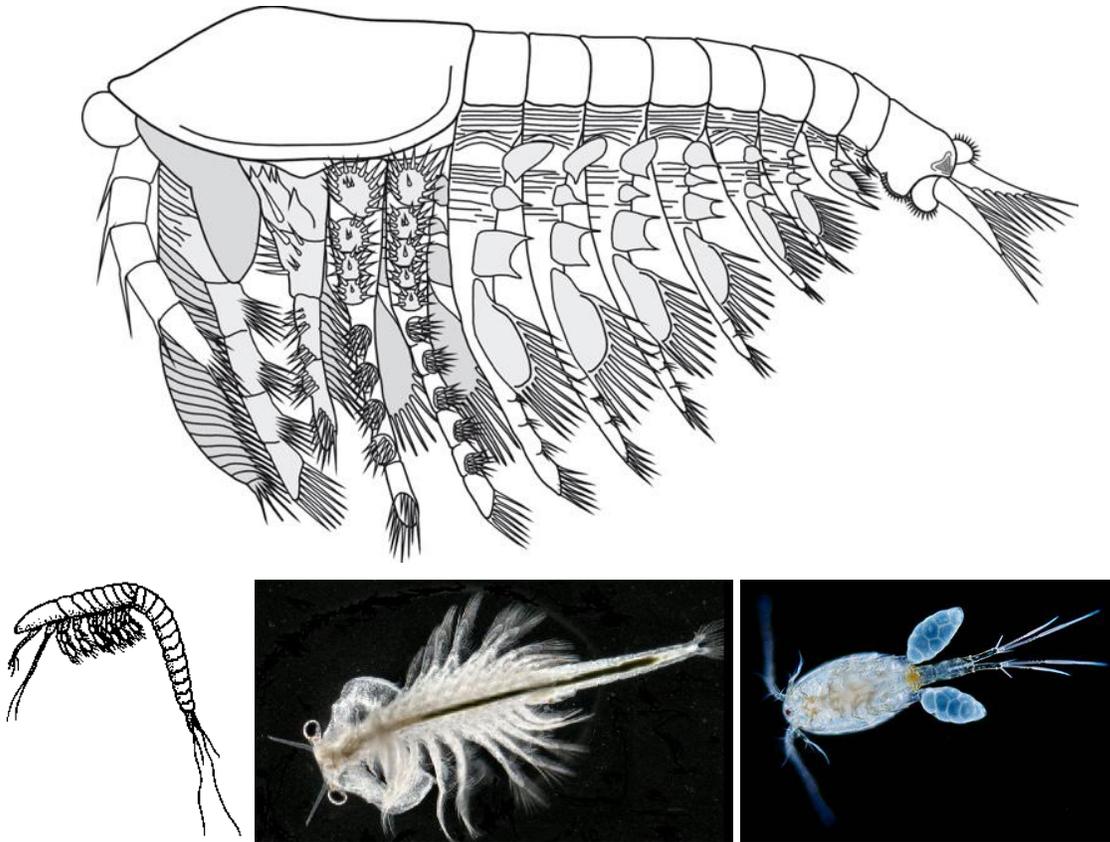


Fig. 1.3.2.1f. (top, left) *Hesslandona* sp., a member of the upper stem group of the crustaceans, from the 498 Ma old Orsten fauna. Scale bar, 50 microm. (*Nature* 457, 812, 2009). (top, right; middle) Fossils and reconstruction of *Yicaris dianensis*, a member of the crown group crustaceans from the 525 Ma old Yu'anshan Formation (Yunnan, China). The limb morphology and other details of this species are very similar to those of living cephalocarids, branchiopods and copepods (bottom, left to right) (*Nature* 449, 595, 2007).

There were at least two mass extinctions during the Cambrian period, Botomian (517 mya) and Dresbachian (502 mya), with about a half of genera of animals disappearing in each of the. Another mass extinction, Cambrian-Ordovician, occurred 488 mya and is accepted as the end of the Cambrian period (Fig. 1.2.4.1a). The causes of all these extinctions remain unknown, although there is evidence of reduced concentration of oxygen in surface ocean water at that time. Of course, marine life kept evolving after Cambrian, with countless species and clades appearing and disappearing. Still, it seems that radical innovation after that time was mostly limited to evolution on the dry land.

### 1.3.2.2. Vertebrates

Vertebrates are one of many groups of metazoans that belong to the deuterostome clade (Figs. 1.3.1.4b, c). Phylogenetic reconstructions based on genomes of extant species show that our closest relatives are urochordates, followed by cephalochordates and by echinoderms and hemichordates (Fig. 1.3.2.2a). The last common ancestor of vertebrates and urochordates probably lived in the Ediacaran (compare Fig. 1.3.1.4b and Fig. 1.3.2.2a). In contrast to even their closest relatives, vertebrates possess a complex brain and well-developed eyes, as well as auditory and olfactory systems.

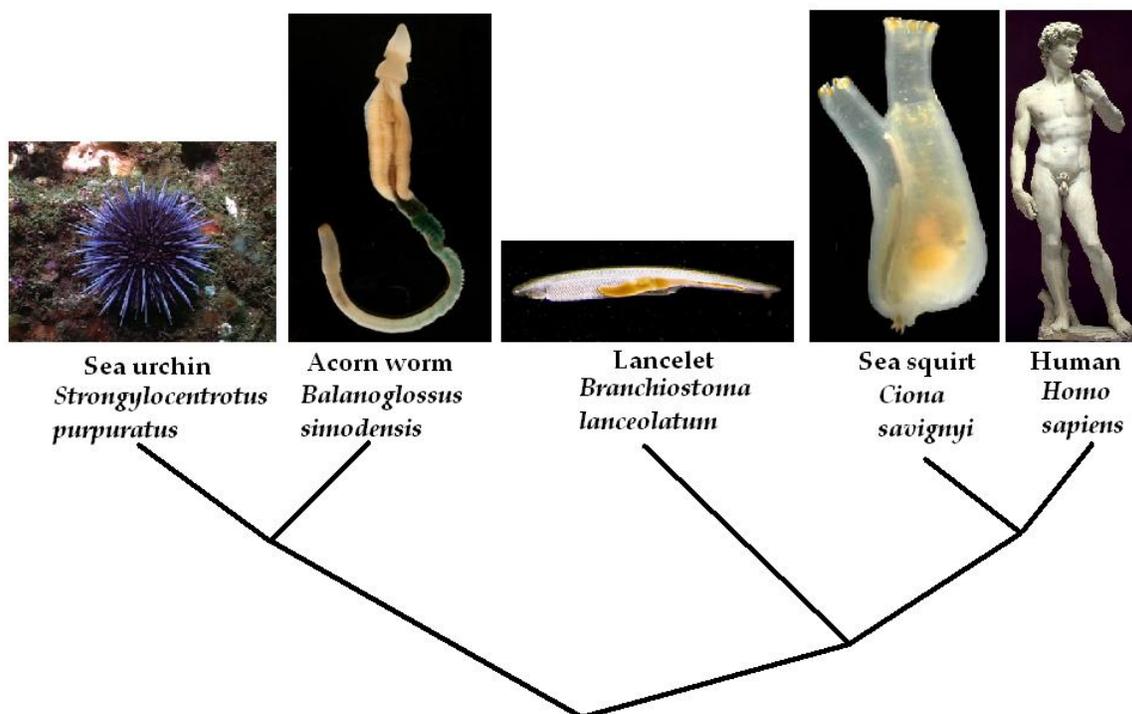


Fig. 1.3.2.2a. Phylogenetic relationships between Vertebrata and their closest relatives (left to right), Echinodermata, Hemichordata, Cephalochordata, and Urochordata (or Tunicata) (*Nature* 453, 1064, 2008).

The earliest known fossils of vertebrates are three substantially different species of agnathan (jawless) fishes, *Haikouichthys ercaicunensis* (Fig. 1.3.2.2b), *Mylokunmingia fengjiao*, and *Zhongjianichthys rostratus*; from Lower Cambrian Yunnan fauna (Section 1.3.2.1); vertebrate affinities of more primitive *Haikouella* and

*Yunnanozoon* from the same fauna remains uncertain. These fishes are already fully-fledged vertebrates, with eyes and possible nasal sacs, as well as otic capsules and a notochord with separate vertebral elements, dorsal fin, myomeres, and branchial arches. It seems that Yunnan vertebrates were close to the common ancestor of extant vertebrates, but still belonged to their crown group, instead of the stem group, because extant hagfishes apparently form even an earlier branch (Fig. 1.3.2.2b).

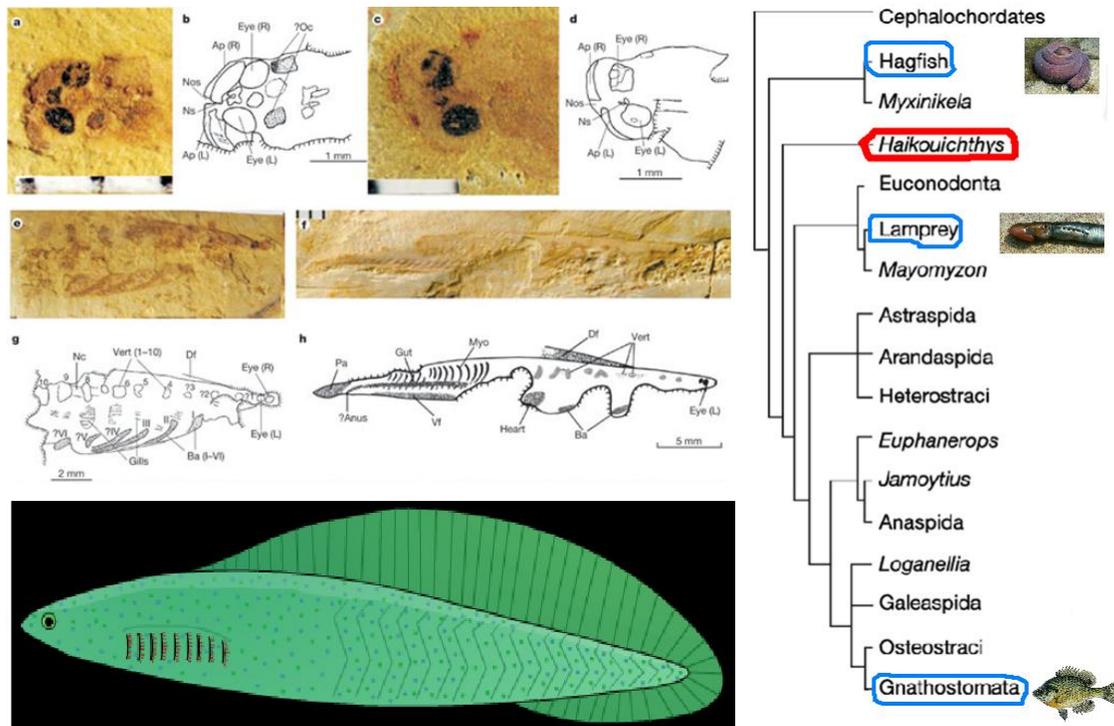


Fig. 1.3.2.2b. (left) The Lower Cambrian vertebrate *Haikouichthys ercaicunensis*, known by numerous specimens from the Yunnan fauna. (right) A likely position of *H. ercaicunensis* on the phylogenetic tree of vertebrates. Extant clades are circled in blue. (*Nature* 421, 526, 2003; *Proceedings of the Royal Society B* 277, 165, 2010).

Almost all living vertebrates belong to Gnatostomata. Still, agnathan fishes hold a key position in vertebrate evolution. From ~500 mya to ~370 mya, there existed a wide diversity of agnathans, all now extinct, except hagfishes and lampreys, which morphologically changed very little since then (Fig. 1.3.2.2c). This is one of very many examples of a rapid diversification of some kind to organisms, followed by complete or almost complete extinction (Chapter 1.5).

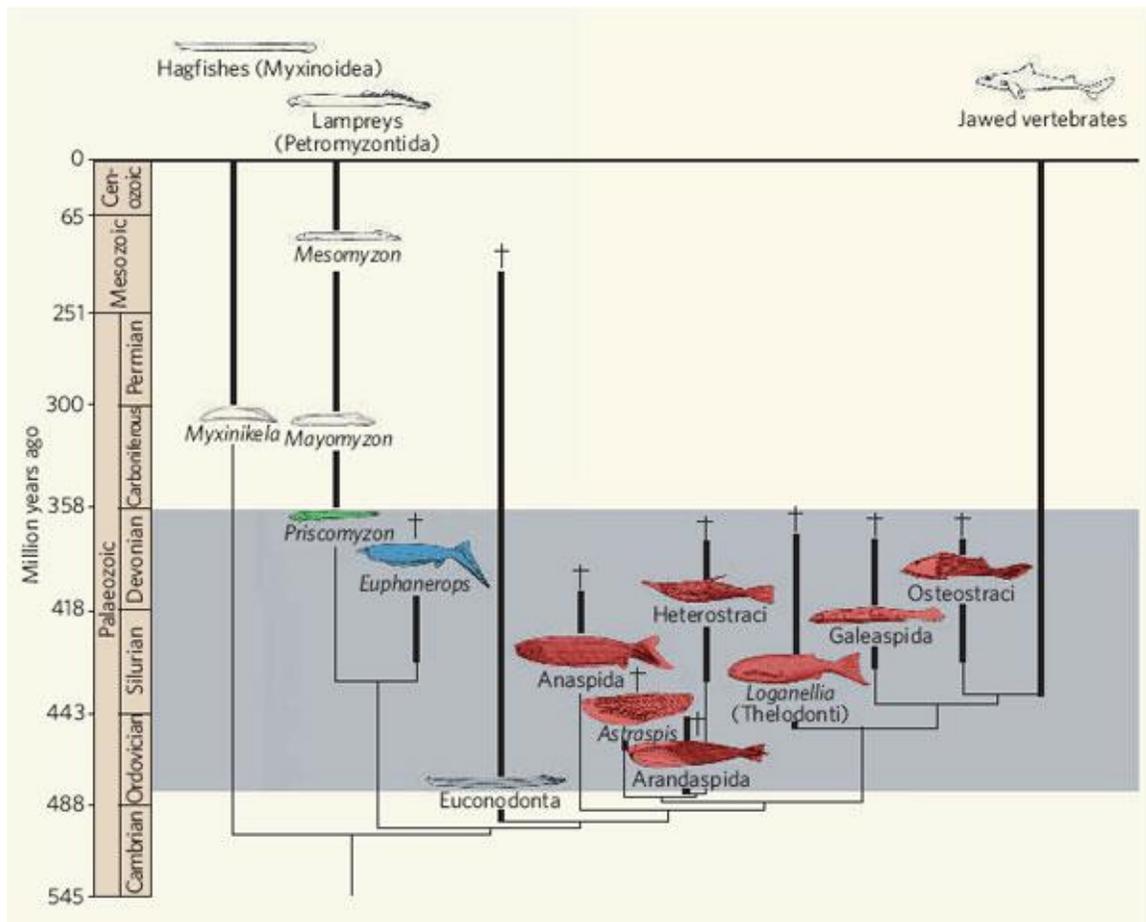


Fig. 1.3.2.2c. Diversification and extinction of jawless fishes in Ordovician, Silurian, and Devonian periods (*Nature* 443, 981, 2006).

The two key events in the evolution of vertebrates after the origin of the agnathans were the acquisitions of jaws and of bones, although many other important changes also occurred. Jaws evolved from gill support arches, probably ~450 mya (Fig. 1.3.2.2d). The earliest clade among the jawed vertebrates, are the extinct fishes Placodermi. In fact, it cannot be ruled out that Placodermi acquired their jaws independently of other Gnathostomata. At least some placoderms bore live offspring (Fig. 1.3.2.2e).

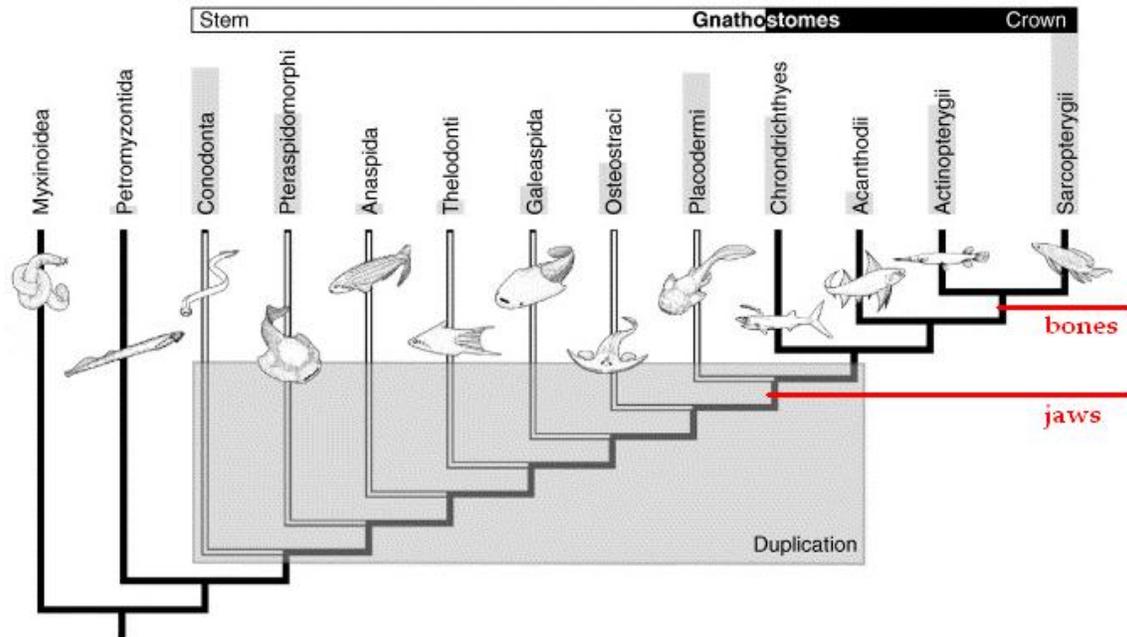


Fig. 1.3.2.2d. Acquisition of jaws and bones (red lines) in the evolution of vertebrates. Stem group of gnathostomes is shown in grey (*Trends in Ecology and Evolution* 20, 312, 2005; *Nature* 457, 305, 2009).

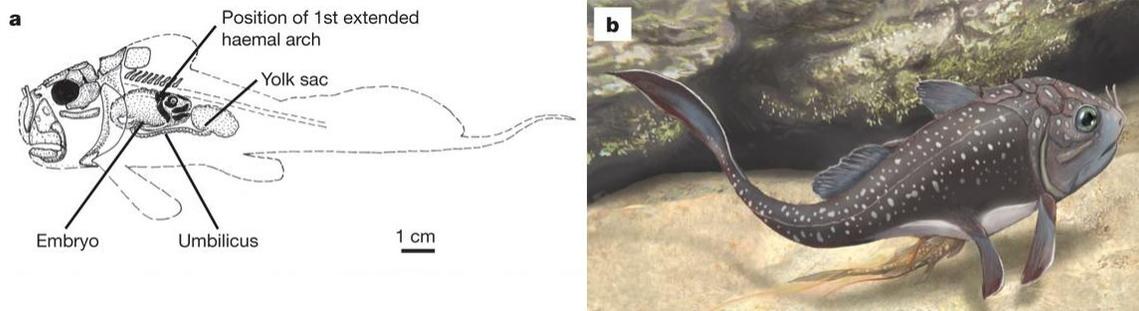


Fig. 1.3.2.2e. A placoderm *Materpiscis attenboroughi* who lived ~380 Ma ago in the Late Devonian in Australia is represented by the specimen, remarkably preserved in three dimensions, which contains a single, intra-uterine embryo connected by a permineralized umbilical cord (*Nature* 453, 650, 2008; *Nature* 457, 1124, 2009).

In addition to placoderms, gnathostomes are represented by cartilaginous fishes, or Chondrichthyes (Fig. 1.3.2.2f), extinct Acanthodii, and bony fishes or Osteichthyes (Fig. 1.3.2.2d.) The oldest fossils of cartilaginous fishes are ~440 Ma old, indicating that Chondrichthyes and Osteichthyes diverged before that time. Bones evolved in the

common ancestor of Osteichthyes at least 420 mya, because there are several fossils from that time that belong to bony fishes (Fig. 1.3.2.2g). Osteichthyes represent a vast majority of modern vertebrates, and are subdivided into Sarcopterygii (lobe-finned fishes) and Actinopterygii (ray-finned fishes) (Fig. 1.3.2.2h). The split of these two clades must have occurred before 420 mya, because *Guiyu oneiros* was a sarcopterygian fish (Fig. 1.3.2.2g).

**Chondrichthyes:**



Fig. 1.3.2.2f. Extant Chondrichthyes are chimeras, sharks, and rays.

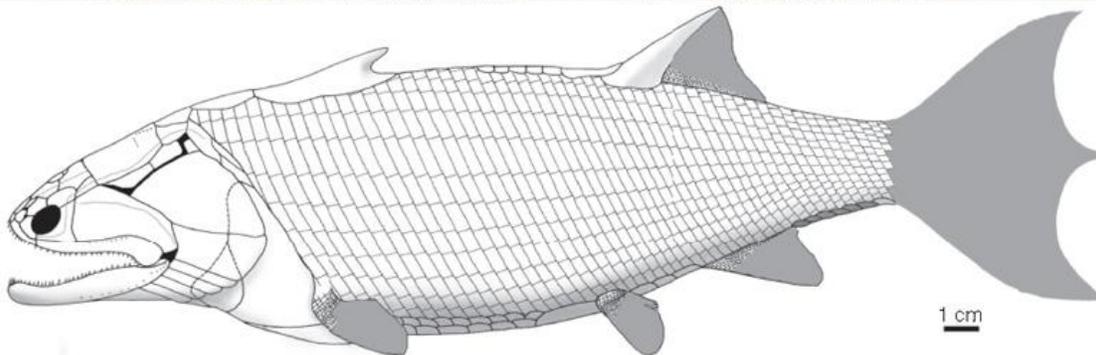


Fig. 1.3.2.2g. Fossil and reconstruction of *Guiyu oneiros*, a basal sarcopterygian fish that lived in Late Devonian 418 mya. This fish presents a mixture of ancestral and derived trait states and, thus, sheds light on the order in which derived trait states were

acquired in the course of evolution of the bony fishes (*Nature* 448, 583, 2007; *Nature* 458, 469, 2009).

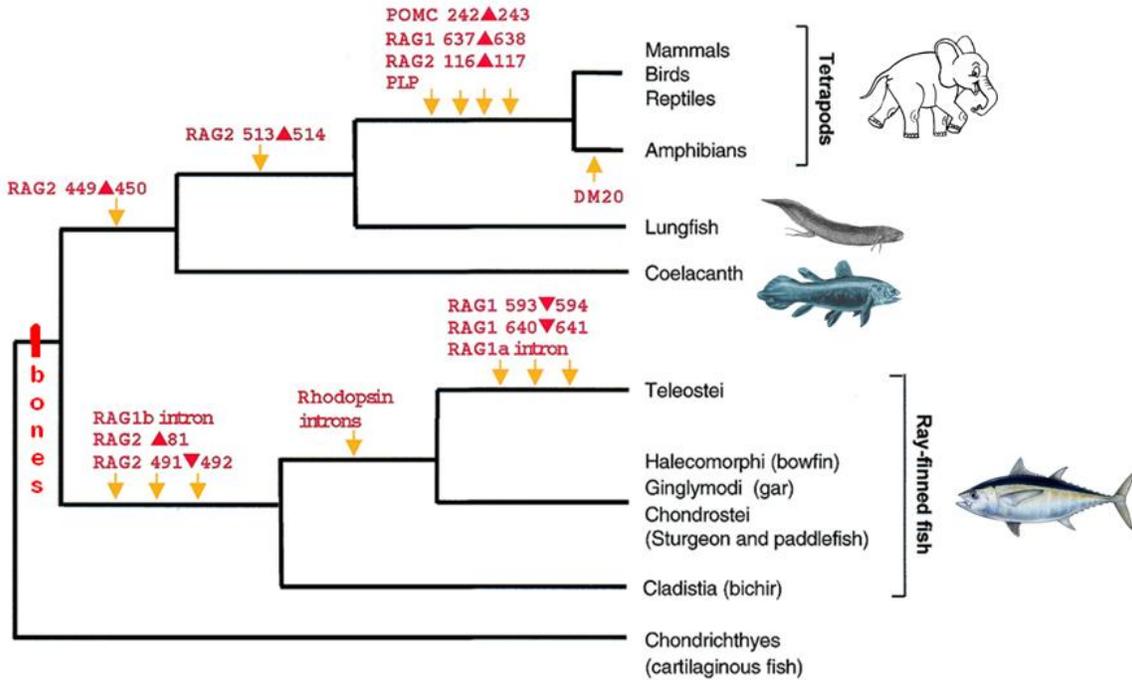


Fig. 1.3.2.2h. Phylogeny of bony fishes, created on the basis of acquisitions of introns, which are relatively homoplasy-free traits (*PNAS* 98, 11382, 2001).

Lobe-finned fishes appeared in the fossil record 418 mya. Almost all extant bony fishes are ray-finned, and lobe-finned fishes are currently represented only by two species of coelocanths, three species of lungfishes, and by tetrapods (Fig. 1.3.2.2h). However, there existed a wide diversity of lobe-finned fishes in the Devonian (Fig. 1.3.2.2i). Ray-finned bony fishes, as well as sharks, continued to evolve and diversify in the ocean in the late Paleozoic and afterwards; ray-finned fishes also were very successful in adapting to fresh water. In contrast, lobe-finned fishes, which were also very diverse in Paleozoic, almost all went extinct in the water but achieved great success colonizing dry land (Section 1.3.2.5).

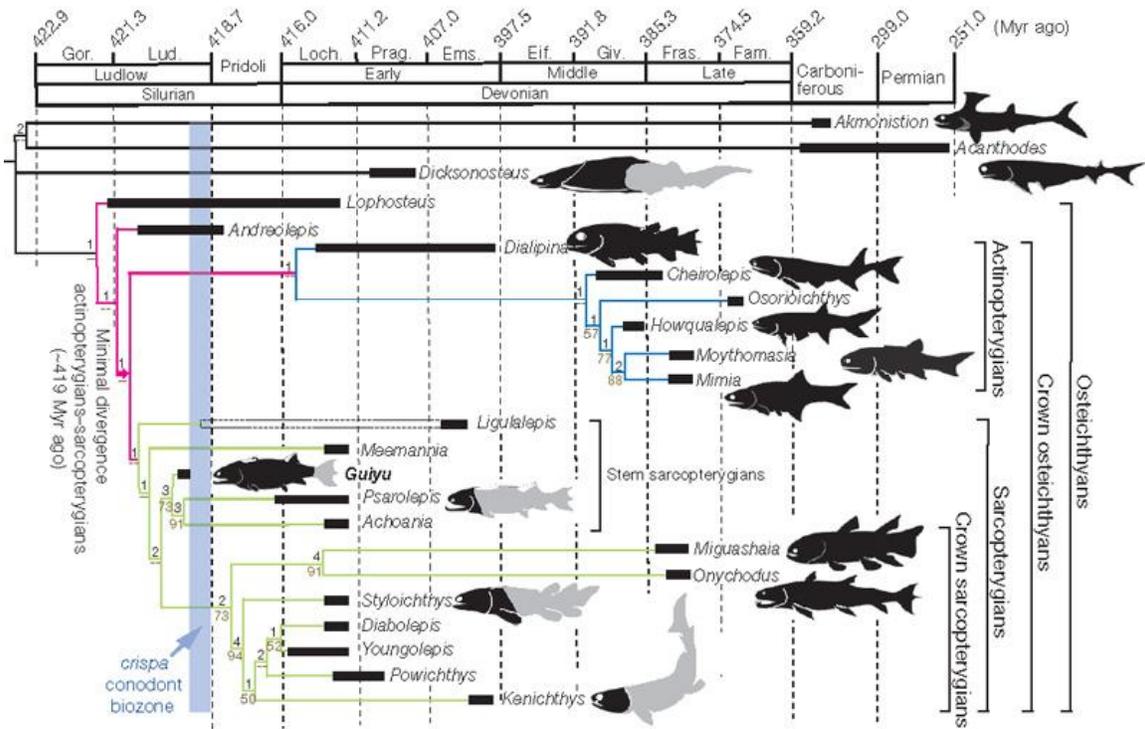


Fig. 1.3.2.2i. Evolution of bony fishes (*Nature* 458, 469, 2009).

After its divergence from the common ancestor with tunicates, the ancestral lineage of vertebrates underwent two successive whole-genome duplications (collectively known as 1R/2R quadruplication), followed by some gene loss, similar to that happened after one duplication in the ancestry of some *Saccharomyces* species (Fig. 1.1.2.7d) and tree duplications in the ancestry of *Paramecium tetraurelia* (Fig. 1.1.2.7e). These processes affected, in particular, evolution of the body plan-determining Hox genes (Fig. 1.3.1.4k) of vertebrates. Parsimony-based (Section 1.1.3) reconstruction of the ancestral state of the repertoire of Hox genes in gnathostomes indicates that their common ancestor possessed four clusters of Hox genes, derived by the 1R/2R quadruplication from the single ancestral cluster, observed in other deuterostomes and that each of these clusters lost some of the duplicated genes (Fig. 1.3.2.2j). In contrast to the early evolution of metazoans (Fig. 1.3.1.4k), evolution of gnathostomes was not involved with diversification of Hox genes through gene duplication. Instead, sporadic loss of redundant genes continued, proceeding independently among Chondrichthyes and sarcopterygian and actinopterygian Osteichthyes (Fig. 1.3.2.2k). This process intensified within Teleostei, the largest clade of ray-finned fishes Actinopterygii that originated ~250 mya, after yet

another whole-genome duplication occurred in their ancestral lineage, creating eight Hox gene clusters. In fact, the whole Hox cluster has been independently lost twice within teleosts, reducing their number of Hox clusters to seven (Fig. 1.3.2.2k).

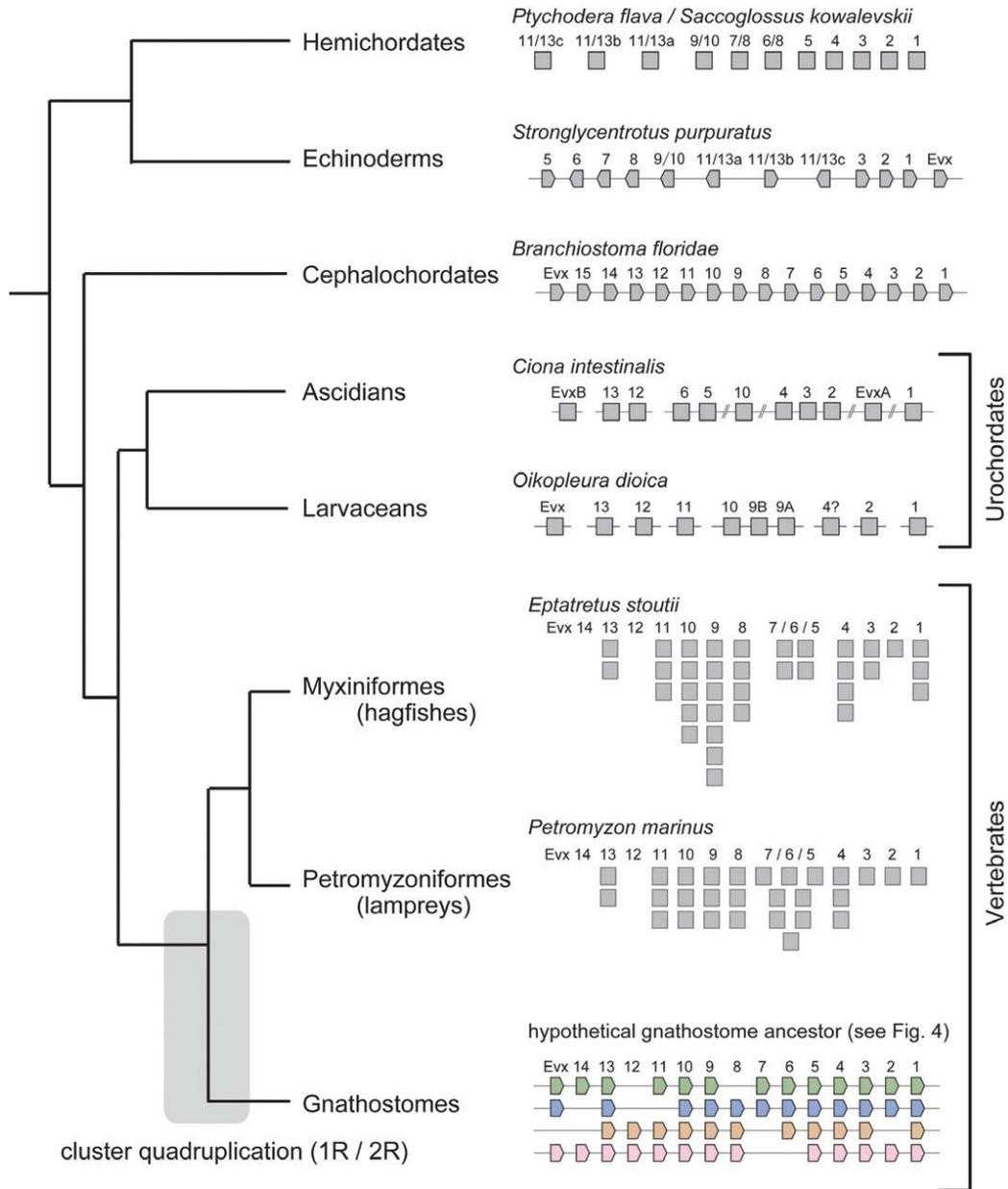


Fig. 1.3.2.2j. Origin of the four clusters of Hox genes in the common ancestor of gnathostomes (jawed fishes). Hox genes of agnathan fishes, hagfishes and lampreys, are also apparently organized into four clusters, but are not well-studied (*International Journal of Developmental Biology* 53, 765, 2009).

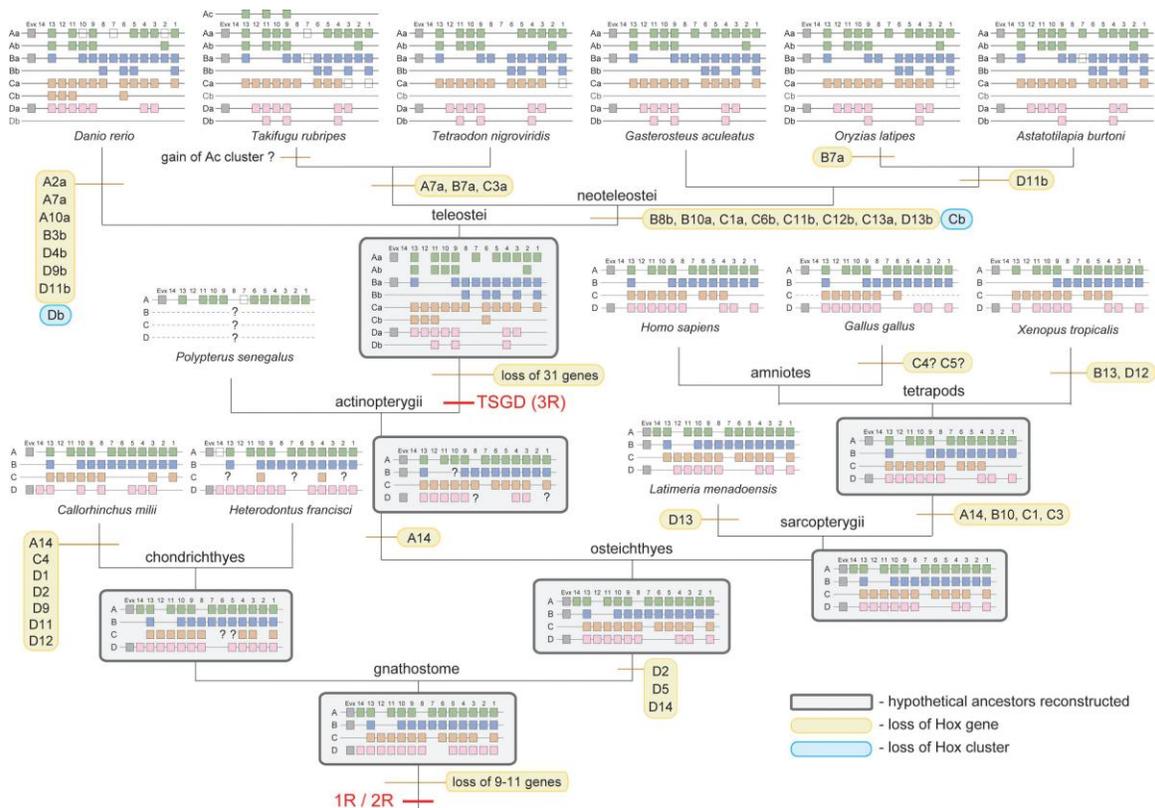


Fig. 1.3.2.2k. Evolution of Hox genes, ancestrally organized into four clusters, within gnathostomes. TSGD (3R) stands for teleost-specific genome duplication (*International Journal of Developmental Biology* 53, 765, 2009).

### 1.3.2.3. Origin and evolution of land plants

In the Proterozoic eon, land was initially populated only by prokaryotes (Fig. 1.3.1.2i) which were very likely joined by various unicellular eukaryotes ~1,000 mya. The most spectacular evolutionary innovations that occurred during the Phanerozoic eon were concerned with adaptation of multicellular eukaryotes to terrestrial habitats. These innovations created our familiar environment, dominated by land plants, insects, and tetrapods.

Phylogenetic reconstructions based on the genomes of modern organisms (Fig. 1.3.1.3r) show that land plants originated from Charophyta (or Streptophyta), a relatively small clade of freshwater green algae ranging from scaly, unicellular flagellates (Mesostigma) to complex, filamentous thalli with branching, cell differentiation and

apical growth (Charales) (Figs. 1.3.1.3q, r). Thus, one of the multiple origins of multicellularity occurred, perhaps ~1,000Mya, in the course of evolution of Charophyta, together with many other innovations (Fig. 1.3.2.3a).

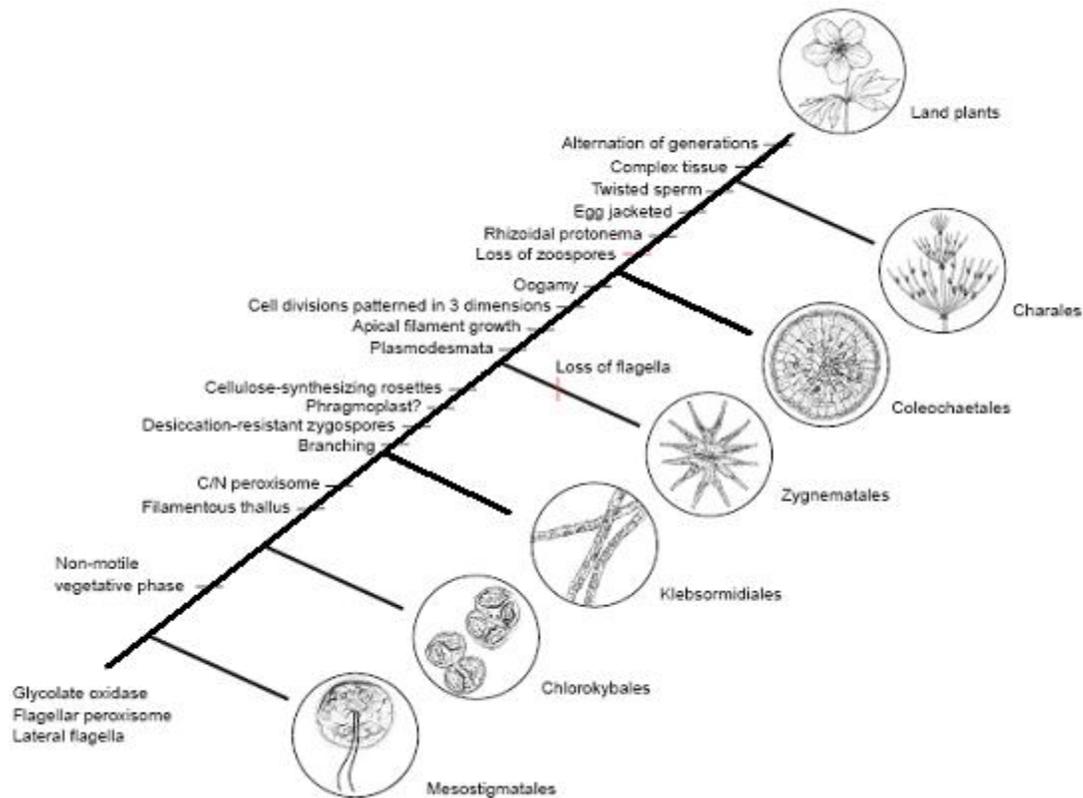


Fig. 1.3.2.3a. Innovations during the evolution of Charophyta, culminated by the origin of land plants (*Trends in Ecology and Evolution* 19, 661, 2004).

Currently, no transitional fossils between the land plants (embryophytes) and their aquatic ancestors are known. The earliest fossils of land plants are spore-containing fragments from ~460 Ma old Ordovician rocks of Oman. They show that the earliest spores developed in large numbers within sporangia. Analysis of spore wall ultrastructure supports liverwort affinities of these fossils (Fig. 1.3.2.3b).

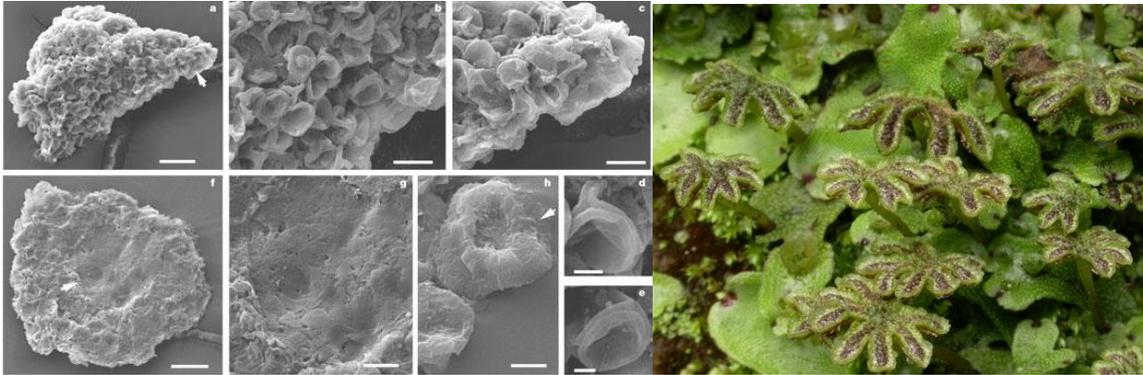


Fig. 1.3.2.3b. (left) Fragment of a sporangium containing permanent tetrads of an apparent 460 Ma old liverwort.(right) An extant liverwort, *Marchantia polymorpha*.

Molecular phylogenetics demonstrated that extant liverworts represent the earliest clade on the tree of land plants (Figs. 1.3.2.3c, d). We do not know whether the Ordovician fossil "liverworts" indeed belonged to this clade or if they lived before the cladogenesis event that produced it. The second situation is possible if modern liverworts retained the ancestral trait states. Anyway, colonization of the dry land by Charophyta is rather unlikely to occur before the Phanerozoic eon, so that fossils shown in Fig. 1.3.2.3b must be not too far from the common ancestor of land plants.

Except the first three clades, liverworts, mosses, and hornworts, collectively referred to as bryophytes, all other land plants have vascular tissue and are called vascular plants. Lycophytes and monilophytes, collectively referred to as pterydophytes, are the only two clades in which both phases of the amphimictic life cycle are represented by independent organisms, haploid gametophyte and diploid sporophyte (Fig. 1.3.2.3e). The remaining vascular plants are seed plants because they lack independent gametophytes and produce seeds (Figs. 1.3.2.3c, d).

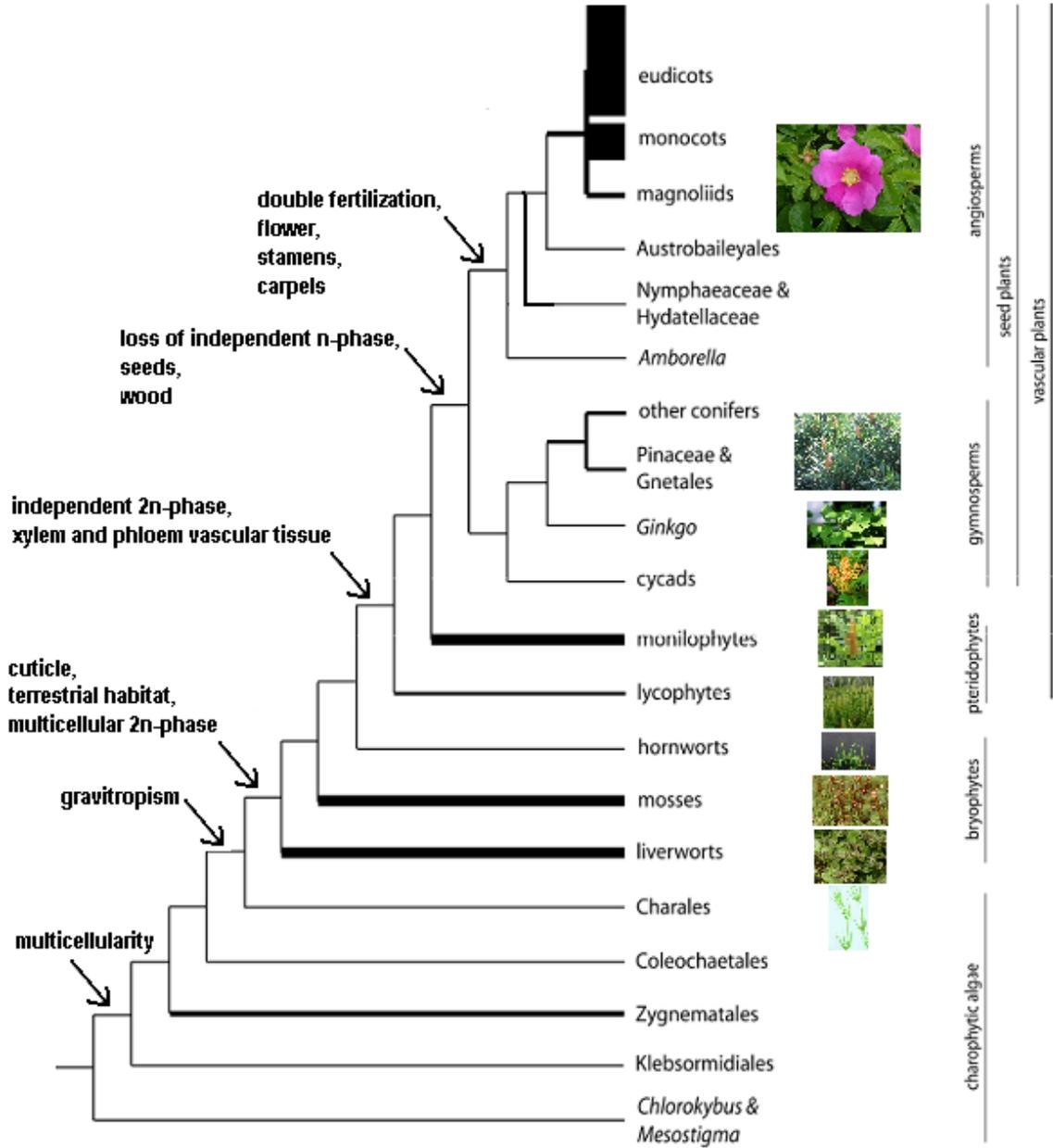


Fig. 1.3.2.3c. Phylogeny of charophytic algae and land plants, with some key evolutionary innovations labeled. The thickness of a line reflects the number of extant species within the clade (*Journal of Systematics and Evolution* 46, 287, 2008).



Fig. 1.3.2.3d. Diversity of land plants. (top, left to right): non-vascular plants with sporophyte living on gametophyte ("bryophytes"): *Marchantia polymorpha* (liverwort), *Polytrichum commune* (moss), and *Antoceros sp.* (hornwort), (middle): vascular plants with independent gametophyte and sporophyte ("pteridophytes"): *Lycopodium annotinum* (lycophyte), *Osmunda regalis* (monilophyte), *Equisetum arvense* (monilophyte), *Ophioglossum vulgatum* (monilophyte), (bottom): vascular plants with gametophytes living on sporophytes and producing seeds (seed plants): *Encephalartos longifolius* (cycad, gymnosperm), *Ginkgo biloba* (ginkgo, gymnosperm), *Gnetum urens* (gnetalian, gymnosperm), *Pinus silvestris* (conifer, gymnosperm), *Rosa rugosa* (eudicot, angiosperm).

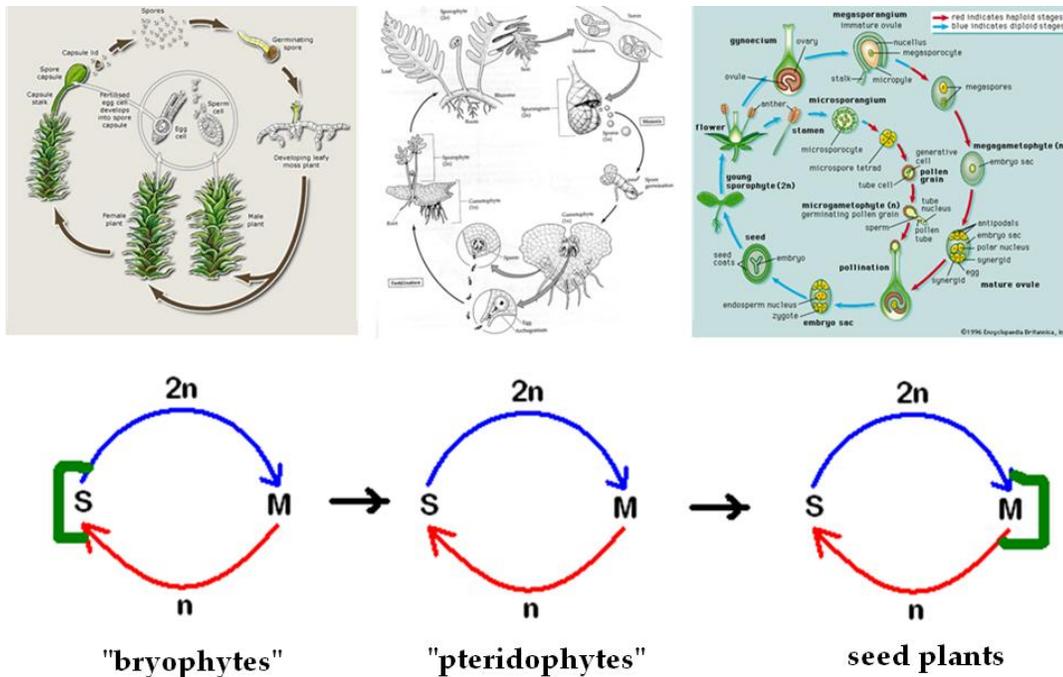


Fig. 1.3.2.3e. Evolution of the life cycle of land plants. In the lineage that gave rise to vascular plants sporophyte (multicellular organism representing the diploid phase) became independent, and in the lineage that gave rise to seed plants gametophyte (multicellular organism representing the haploid phase) lost its independence.

Vascular plants originated at least 420 mya, because there are reliable lycophyte fossils from late Silurian. Pteridophytes were widespread in the Carboniferous. Seed plants originated at least 350 mya, because the now extinct seed ferns Pteridospermatophyta were diverse and common from the late Devonian (Fig. 1.3.2.3f). The last known seed ferns went extinct ~50 mya in Tasmania. Clades of gymnosperms and angiosperms (or flowering plants) diverged at least ~300 mya, because there are Permian fossils that belong to total groups of all the three extant clades of gymnosperms, cycads, ginkgo, as well as conifers and gnetales (Fig. 1.3.2.3g). The earliest known angiosperm fossils are only 125 Ma old (Fig. 1.3.2.3g). However, angiosperms were already rather diverse at that time, and it is likely that the key derived angiosperm trait states evolved much earlier, perhaps ~200 mya. It is not yet clear, in which order these trait states evolved after the gymnosperm-angiosperm cladogenesis.

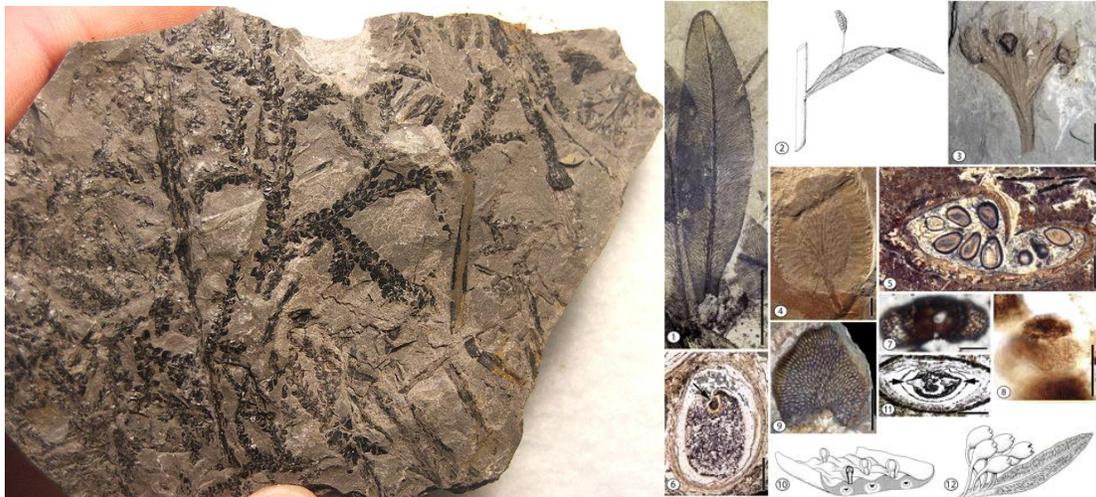


Fig. 1.3.2.3f. (left) *Lycopodites*, an early lycopod-like fossil. (right) Vegetative and reproductive organs of fossil seed ferns from the order Glossopteridales (see Fig. 1.2.2.3a) (*American Journal of Botany* 96, 237, 2009).

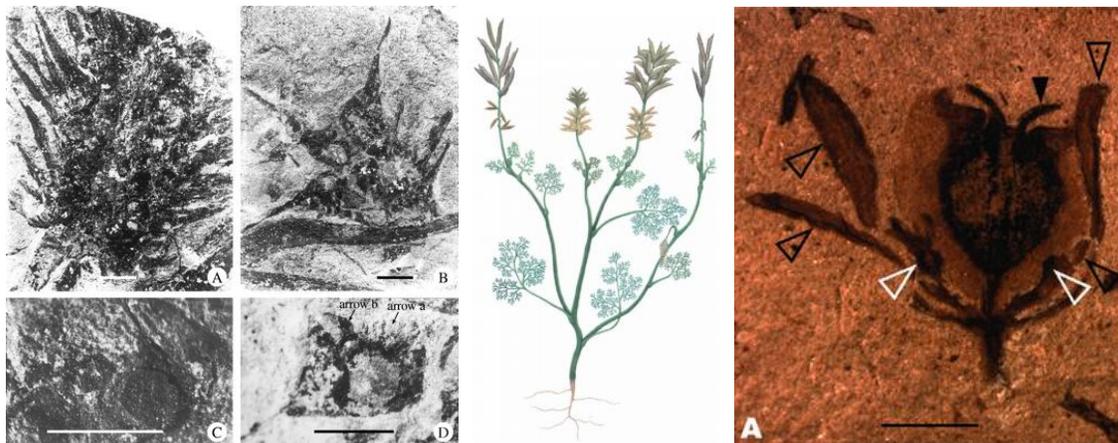


Fig. 1.3.2.3g. (left) *Palaeognetaleana auspicia* from Late Permian, a 270 Ma old member of the order Gnetales (*Annals of Botany* 94, 281, 2004). (center) Reconstruction of *Archaeofructus sinensis* from early Cretaceous, a 125 Ma old angiosperm fossil (*Science* 296, 899, 2002). (right) Flower of *Callianthus dilae*, another 125 Ma old angiosperm fossil (*Journal of Integrative Plant Biology* 51, 800, 2009).

Currently, there are hundreds of thousands of species of flowering plants, and phylogenetic relationships within them are close to being fully resolved (Figs. 1.3.2.3h,i). The basal clade among the extant flowering plants is represented by a single species

*Amborella trichopoda* from the island of New Caledonia. Coevolution with insects obviously played a major role in diversification of flowering plants (Chapter 1.5).

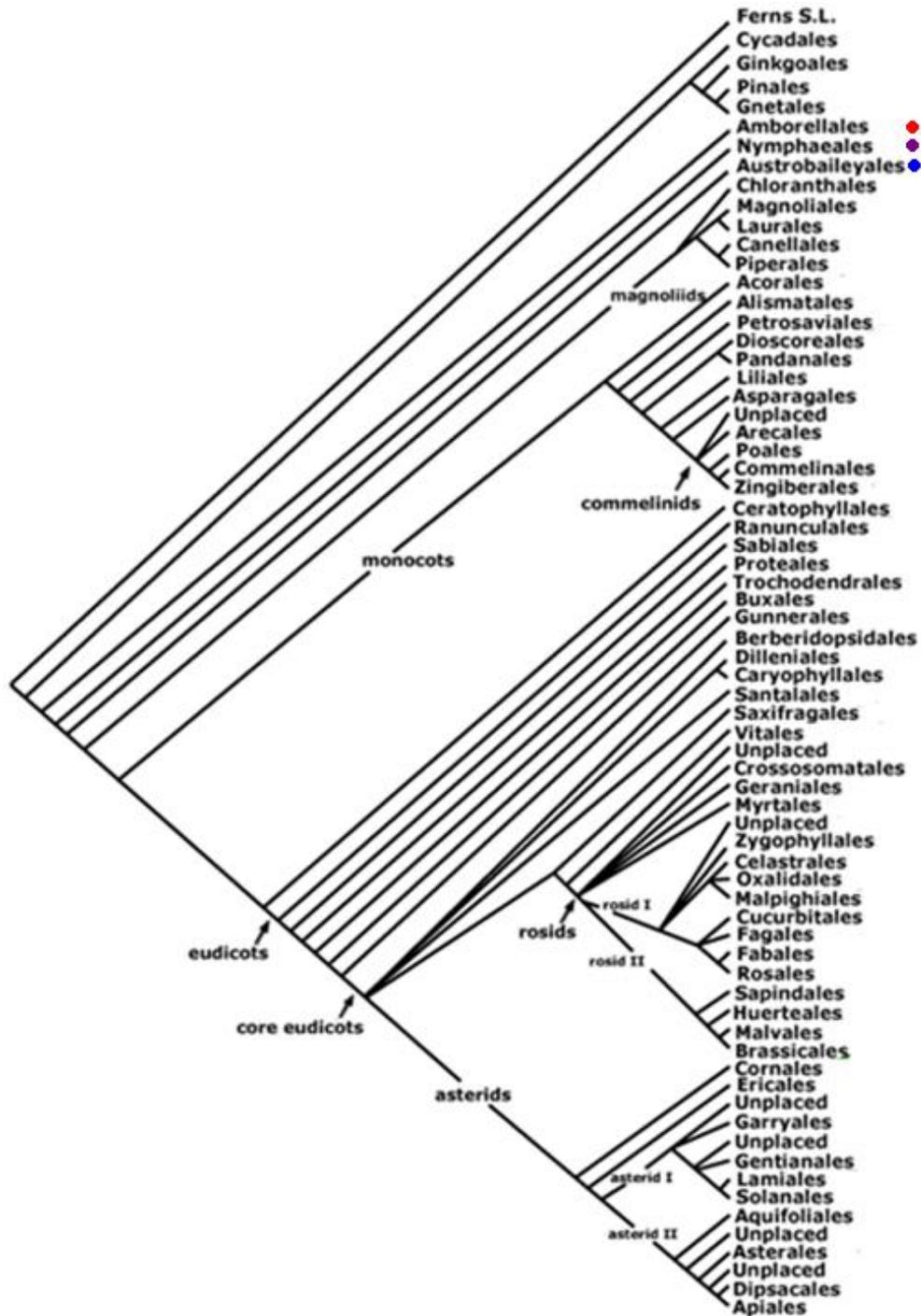


Fig. 1.3.2.3h. Phylogeny of flowering plants, or angiosperms. The three most basal clades are marked by colored dots.

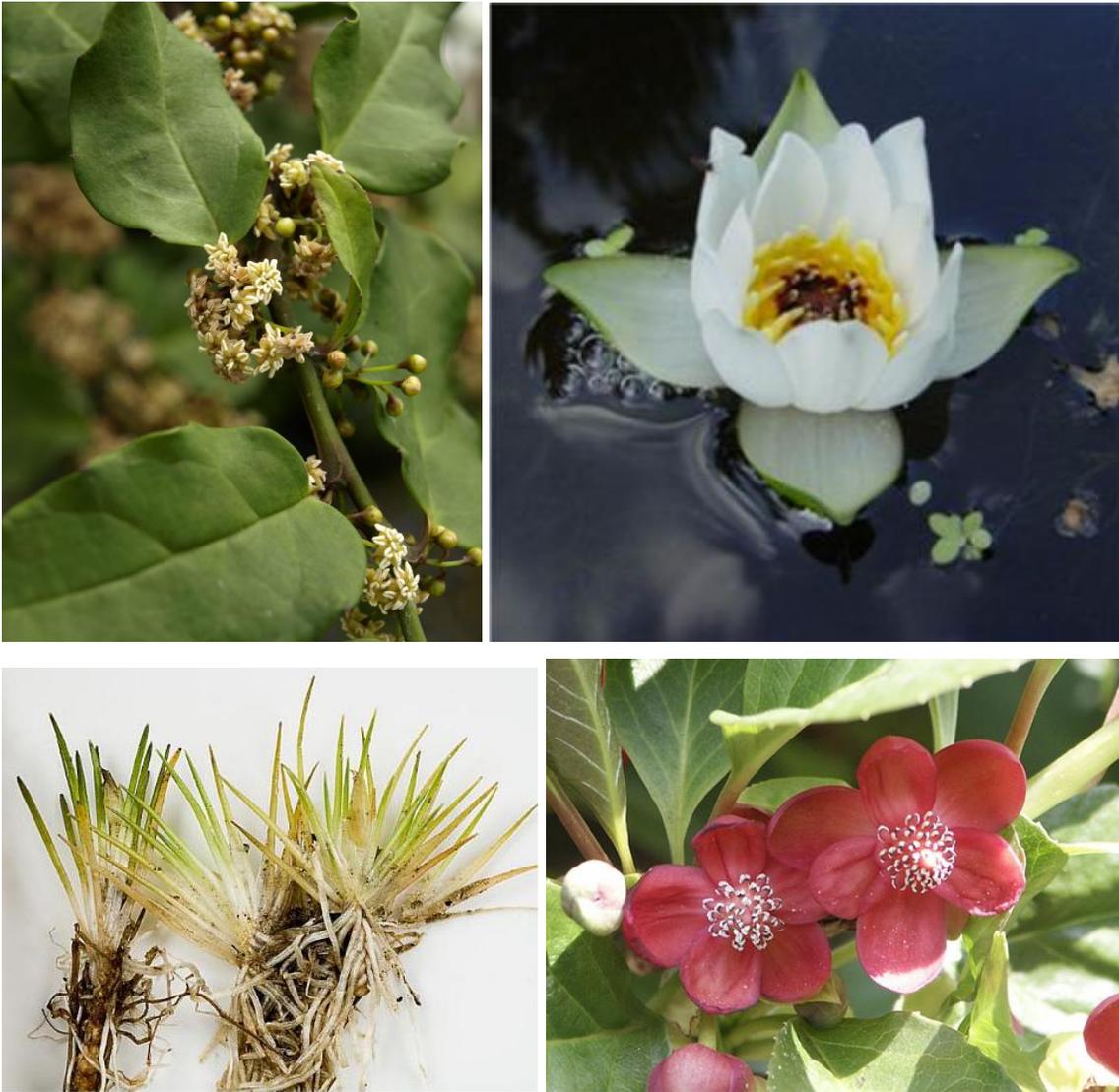


Fig. 1.3.2.3i. Representatives of the three basal clades of extant angiosperms. *Amborella trichopoda* (Amborellales), *Nymphaea tetragona* (Nymphaeales and Hydatellales), *Hydatella filamentosa* (Nymphaeales and Hydatellales), *Schisandra rubriflora* (Astrobaileyales).

Metazoans and land plants represent the only two instances of independent evolution of multicellularity, which culminated in very complex macroscopic organisms. Thus, comparison of the genetic and molecular mechanisms of metazoan and plant complexity is of great interest. Indeed, there are several profound similarities between these two cases.

First, evolution of complex multicellularity in plants was not accompanied by a large increase in the number of protein-coding genes. Thus, as in animals, the complexity of multicellular plants must be primarily due to complexity of interactions between genes. In fact, angiosperms have 1.5-2.5 times more protein-coding genes than mammals (30,000 - 45,000), apparently because of a number of relatively recent whole-genome duplications (Fig. 1.3.2.3j). Still, a ciliate *Paramecium tetraurelia* also has ~40,000 genes, for the same reason (Fig. 1.1.2.7e).

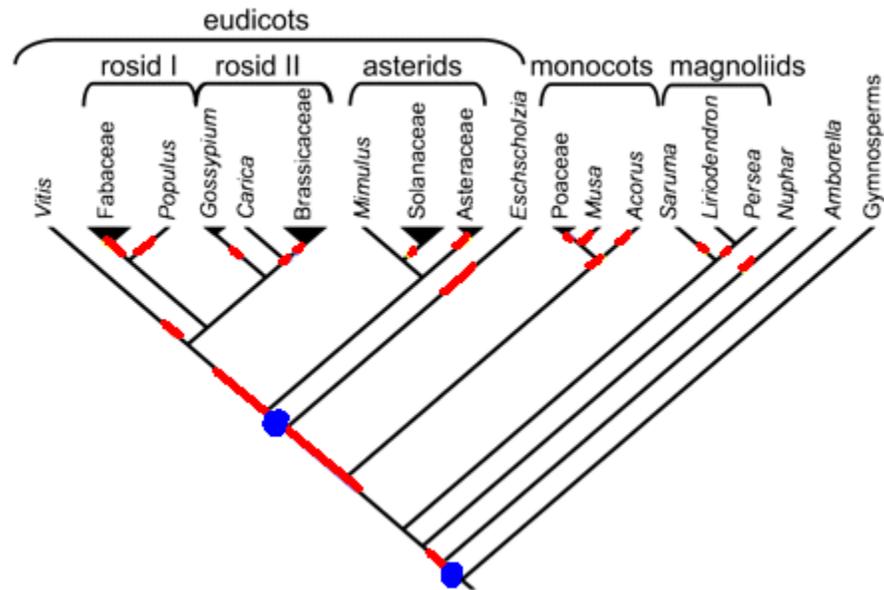


Fig. 1.3.2.3j. Simplified phylogeny of angiosperms depicting whole-genome duplication events in their ancestry (red bars); bar lengths reflect uncertainty of the available estimates. Blue dots show likely places of duplication of B-kind MADS genes (see below) (*American Journal of Botany* 96, 336, 2009; *Molecular Biology and Evolution* 26, 2229, 2009).

Second, plants, as animals, do possess a number of homeiotic genes that individually play a key role in their development (Fig. 1.3.2.3k), and plant homeiotic genes also are transcription factors and their mutations can affect the development drastically (Fig. 1.3.2.3l). Plant homeiotic genes that regulate the development only of flowers of angiosperms, instead of the whole organism, apparently demonstrate the closest similarity to the Hox genes in animals. Almost all of these plant genes belong to

the same family of paralogs, called MADS. Still, MADS and Hox transcription factors apparently are not related to each other, and bind DNA using different mechanisms, which is consistent with independent origin of multicellularity in plants and animals.

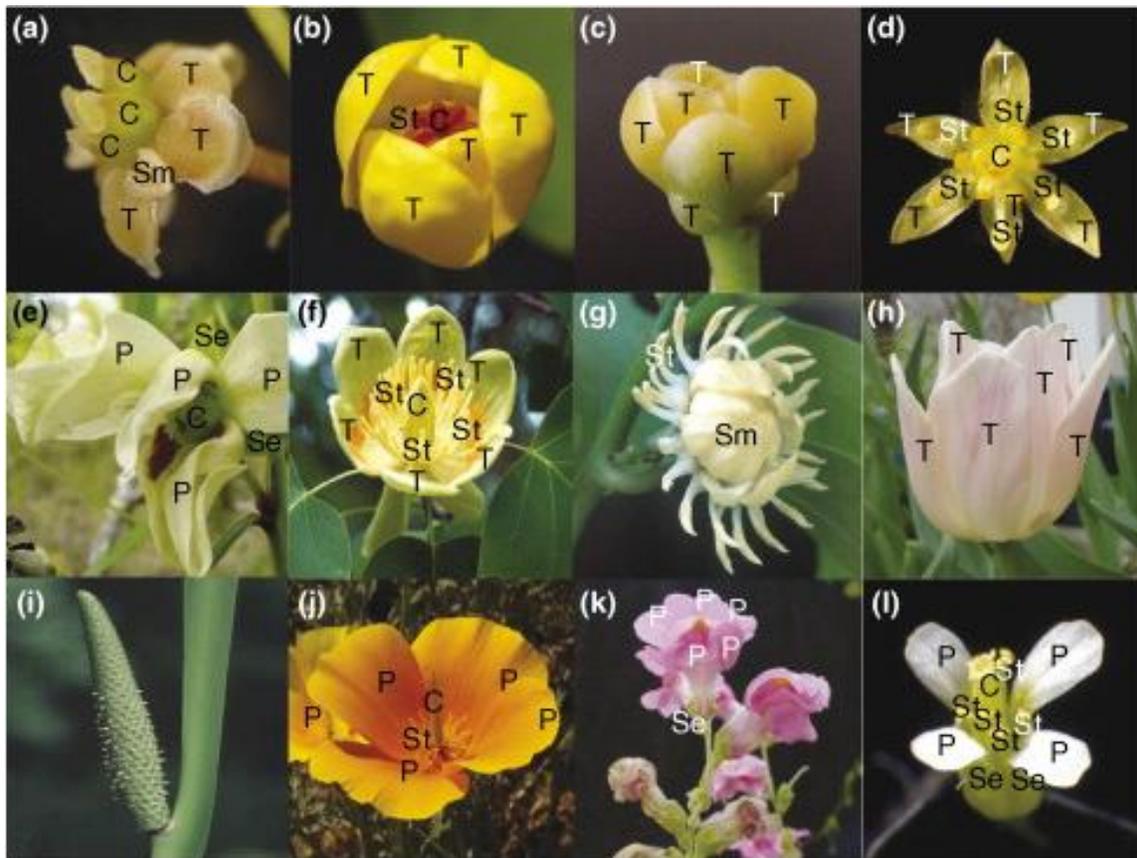
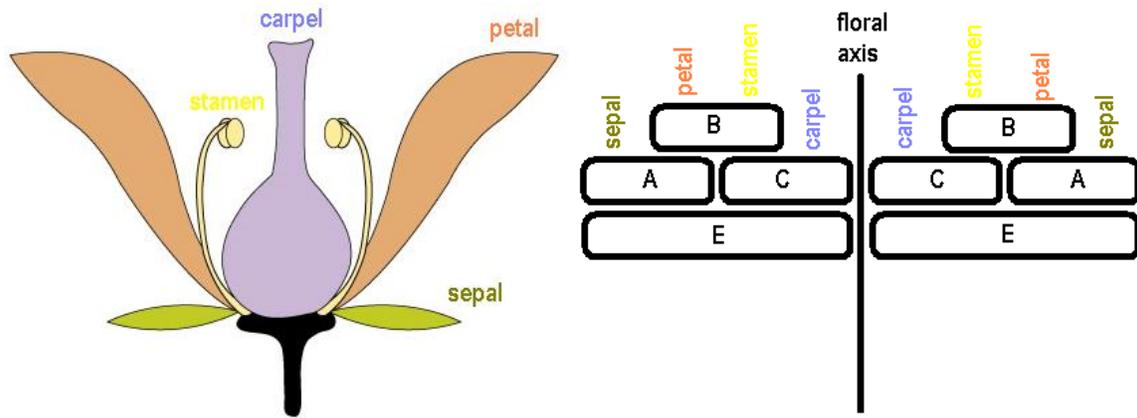


Fig. 1.3.2.3k. (top, left) A prototypical flower with carpels (C, collectively constituting gynoecium), stamens (St, androecium), petals (P, corolla), and sepals (Se, calyx); elements that are not differentiated into petals and sepals are called tepals (T), and sterile

stamens are staminodia (Sm). (top, right) A simplified model of regulation of flower development in many angiosperms. There are 4 kinds of homeiotic genes, A, B, C, and E, expressed differently relatively to the floral axis. E must be expressed throughout the whole flower, C is expressed only in the inner whorls of the flower, A only in the outer whorls, and B in between. Expression of C alone produces carpels, of C and B stamens, of A and B petals, and of A alone sepals. (bottom) – structures of various flowers.



Fig. 1.3.2.3l. Mutations of homeiotic MADS genes in *Arabidopsis thaliana* (compare to Fig. 1.3.1.4j). (left) Wild type. (center) Loss-of-function mutation of the gene of kind C. Its expression is substituted with the expression of A, and a flower with whorls of sepals, petals, petals, and sepals results. (right) Loss of function mutations in the genes of kinds A, B, and C, collectively leading to replacement of all elements of the flower with leaf-like structures.

Third, duplications of MADS genes played a major role in the evolution of flowers (e. g., Fig. 1.3.2.3j). Thus, in this respect angiosperms are more similar to metazoans in general (Fig. 1.3.1.4k), and not to animals, in which evolution of Hox genes repertoire was dominated by gene loss (Fig. 1.3.2.2k). The most obvious difference between Hox and MADS genes is that MADS genes do not have a tendency to form large clusters. Still, independent evolution of a compliment of paralogous transcription factors with major impacts on general patterning of the body in metazoans and in land plants is a striking example of parallelism, which certainly sheds some light on how complex multicellular organisms could possibly evolve (Chapter 3.2).

#### 1.3.2.4. Origin and evolution of insects

Evolution of full adaptation to terrestrial environments occurred only within three animal clades: vertebrates (tetrapods, Section 1.3.2.5), gastropod molluscs (pulmonates, not considered here), and arthropods. Several lineages of arthropods evolved such adaptations independently, including onychophores, chelicerates, myriapods, and isopod crustaceans (Fig. 1.3.2.4a). Still, insects and other hexapods are by far the most numerous and important clade of fully terrestrial arthropods.

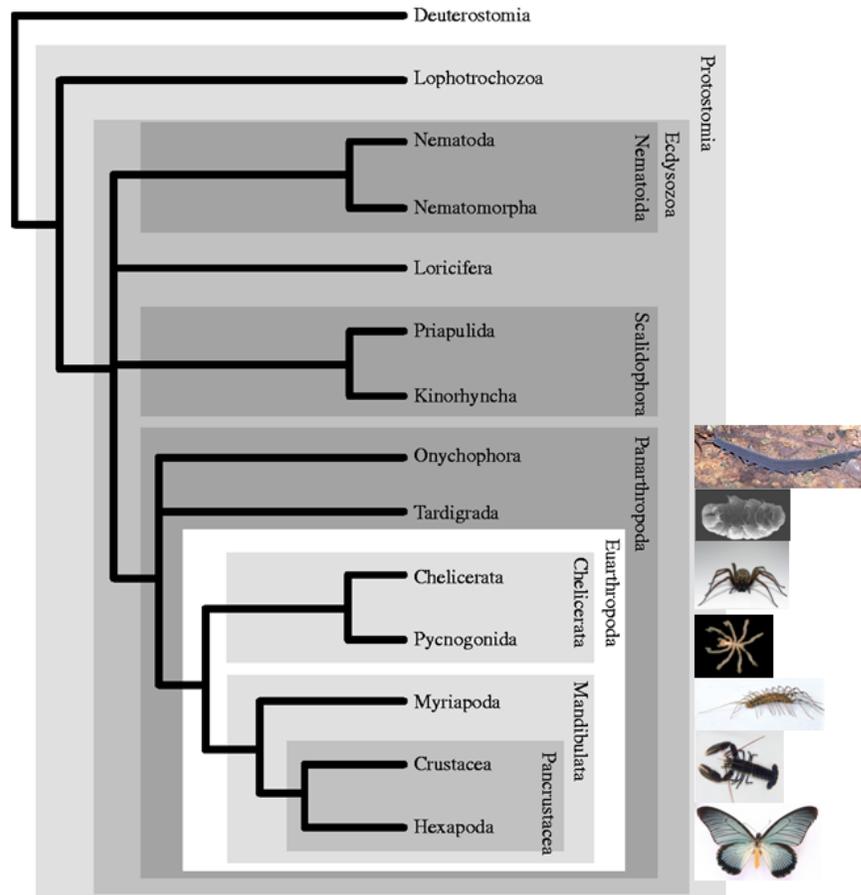


Fig. 1.3.2.4a. Phylogeny of Ecdysozoa, a clade comprising molting animals with exoskeleton (*Phil. Trans. Roy. Soc. B* 363, 1529, 2008; *Nature* 457, 812, 2009).

There are no known fossils that directly shed light on the origin of hexapods. However, phylogenetic reconstructions support their tight relatedness to one clade of crustaceans, branchiopods (Fig. 1.3.2.4b). This clade of crustaceans already existed 525 mya (Fig. 1.3.2.1f). However, hexapod remains are found only in freshwater or terrestrial

strata no earlier than the Devonian, ~410 mya. The last common ancestor of hexapods and branchiopods probably lived in fresh water during the Late Silurian, giving rise to extant freshwater dwelling branchiopods (fairy shrimps, water fleas, and tadpole shrimps) and insects.

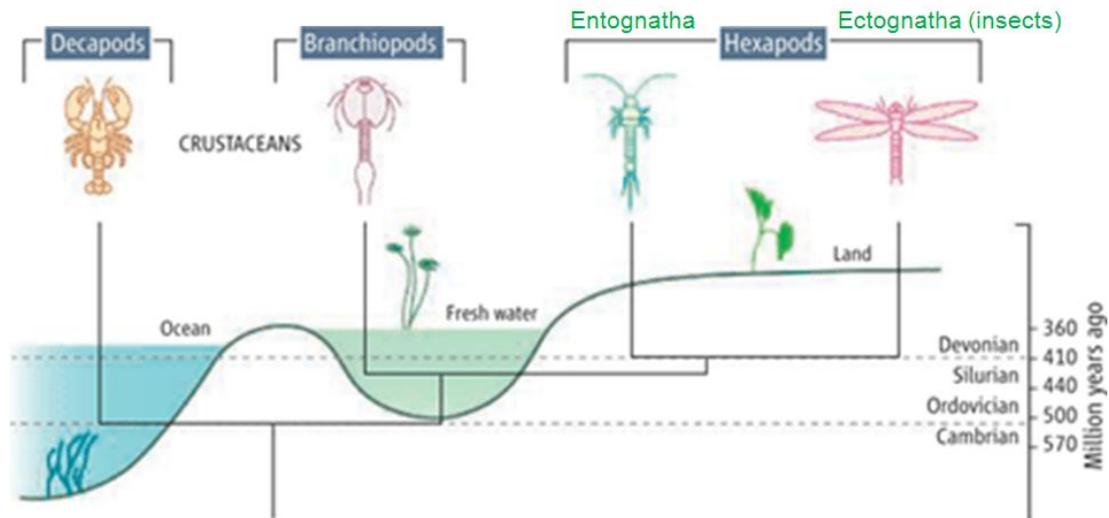


Fig. 1.3.2.4b. Phylogenetic position of insects and other hexapods within the crustaceans (*Science* 314, 1883, 2006).

Fossils representing the earliest stages of insect evolution are found in the chert from Rhynie, Scotland's Old Red Sandstone (Devonian, ~400 mya). Rhynie fauna includes the springtail *Rhyniella praecursor* (Entognatha, Collembola), the oldest known hexapod and a fragmentary fossil *Rhyniognatha hirsti*, the oldest known true insect (Ectognatha), which may be relatively derived within basal Ectognatha (Fig. 1.3.2.4c). Thus, insects were already present in some of the earliest terrestrial faunas.

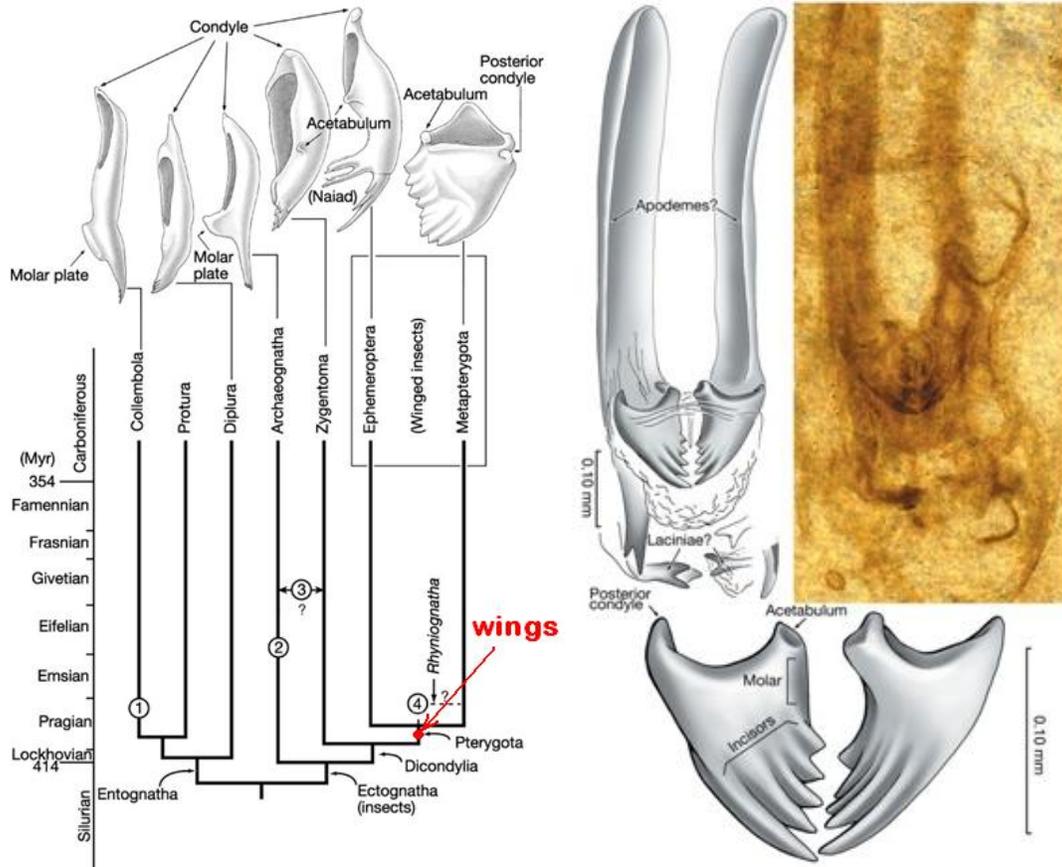


Fig. 1.3.2.4c. Phylogeny of basal hexapod orders (*Nature* 427, 627, 2004) and the earliest fossil of a true insect *Rhyniognatha hirsti*.

The first radical innovation after the origin of true insects Ectognatha was the origin of wings. It occurred relatively early: so far the earliest pterygote (winged insect) was found in the Lower Carboniferous ~325 mya in the Czech Republic (Fig. 1.3.2.4d). On the basis of its wing venation, this fossil is attributed to the Orthoptera (locust) lineage. Thus, the origin of winged insects must have happened well before that.

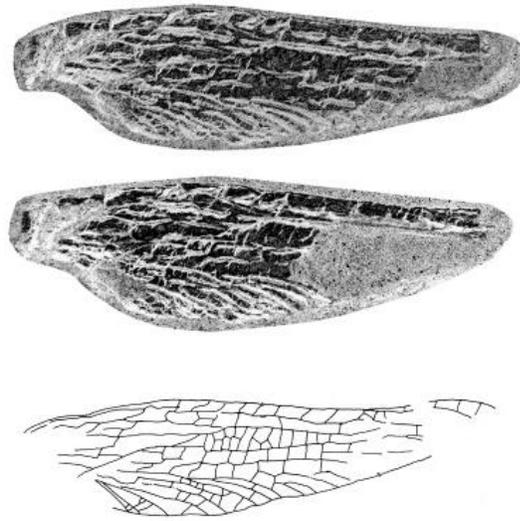


Fig. 1.3.2.4d. The earliest known fossil insect wings (*Geobios* 38, 383, 2005).

After the origin of wings, the next innovation was metamorphosis (larva, pupa, imago). The most diverse orders of modern insects have metamorphosis. The first known fossil of an insect with metamorphosis is from Carboniferous in France, ~310 Ma old. (*Annal. Soc. Entomol. France* 43 349, 2007). After this, diversification of insects continued, becoming especially rapid after the origin of flowering plants (Fig. 1.3.2.4e).

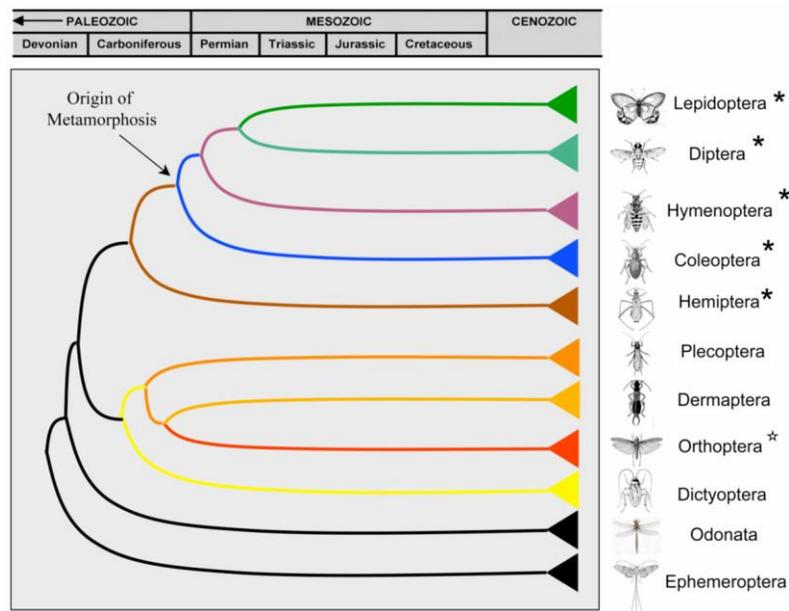


Fig. 1.3.2.4e. Phylogeny of some of the modern orders of insects.

### 1.3.2.5. Tetrapods

We are now returning to the evolution of vertebrates. The origin of tetrapods from sarcopterygian fishes (Fig. 1.3.2.2h) was one of the most dramatic events in the evolution of life. In recent years, a number of truly transitional fossils that document this process have been discovered (Fig. 1.2.3.3c). Although direct ancestor - descendant relationships between these fossils are not very likely (Section 1.2.3.4), more ancient fossils tend to represent ancestral trait states, and having enough fossils will make it possible to reconstruct the course of this evolutionary transition (Fig. 1.3.2.5a).

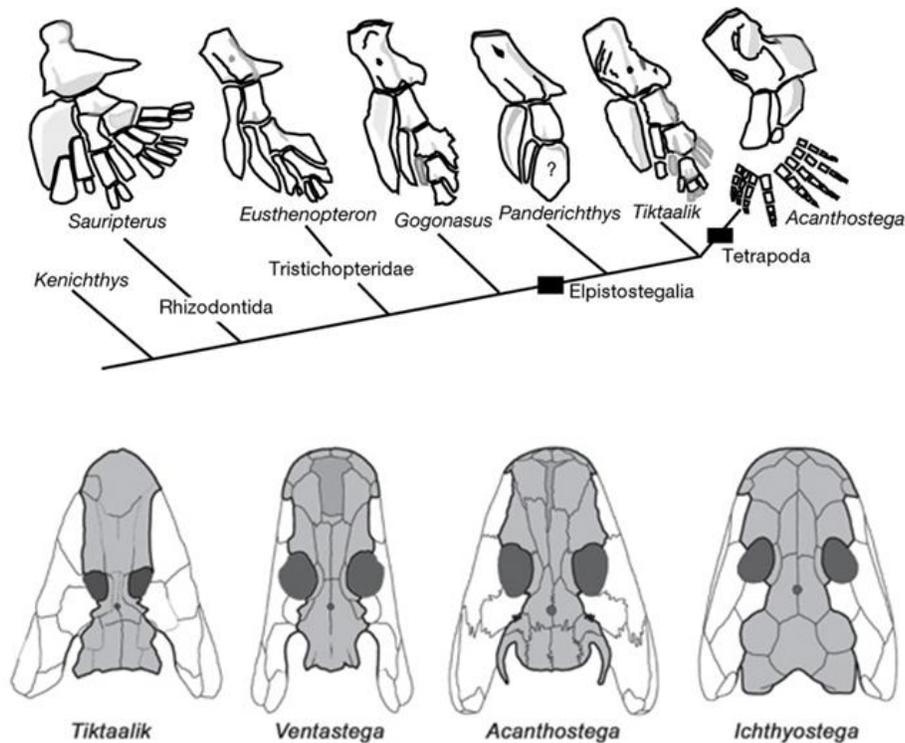


Fig. 1.3.2.5a. Evolution of forelimb from pectoral fin (top, *Nature* 444, 199, 2006) and of tetrapod cranium from fish cranium (bottom, *Nature* 453, 1199, 2008).

Let us briefly review some of these transitional fossils. *Gogonasmus*, discovered in a limestone concretion of Gogo Formation of Western Australia in Devonian (~385 Ma old) was a tetrapodomorph sarcopterygian fish (Fig. 1.3.2.5b). It possessed a mosaic of

ancestral and derived tetrapod-like features. As a result, some aspects of the tetrapod limb skeleton and middle ear architecture can now be traced further back to their aquatic ancestors. The pectoral fin skeleton of *Gogonasmus* shares several features with that of *Tiktaalik*, the most tetrapod-like fish.



Fig. 1.3.2.5b. *Gogonasmus*, a ~385 Ma old tetrodomorph fish (*Nature* 444, 199, 2006).

A well-preserved fossil *Tiktaalik roseae*, of approximately the same age as *Gogonasmus* found Arctic Canada, represents an intermediate between fish with fins and tetrapods with limbs. Although the body scales, fin rays, lower jaw and palate are comparable to those in sarcopterygians, *Tiktaalik* also has a shortened skull roof, a modified ear region, a mobile neck, a functional wrist joint, and other features that presage tetrapod conditions (Fig. 1.3.2.5c). The morphological features and geological setting of *Tiktaalik* suggest life in shallow-water habitats.

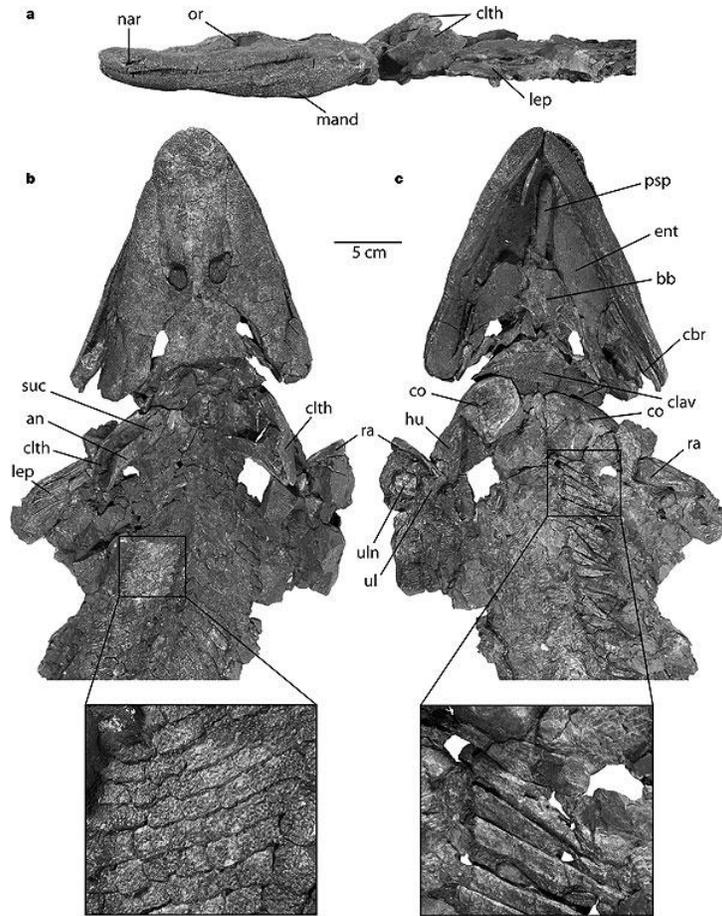


Fig. 1.3.2.5c. *Tiktaalik roseae*, ~385 Ma old, an intermediate between fish with fins and tetrapods with limbs (*Nature* 440, 757, 2006).

*Ventastega curonica*, found in Latvia, lived a little later, in Late Devonian ~360 mya, and is a transitional intermediate form between the fishes *Panderichthys* and *Tiktaalik* and the Devonian tetrapods (limbed vertebrates) *Acanthostega* and *Ichthyostega* (Fig. 1.3.2.5d). *Ventastega* is the most primitive Devonian tetrapod represented by extensive remains, and it illuminates the origin of principal tetrapod structures.

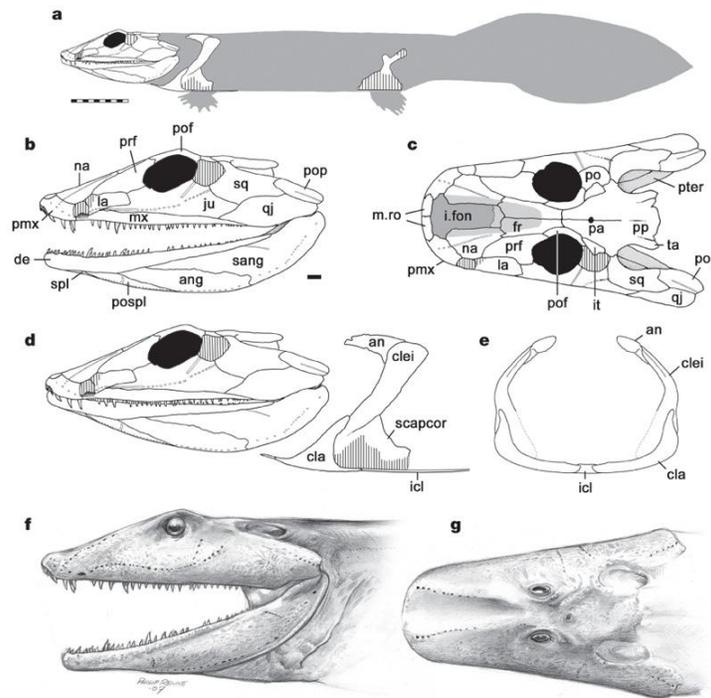


Fig. 1.3.2.5d. The skull, exceptionally preserved braincase, shoulder girdle and partial pelvis of *Ventastega curonica* from the Late Devonian (*Nature* 453, 1199, 2008).

Thus, the whole transition of aquatic sarcopterygian fishes into terrestrial tetrapods apparently took only ~20-30 Ma. However, the primitive tetrapods still lacked embryo-protecting membranes and depended on water for reproduction. Such tetrapods are called anamniotes and are attributed to class Amphibia. There was a wide radiation of anamniotes soon after the origin of tetrapods, in the Carboniferous (Fig. 1.3.2.5e). Still, almost all of these early anamniotes left no living descendants, and modern amphibians belong to 3 clades which diverged later (Fig. 1.3.2.5f).



*Diplocaulus* sp., 275Mya



*Eryops megacephalus*, 295Mya

Fig. 1.3.2.5e. Two extinct anamniotes.

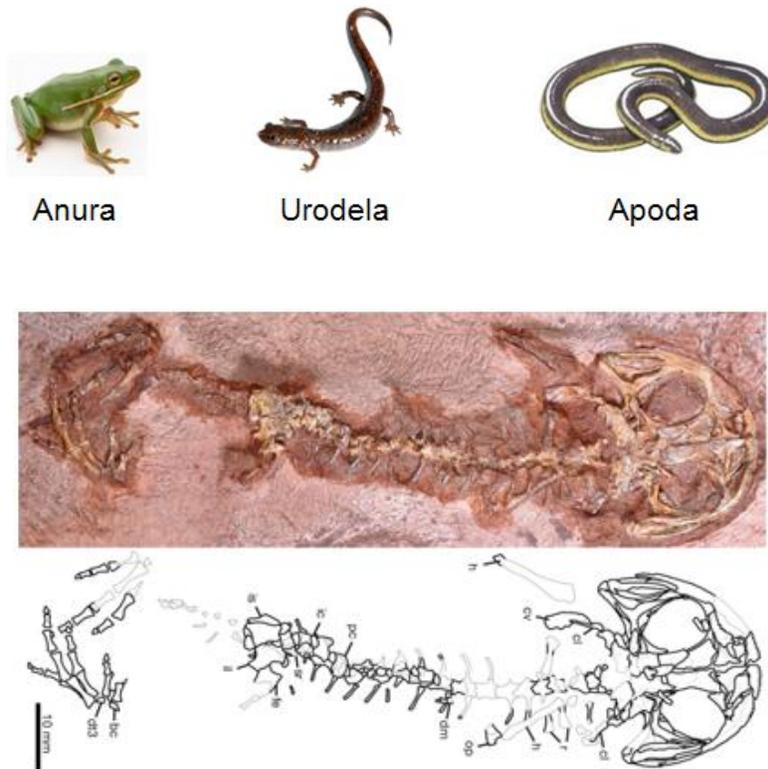


Fig. 1.3.2.5f. (top) Three clades of modern amphibians. (bottom) *Gerobatrachus hottoni*, a species probably close to the common ancestor of Anura and Urodela, lived in Early Permian, 290 mya. The lineage of Apoda diverged earlier (*Nature* 453, 515, 2008).

The first crucial innovation in the evolution of tetrapods was the origin of embryo-protecting membranes (amnion, chorion, and allantois). Except the 3 orders of amphibians, all other modern tetrapods are amniotes (Fig. 1.3.2.5g). The earliest definite fossil amniotes (reptiles) are from Middle Carboniferous, ~314 Ma, and some fossils from Lower Carboniferous, ~340 Ma, may also be amniotes (Fig. 1.3.2.5h). Thus, amnion evolved in less than 30-40 Ma after the origin of tetrapods. Amniotes became very diverse beginning from Permian, 290 mya (Fig. 1.3.2.5i). Those amniotes that are not mammals or birds are collectively called Reptilia. Below, we will briefly consider the origins of mammals and birds, ignoring the other 3 living clades of reptiles.

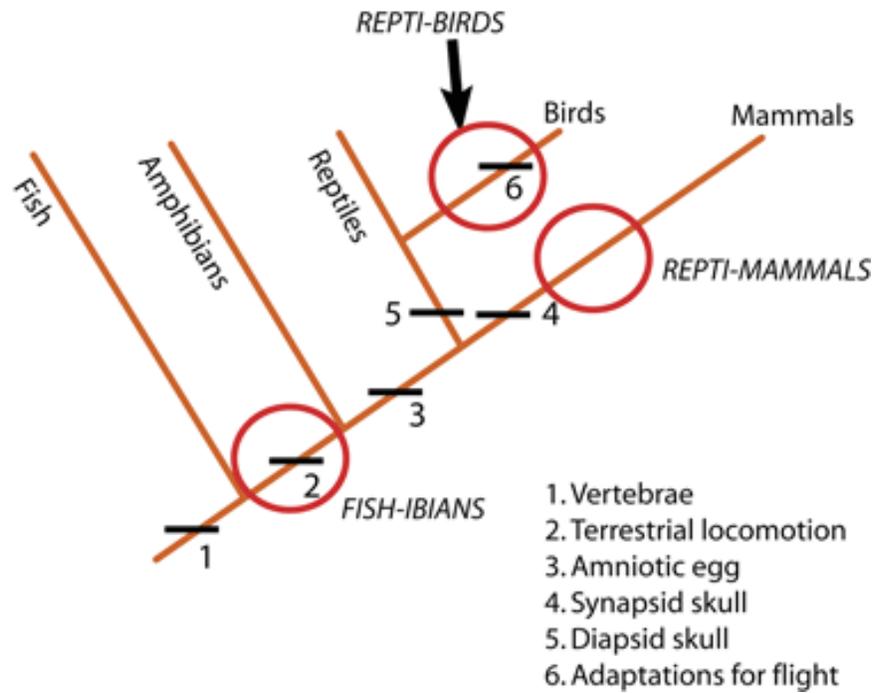


Fig. 1.3.2.5g. Some important innovations in the evolution of tetrapods.

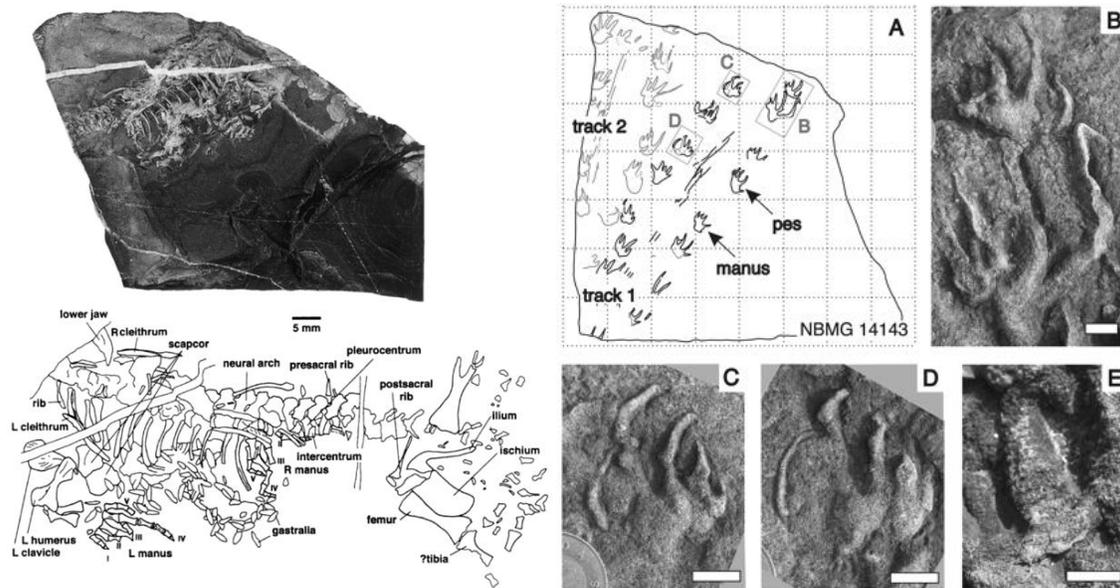


Fig. 1.3.2.5h. (left) *Casineria kiddi*, Scotland, probably amniote, 340 Ma (*Nature* 398, 508, 1999). (right) Trace fossils of reptiles, 314 Ma (*Journal of Geological Society* 164, 1113, 2007).

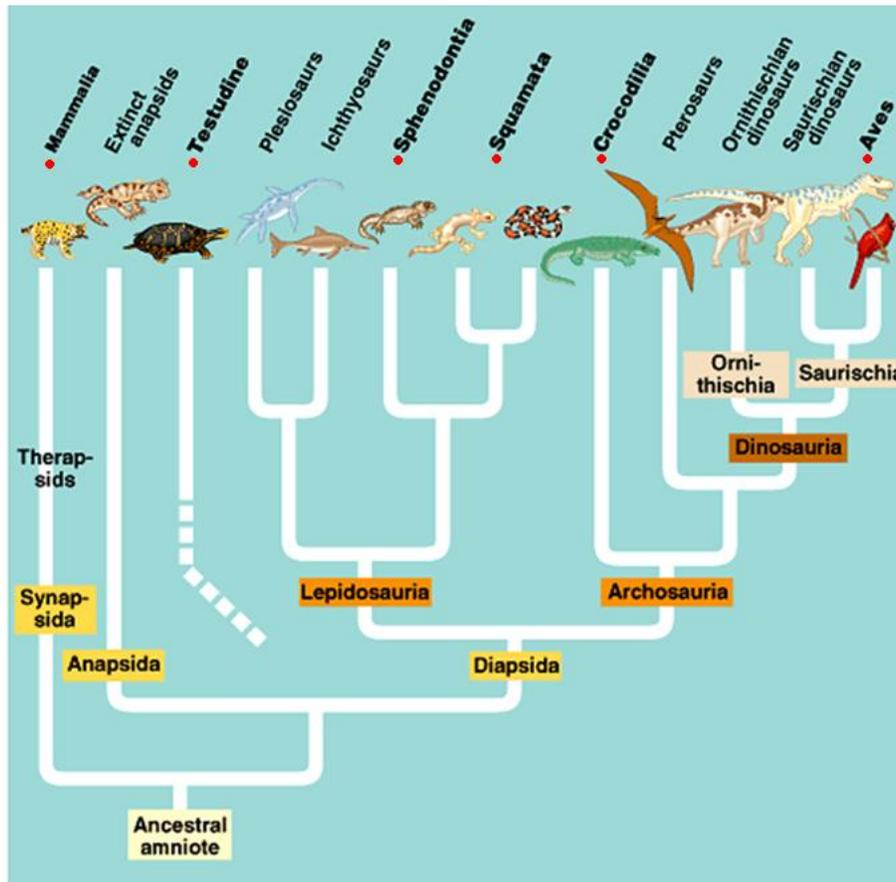


Fig. 1.3.2.5i. Diversity of amniotes, both extinct and extant (marked by red dots). Terms synapsida, anapsida, and diapsida refer to the basic anatomy of the skull.

### 1.3.2.6. Mammals

The key fact about the origin of mammals is that a lot of traits that distinguish extant mammals and "reptiles" evolved very early, in Early Permian (290 mya), but the first "true" mammals appeared only in Early Jurassic (200 mya). Mammals belong to Synapsida ("fused arch"), a clade of amniotes that evolved one opening in their skull (temporal fenestra) behind each eye, ~310 mya, in the late Carboniferous. Synapsida consist of the stem and crown group mammals; fossils are known that together span the morphological distance from the common ancestral amniote to the Mammalia. Synapsida include the basal group Pelycosauria and the derived group Therapsida, nested within the Pelycosauria; Mammalia in turn is nested within Therapsida (Fig. 1.3.2.6a).

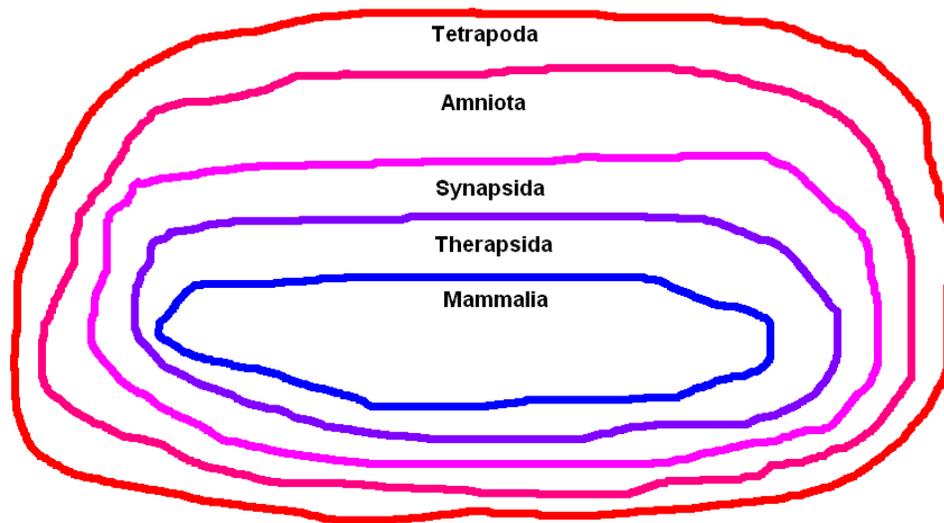
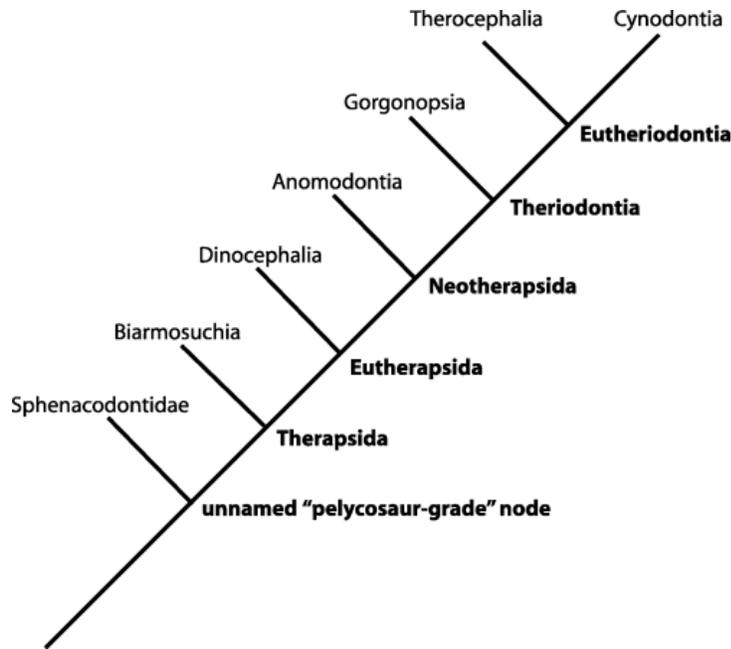
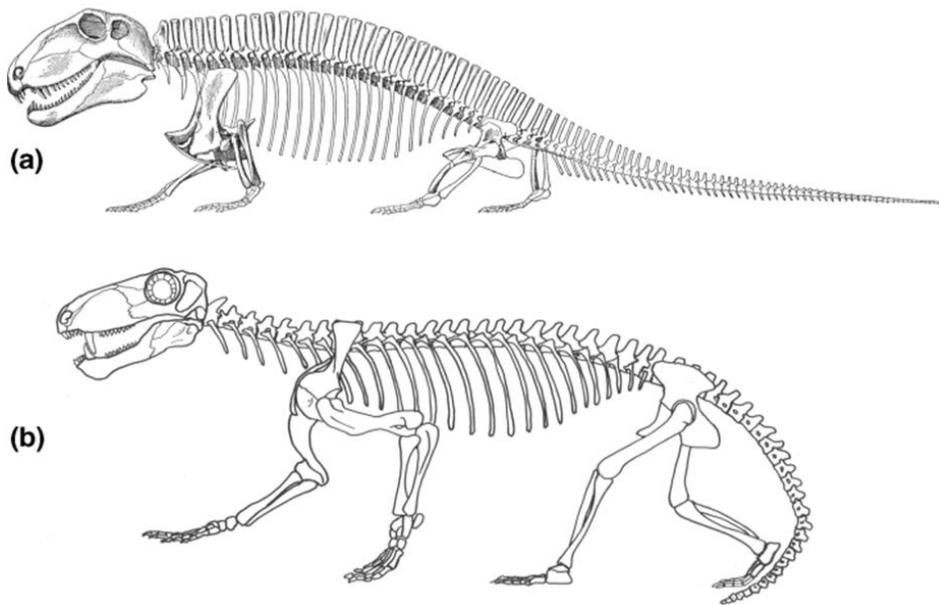


Fig. 1.3.2.6a. The place of mammals within tetrapods.

Therapsids (or "mammal-like reptiles"), are a group of synapsids, which flourished in the Permian. Therapsids evolved from a group of pelycosaurs, the Sphenacodontia, in Early Permian (~290 mya) and became the dominant land animals in the Middle Permian (~270 mya), replacing the pelycosaurs and apparently became warm-blooded by then. Therapsids probably had skin glands, similar to that of mammals, rather than scales as in reptiles. Theriodonts are the only therapsids known to have had fur, which evolved in the Late Permian. Therapsids consisted of three major clades, the dinocephalians, the herbivorous anomodonts and the mostly carnivorous theriodonts (Fig. 1.3.2.6b).



Therapsida, Paleozoic mammal-like reptiles



Skeletal reconstructions of (a) *Sphenacodon* and (b) hypothetical ancestral therapsid.

Fig. 1.3.2.6b. (top) A plausible phylogeny of the Therapsida (*J. Evol. Biol.* 19, 1231, 2006). (bottom) Two therapsids.

Cynodontia, the only clade of Therapsida that survived end-Permian extinction (Section 1.3.2.8), had nearly all the characteristics of mammals (Fig. 1.3.2.6c). Their teeth

were fully differentiated, the braincase bulged at the back of the head, and many of them walked in an upright manner unlike reptiles. Their temporal fenestrae was much larger than in their ancestors, and the widening of the zygomatic arch allowed for more robust jaw musculature. They also had the secondary palate that other primitive therapsids lacked, except the therocephalians, who were the closest relatives of cynodonts. Their dentary was the largest bone in their lower jaw, as other smaller bones moved into the ears. Cynodonts were probably warm-blooded, and covered in hair. However, cynodonts still laid eggs.

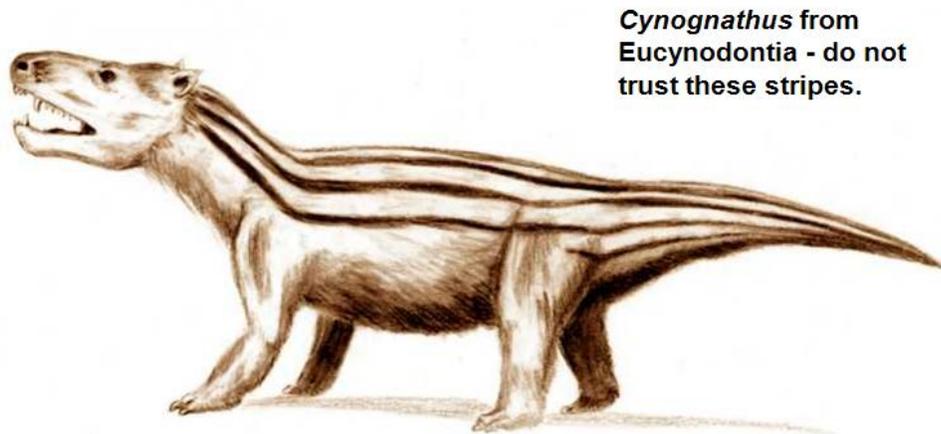


Fig. 1.3.2.6c. An advanced cynodont.

The most derived cynodonts are found within Eucynodontia clade (lower Triassic, ~250 Ma), which also contains the members of Mammalia. Milk evolved in Jurassic (200-150 mya, *Nature* 450, 1011, 2007), and during this period there lived a wide diversity of Mammalia and their close relatives, mammaliaforms. By the Late Jurassic, diverse mammals mostly displaced several more primitive mammaliaform lineages (Fig. 1.3.2.6d).

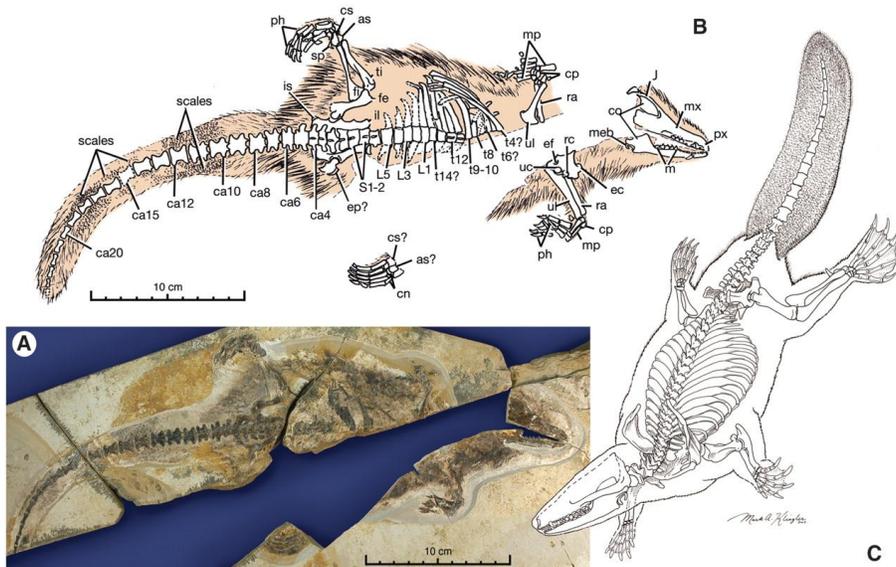


Fig. 1.3.2.6d. A swimming mammaliaform from the Middle Jurassic, *Castorocauda lutrasimilis*. This fossil demonstrates that some mammaliaforms developed diverse locomotory and feeding adaptations. Similarity of this animal with modern aquatic mammals is convergent (*Science* 311, 1123, 2006).

In the Cretaceous (145-65 mya) Mammalia became even more diverse. Eleven species belonging to five major groups of mammals (multituberculates, eutriconodontans, symmetrodontans, metatherians and eutherians) have been described from the 125 Ma old Jehol Biota, China (Fig. 1.3.2.6e). The Early Cretaceous divergence of eutherians is first documented as skull and skeletal fossils. The Jehol mammals indicate a diverse fauna in which species ranged from 25g to 14,000g in body masses, had insectivorous, omnivorous and carnivorous diets (as reflected by their dentitions and by stomach content), and acquired scansorial, possibly arboreal and terrestrial habits (*Geological Journal* 41, 439, 2006; *Nature* 439, 195, 2006). Most of modern mammals belong to two clades, marsupials (nested within metatherians) and placentals (nested within eutherians), and are present in Jehol, so that their divergence must predate 125 mya. Monotremes (egg-laying mammals, currently represented by only two genera) branched off even earlier. Thus, most of the clades of early mammals, and all clades of mammaliaforms, left no extant descendants and would remain unknown without fossils (Fig. 1.3.2.6f).

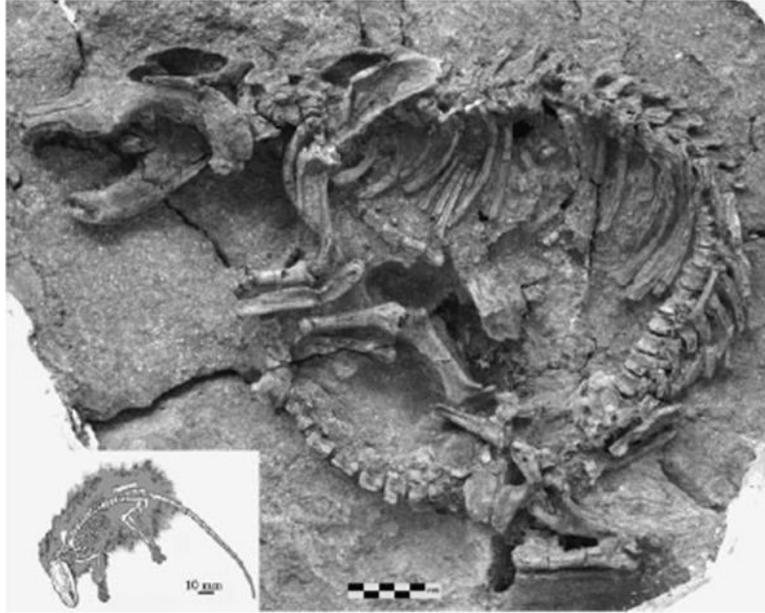


Fig. 1.3.2.6e. Body size contrast of two Jehol mammals: the large *Repenomamus giganticus* and the small *Eomaia scansoria*.

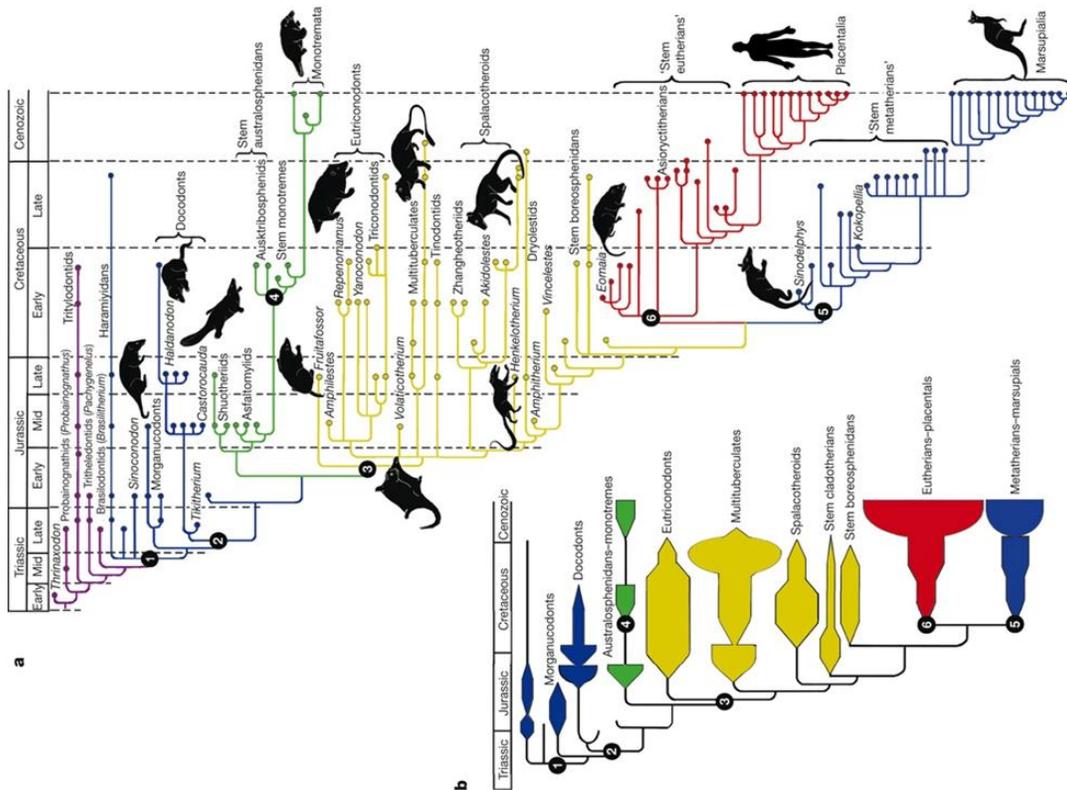


Fig. 1.3.2.6f. Overview of the Mesozoic mammals.

The Jurassic and Cretaceous mammals developed, iteratively, similar niche specializations to modern Australasian monotremes and marsupials, and are no less ecologically diverse than the early Cenozoic mammals of similar body-size range. Splits of Mesozoic mammal groups were accompanied by ecological diversification (Fig. 1.3.2.6g). We already observed this pattern of repeated diversifications and extinctions in the course of evolution of other clades.

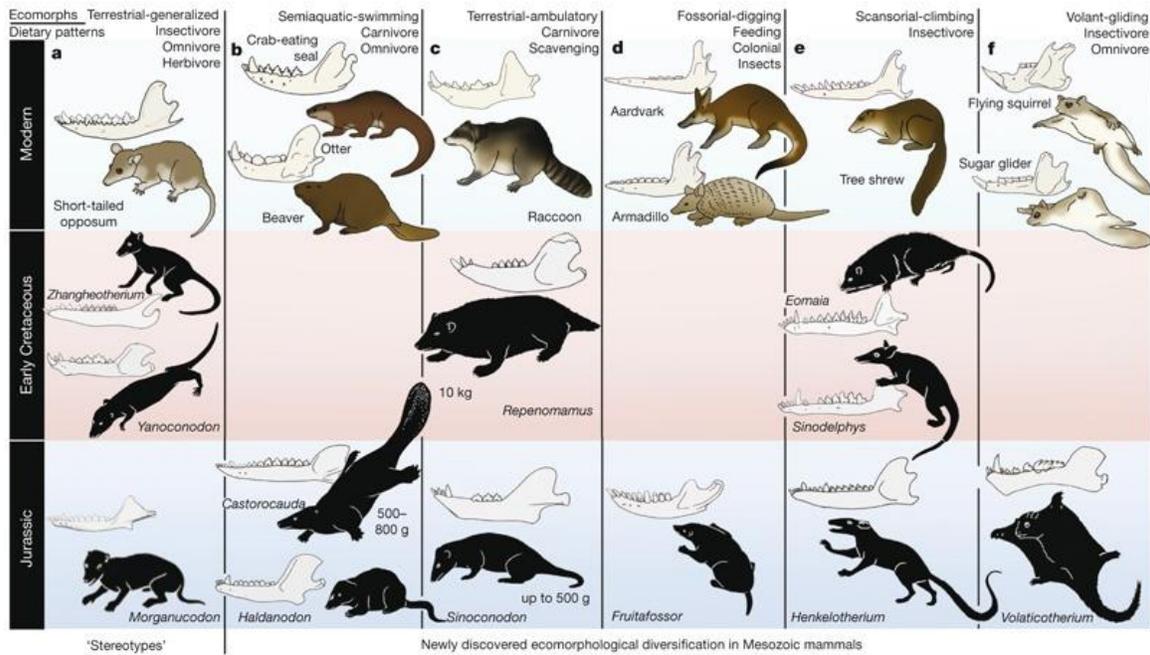


Fig. 1.3.2.6g. Ecological convergence of Mesozoic mammals and modern mammals (*Nature* 450, 1011, 2007).

Cladogeneses that produced extant marsupial and placental mammals began in the Cretaceous, and their phylogeny has mostly been resolved (Fig. 1.1.3.6a). Fig. 1.3.2.6h presents a closer view on the phylogeny of Afrotheria, the earliest extant clade of placental mammals. Phylogeny of Primates will be considered in Chapter 1.4.

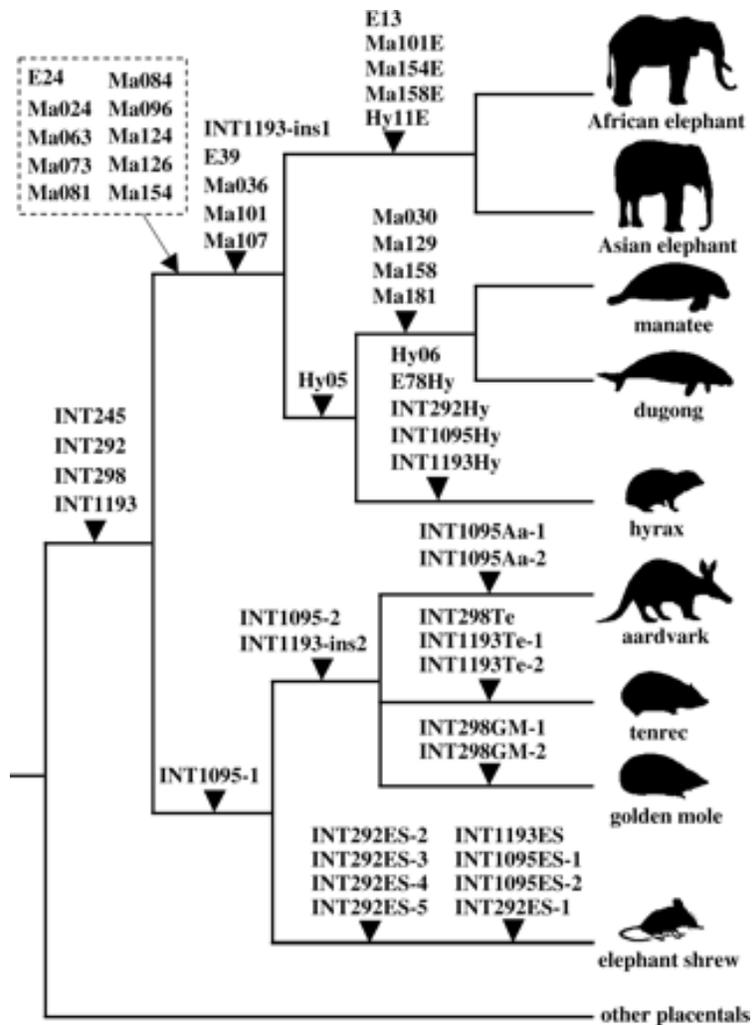


Fig. 1.3.2.6h. Phylogeny of Afrotheria, based on acquisitions of introns (*Mol. Biol. Evol.* 22, 1823, 2005).

### 1.3.2.7. Birds

Birds originated from dinosaurs in the Lower Cretaceous. Dinosaurs evolved ~230 mya during the Middle Triassic, were very diverse in Jurassic and Cretaceous, and disappeared (except birds!) in the K-T extinction 65 mya (Fig. 1.3.2.7a). Within the stem group of birds, feather evolved before flight, perhaps for thermoregulation, as dinosaurs were warm-blooded (Fig. 1.3.2.7b).

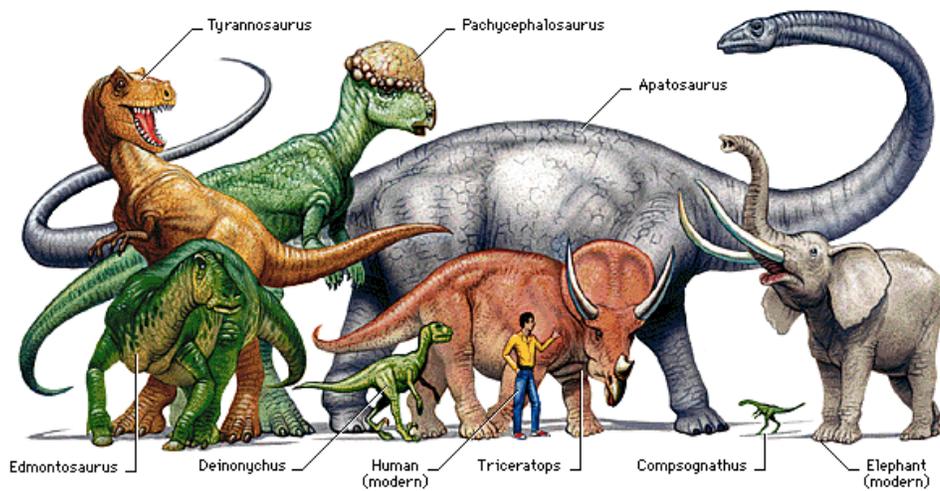
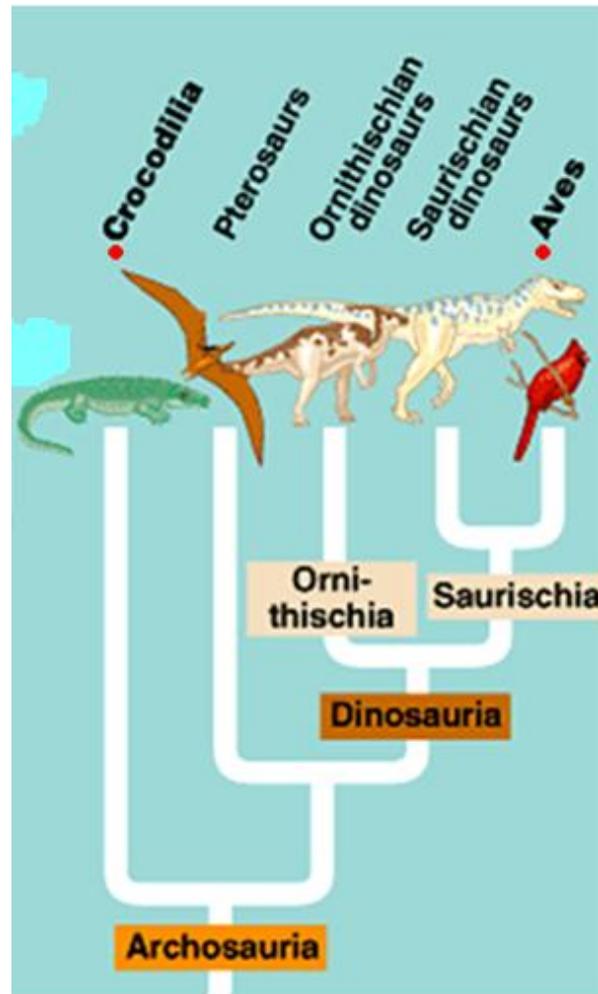


Fig. 1.3.2.7a. (top) Position of birds among the major clades of dinosaurs. (bottom) A small sample from the diversity of dinosaurs.

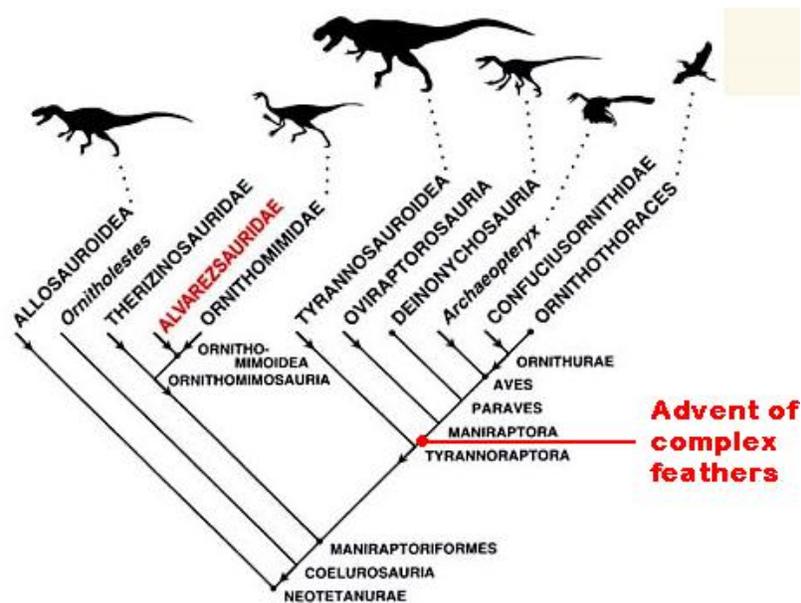
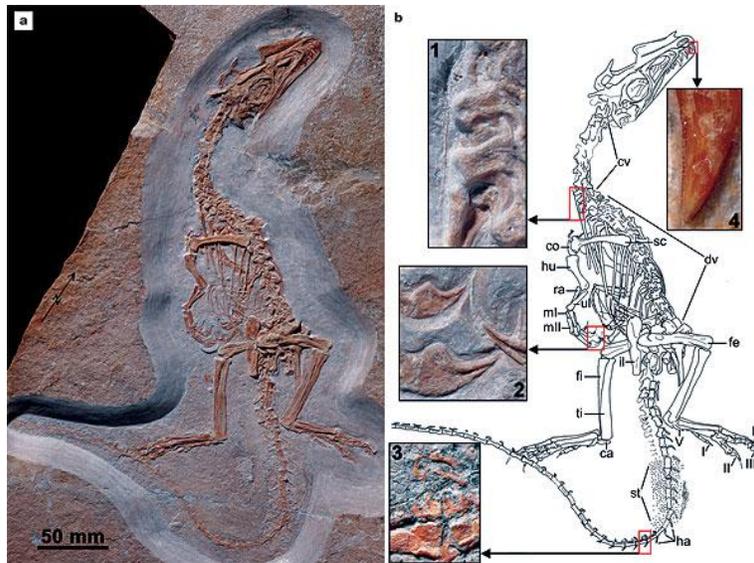


Fig. 1.3.2.7b. A plausible moment of the origin of feathers and the position of birds among related dinosaurs (*Nature* 440, 287, 2006).

A number of fossils represent different stages in the evolution of birds from ground-living, bipedal dinosaurs from the clade Therapoda (Fig. 1.3.2.7c). *Archaeopteryx lithographica*, the first known bird from Late Jurassic, ~150 Ma old, had a skeleton similar to that of nonavian theropod dinosaurs (Fig. 1.3.2.7d). *Archaeopteryx* had a primitive tetraradiate palatine bone and no fully reversed first toe. The second toe was hyperextendible as in dromaeosaurs and troodontids. *Pengornis houi*, a 120 Ma old Early Cretaceous bird, is more advanced and closer to extant birds (Fig. 1.3.2.7e).



***Sinosauropteryx prima*** is the most primitive of the Liaoning 140My old theropods with integumentary covering, visible as a crest along the top of the head, back, and tail.



***Sinornithosaurus milleni***, a dromaeosaurid, from 130My old Lingyuan that shows a complete body covering of various types of integumentary covering.



***Microraptor gui***, a dromaeosaurid from 130My old Liaoning with extremely long pennaceous feathers on both its front and hind limbs.

Fig. 1.3.2.7c. (top) A small 150 Ma old featherless theropod predatory dinosaur from the Late Jurassic in southern Germany (*Nature* 440, 329, 2006). (bottom) Three feathered non-avian dinosaurs from the Cretaceous in China. They cannot be direct ancestors of birds, because *Archeopteryx* lived earlier (*Ann. Rev. Earth Planet. Sci.* 33, 277, 2005).

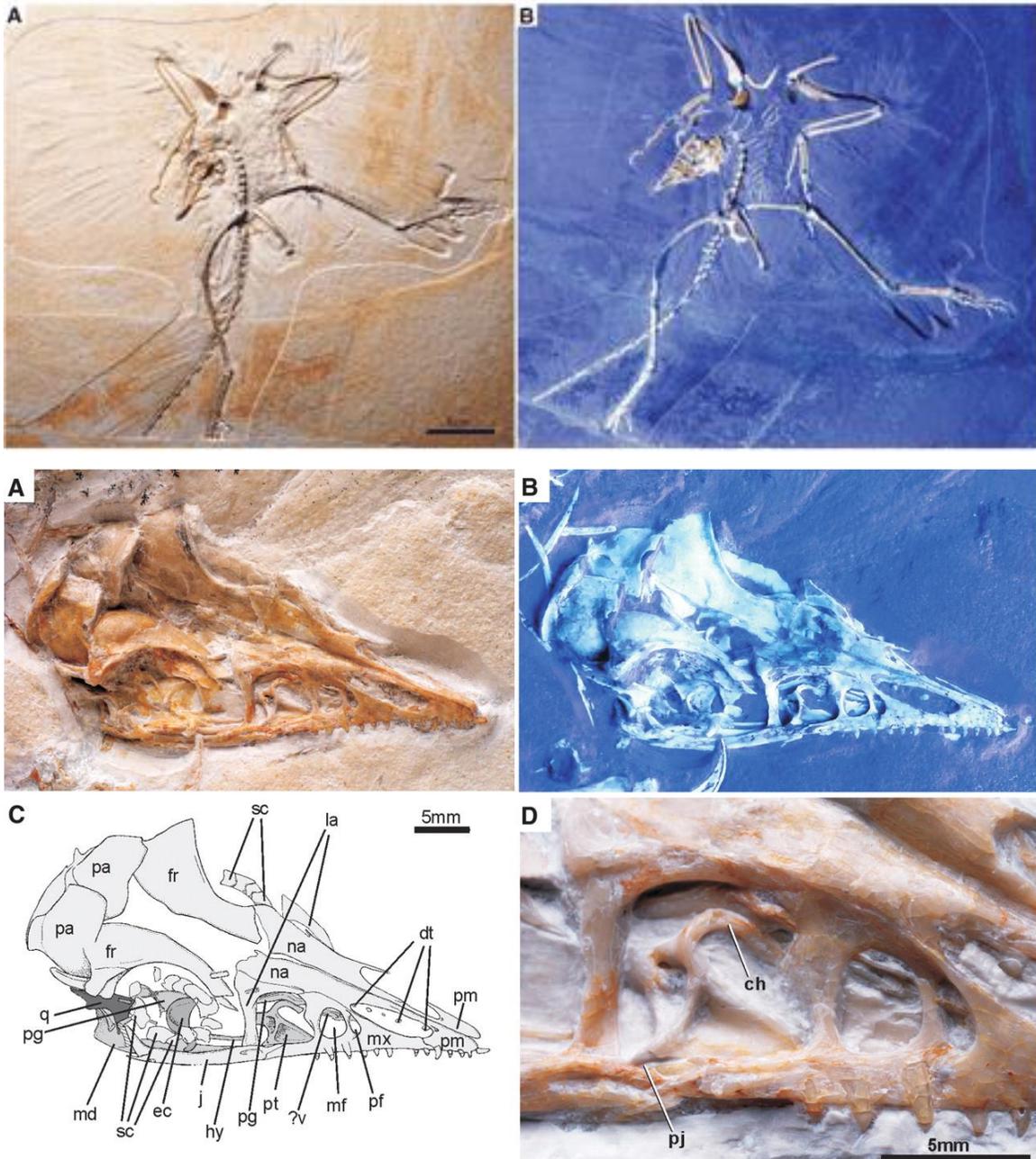


Fig. 1.3.2.7d. *Archaeopteryx* fossils: skeleton with wing and tail feather impressions and skull. Ultraviolet-induced fluorescence photograph shows the preserved bone substance (*Science* 310, 1483, 2005).

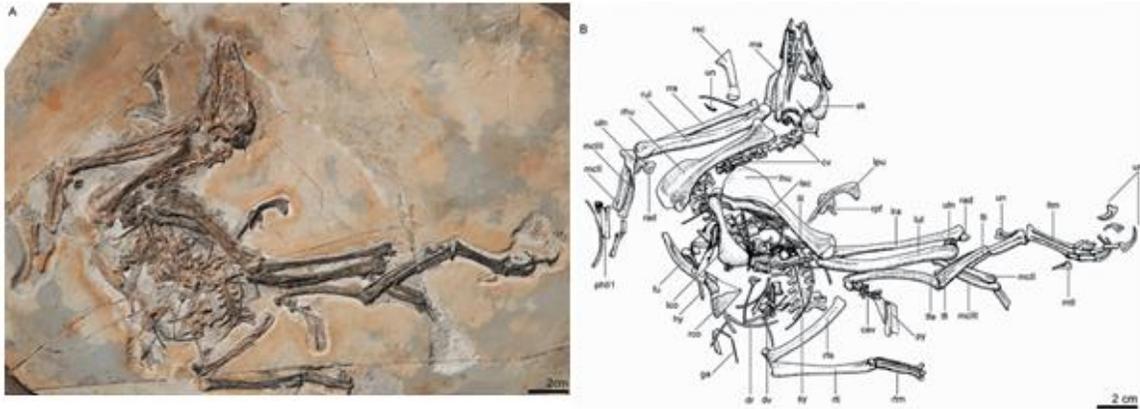


Fig. 1.3.2.7e. *Pengornis houi* (*Journal of Anatomy* 212, 565, 2008).

Soon after their origin, Cretaceous birds became diverse, but most of their lineages went extinct (Fig. 1.3.2.7f). Diversification of modern birds began in the Cretaceous. This follows from placement of *Vegavis iaai*, a fossil from the Cretaceous of Antarctica, within the extant bird radiation. *Vegavis iaai* is a part of Anseriformes (waterfowl) clade, most closely related to modern ducks (Fig. 1.3.2.7g). Thus, at least five cladogeneses within Aves before the K/T boundary: duck, chicken and ratite bird ancestors lived alongside non-avian dinosaurs. The phylogeny of extant birds has been mostly resolved.

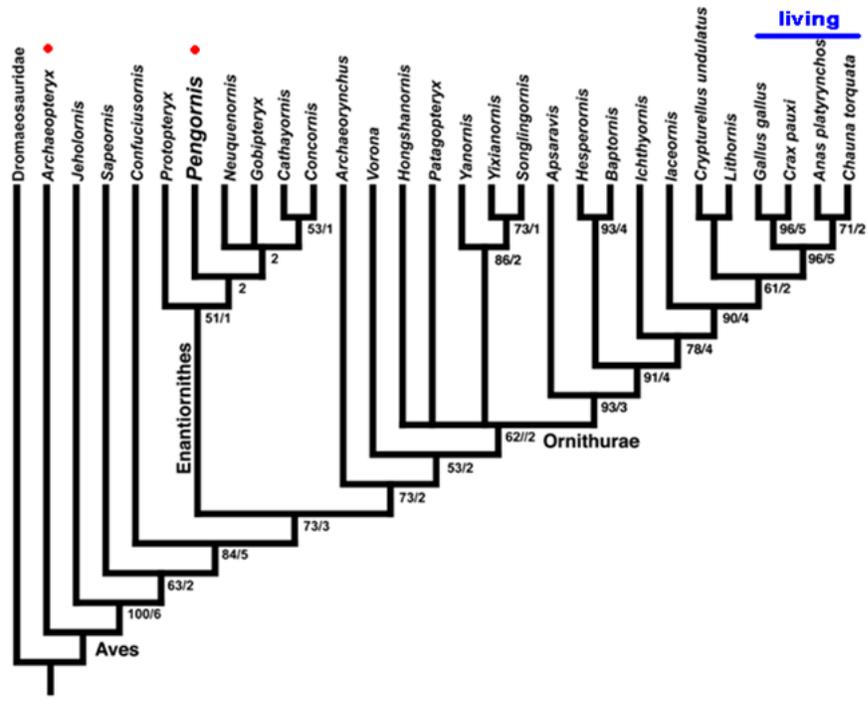
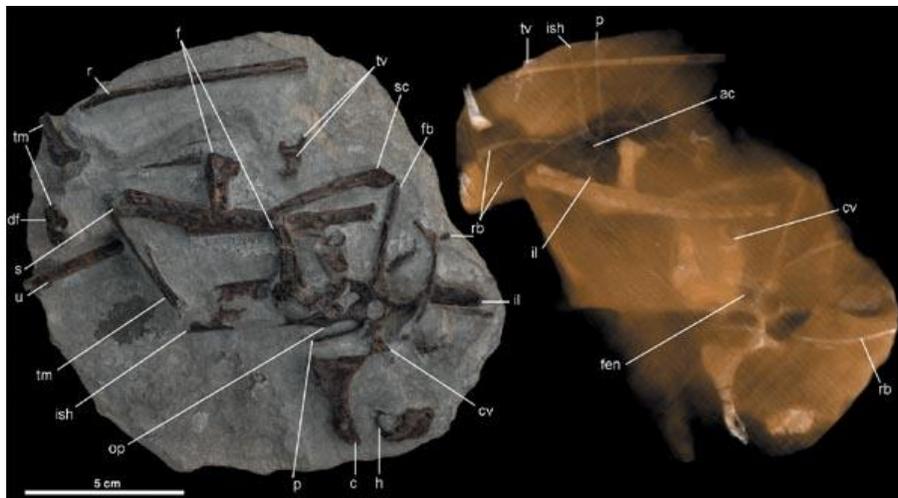


Fig. 1.3.2.7f. Phylogeny of major clades of birds, mostly extinct, with the clades of *Archaeopteryx* and *Pengornis* marked by red dots.



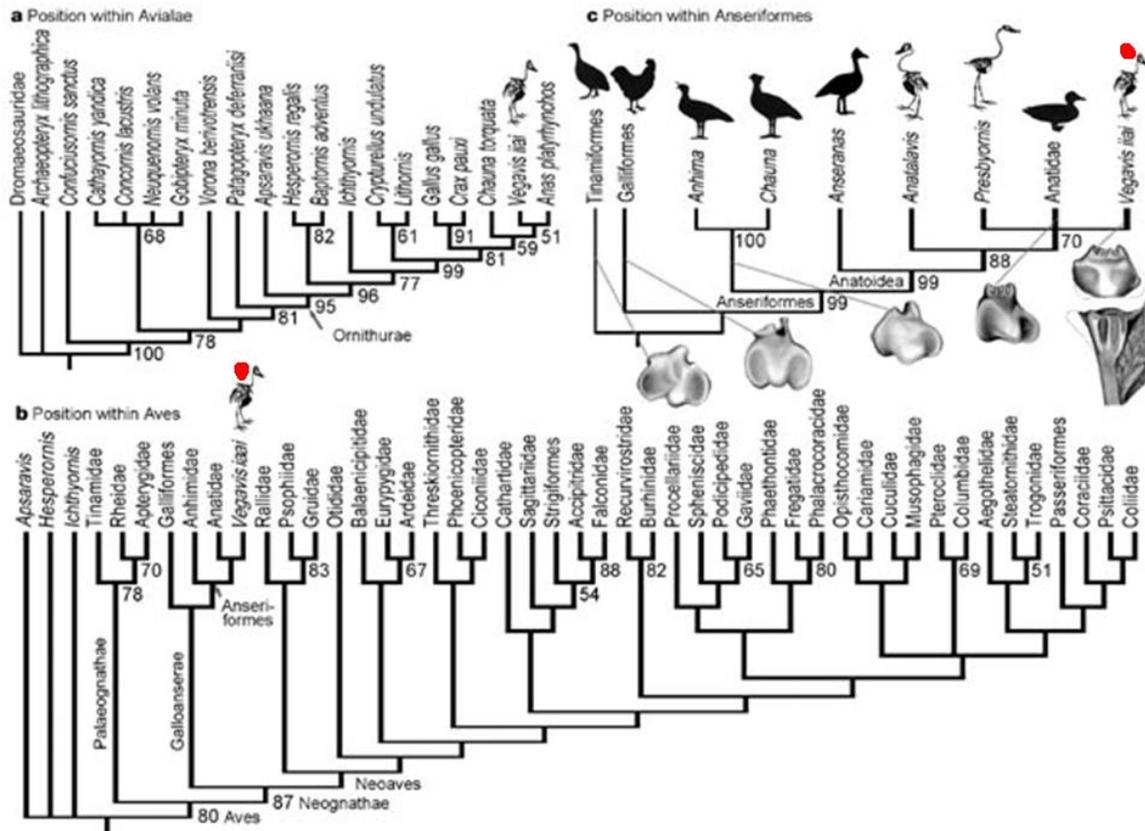


Fig. 1.3.2.7g. (top) *Vegavis iaai*. (bottom) Implications of the phylogenetic position of *V. iaai* for the timing of divergence of birds (*Nature* 433, 305, 2005).

### 1.3.2.8. Mass extinctions

There was a number of episodes in the history of the Earth when a large fraction of biodiversity rapidly went extinct. Fig. 1.3.2.8a shows the dynamics of the percentage of marine animal genera that disappeared from the known fossil record in the course of a million of years in the course of the Phanerozoic eon. Clearly, there are multiple peaks, corresponding to extinction events, separated by periods of low extinction rate, with the overall, and unexplained, trend for the lineages to become more long-lived. Five Phanerozoic mass extinctions ("The Big Five") were particularly severe (Fig. 1.3.2.8b). Mass extinctions, including the one that wiped out the Ediacaran biota (Section 1.2.2.4) definitely occurred in the previous eons, but we currently know very little about them.

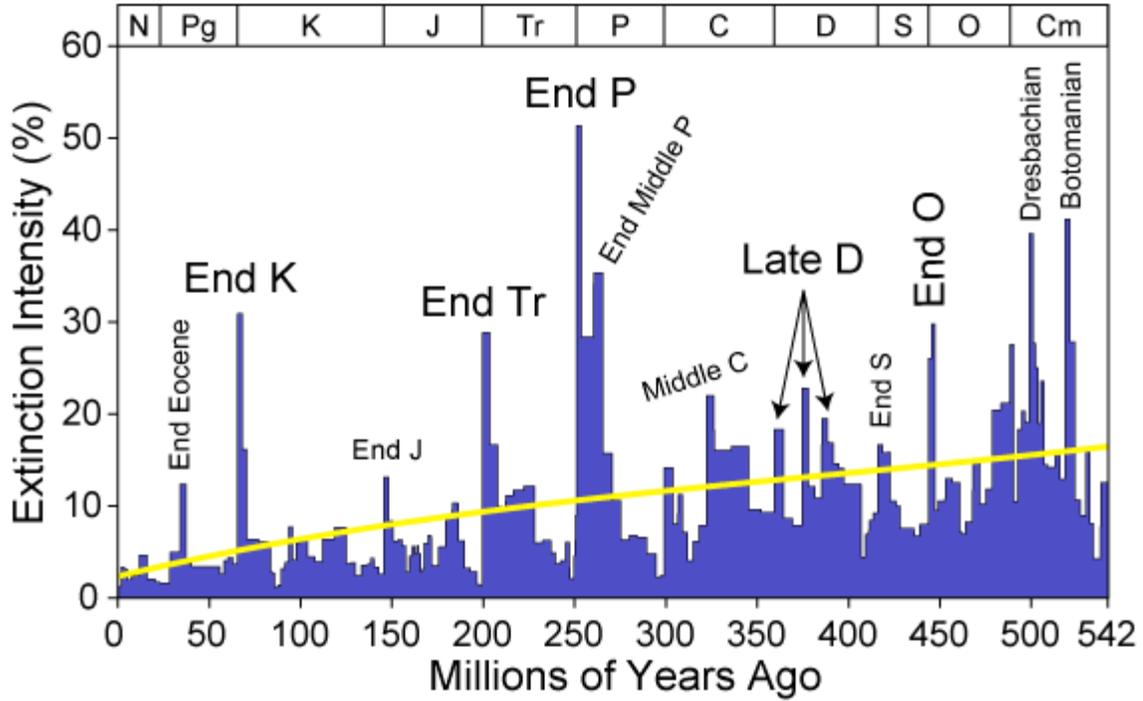


Fig. 1.3.2.8a. Dynamics of phanerozoic extinction of marine animal genera.

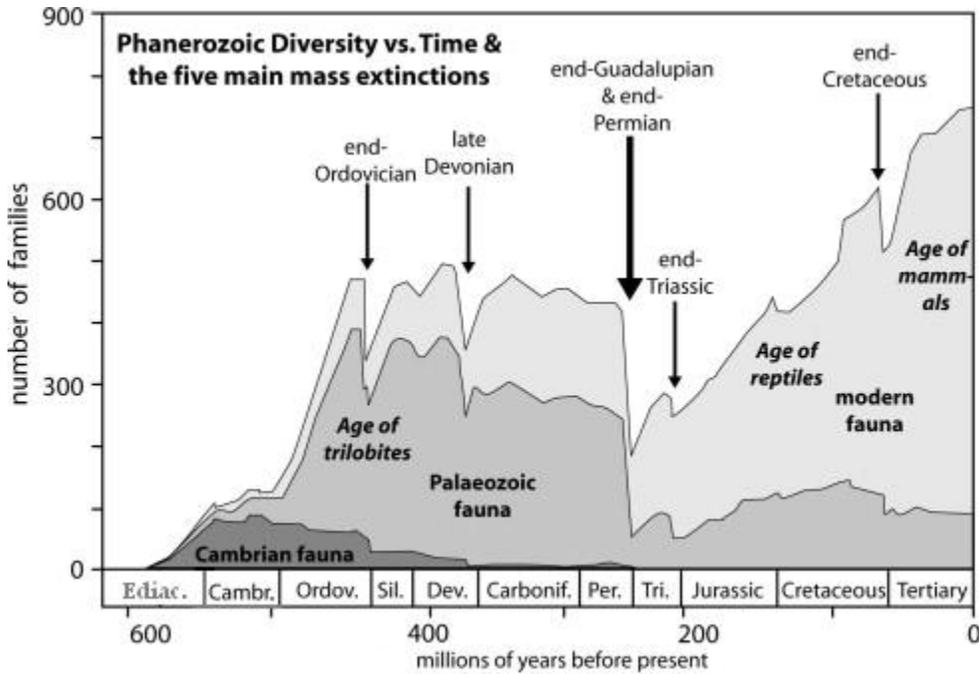


Fig. 1.3.2.8b. Dynamics of Phanerozoic biodiversity showing the three major faunas and five major mass extinctions of the last 600 million years (*Journal of Asian Earth Sciences* 36, 407, 2009).

It is likely that a mass extinction was (almost) always due to deep changes in one or several parameters of the global environment. It is important to distinguish between kill and trigger mechanism(s) of a mass extinction. A kill mechanism is an environmental change that directly harms living beings, and a trigger mechanism is a disturbance that activates kill mechanism(s). Often, it is difficult to establish the cause (or causes) of a particular extinction. Some trigger mechanisms, such as bolide impacts or anomalously high volcanic activity, must leave clear geological traces. However, some other triggers, as well as kill mechanisms may be much harder to detect. Fig. 1.3.2.8c presents data on known past bolide impacts and large-scale volcanic eruptions, in an attempt to correlate them with mass extinctions. Clearly, there is no perfect correlation, although for some of the past mass extinctions, including at least four of "The Big Five", there is a feasible bolide and/or volcanic trigger. Let us briefly review the courses and possible causes of the two greatest Phanerozoic mass extinctions which, not surprisingly, mark the boundaries between its eras.

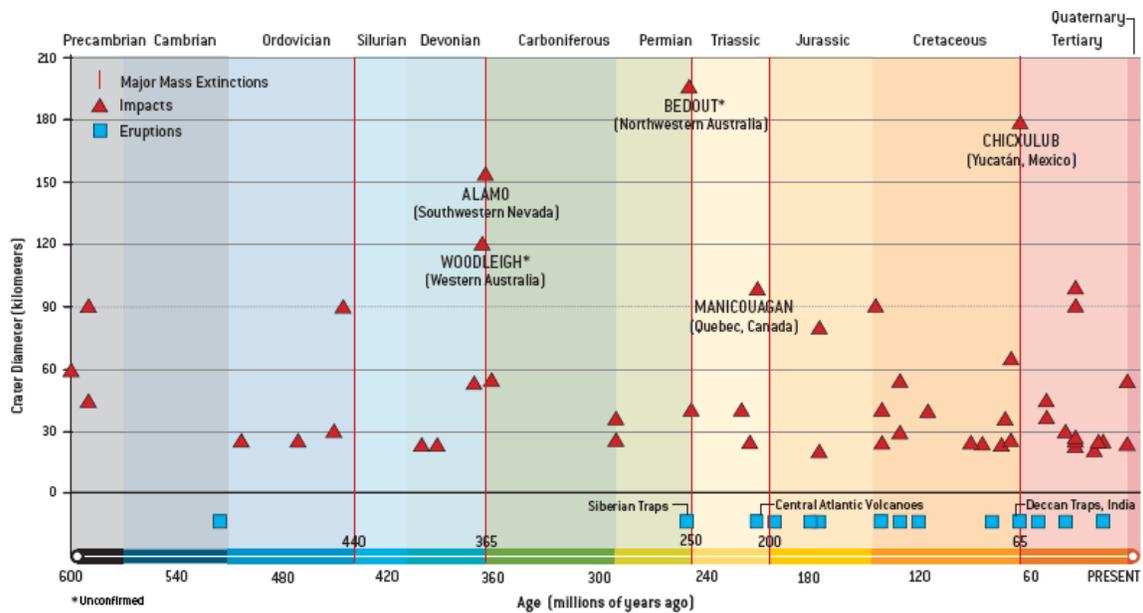


Fig. 1.3.2.8c. Bolide impacts, catastrophic volcanic eruptions, and the five most severe extinctions during the Phanerozoic eon. (*Processes on the Early Earth* 405, 33, 2006).

*End-Permian extinction.* A mass extinction event, currently dated at  $252.6 \pm 0.2$  mya, defines the boundary between the Permian and Triassic periods and the end of the Paleozoic era. End-Permian extinction was perhaps the most severe extinction in the history of life, with >90% of all species of marine animals and ~70% species of terrestrial vertebrates disappearing during a short period of time, no more than 0.5 Ma and perhaps much less. Changes of  $\delta^{13}\text{C}$  at the Still, there is currently no general agreement on either trigger or kill mechanism of the end-Permian extinction.

Currently, it appears that the most plausible trigger mechanism of the end-Permian extinction was Siberian traps (step-like hills) volcanism, the largest known eruption of perhaps ~1 million of cubic kilometers of flood basalt, currently present over large areas in Siberia (Fig. 1.3.2.8d). The age of Siberian traps, as well as of Emeishan Traps, another flood basalt volcanic province in southwestern China, apparently coincides with that of the end-Permian extinction. Global kill mechanisms triggered by massive volcanism would probably be mostly due to the release of  $\text{CO}_2$ ,  $\text{SO}_2$ ,  $\text{CH}_4$  and other volcanic gases which can lead to direct poisoning, acid rain, and a short-term global cooling (due to effects of  $\text{SO}_2$ ) followed by prolonged global warming (due to greenhouse effects of  $\text{CO}_2$ , and  $\text{CH}_4$ ). Other feasible trigger mechanisms of the end-Permian extinction include sudden release of large amounts of  $\text{CH}_4$  from methane hydrates from the sea floor; anoxia; a shift in ocean circulation; and even a bolide impact (Fig. 1.3.2.8c).

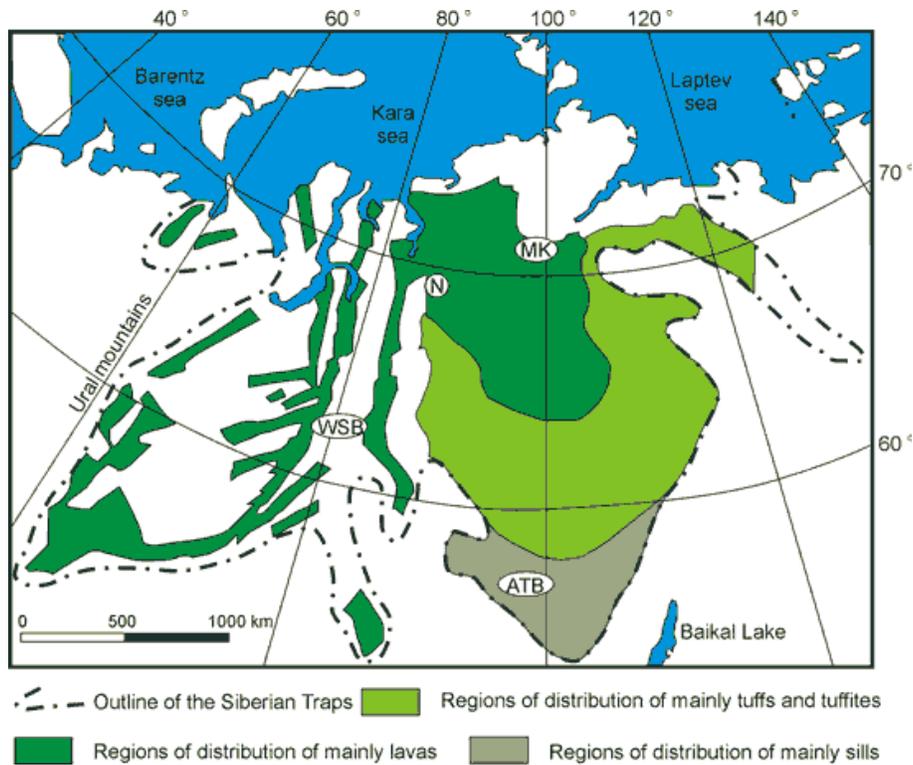


Fig. 1.3.2.8d. Distribution of various igneous rocks that constitute Siberian Traps.

There is a number of locations where uninterrupted deposition of sediments spanned the Permian-Triassic boundary, documenting the end-Permian extinction and enabling rather detailed reconstruction of the post-extinction recovery of the biota. (Fig. 1.3.2.8e). In some clades, such as conodonts, diversity began to grow very soon. In contrast, recovery of sponges and corals did not begin for 5 Ma, and coral reef reappeared only 10 Ma after the extinction (1.3.2.8f). Radiolarite deposition shut down in for millions of years, and full recovery of marine life took about 100 Ma Fig. 1.3.2.8b). Several excursions and persistent ocean anoxia in the Early Triassic (1.3.2.8f) indicate that the physical environment also did not return to its pre-extinction state for along time.

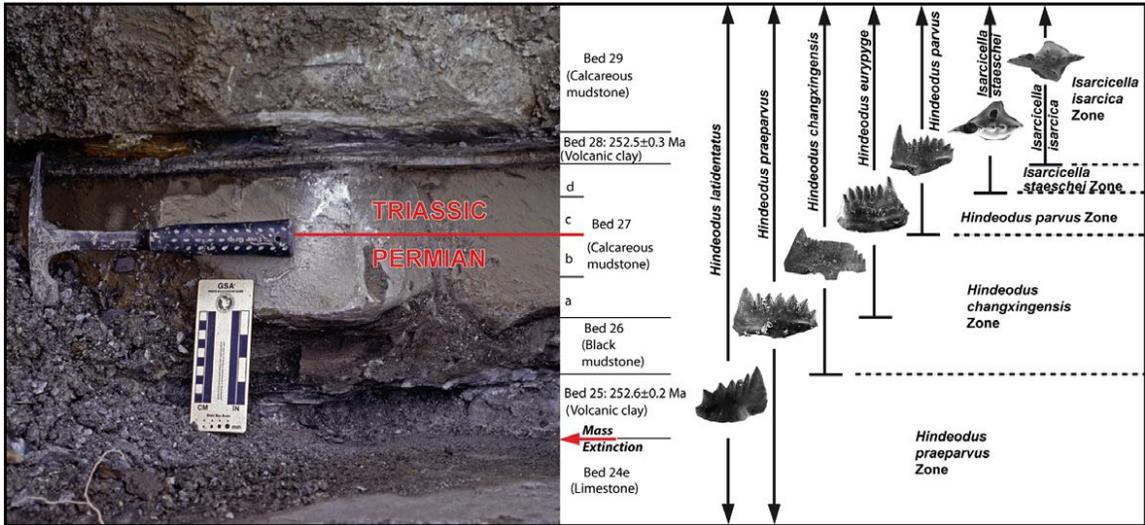


Fig. 1.3.2.8e. Sedimentary rocks spanning the Permian-Triassic boundary in Meishan, China. Temporal ranges of species of *Hindeodus* and *Isarcicella* show the rapid evolution of conodont (an extinct class of fishes) teeth immediately following the mass extinction.

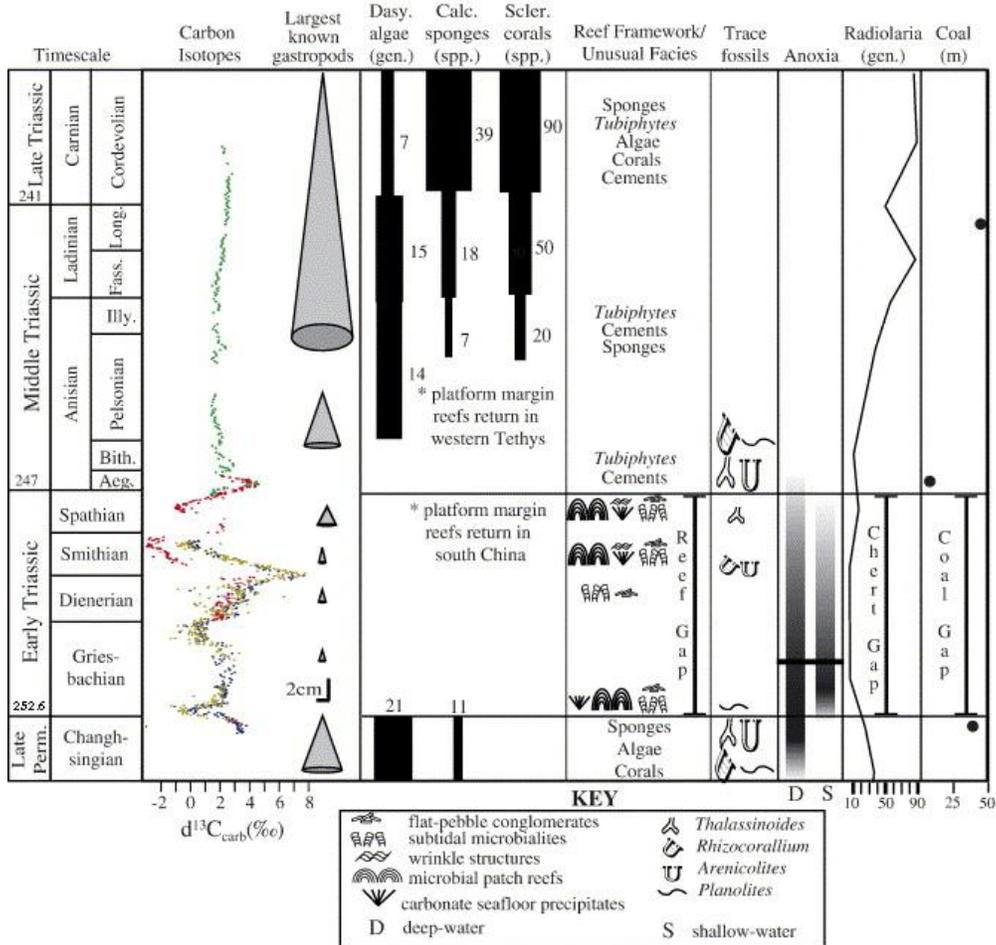


Fig. 1.3.2.8f. Characteristics of the Early Triassic record in comparison to preceding and following intervals (*Earth and Planetary Science Letters* 256, 295, 2007).

*End-Cretaceous, or KT, extinction.* A mass extinction event, currently dated at  $65.81 \pm 0.14$  mya, defines the boundary between the Cretaceous and Paleogene (historically, Tertiary) periods and the end of the Mesozoic era. Although the KT extinction overall was less severe than the end-Permian extinction (Fig. 1.3.2.8b), it led to total extinction of a substantial number of prominent groups of Mesozoic organisms (Fig. 1.3.2.8g). There is a nearly-universal agreement that the main trigger mechanism of the KT extinction was the Chicxulub impact (Section 1.2.2.5). The global kill mechanisms triggered by the Chicxulub impact probably included prolonged global warming due to effects of H<sub>2</sub>O, SO<sub>2</sub>, CO, and CO<sub>2</sub>, released in the atmosphere after the impact. However, in the immediate aftermath of the impact sunlight probably did not reach the surface of the Earth due to a large amounts of dust in the atmosphere, which blocked photosynthesis and led to temporary cooling. Other events that could affect the global biota at the end of the Cretaceous were a deep regression of the sea level, perhaps due to temporary sinking of the mid-ocean ridges, and a massive volcanic eruption that produced Deccan Traps flood basalts. Perhaps, one or both of these event made the biota more vulnerable at the time of the Chicxulub impact.



Fig. 1.3.2.8g. Three groups that went extinct at the end of the Cretaceous period: rudists (a order of Bivalvia), ammonoids (an order of Cephalopoda), and non-avian dinosaurs.

Detailed stratigraphy of the Cretaceous-Paleogene boundary is available from many locations (Fig. 1.3.2.8h). Analysis of fossil pollen and spores made it possible to reconstruct the succession of changes in several floras across the globe. For example, in

the New Zealand the high-diversity Late Cretaceous flora is separated from post-extinction low-diversity Early Paleogene flora by a 4-mm layer that almost exclusively contains fungal spores (Fig. 1.3.2.8i). This layer coincides with the iridium anomaly (Section 1.2.2.4) and must have been deposited in the course of no more than a few years, because fungi disappeared while the iridium concentration remained anomalously high. Thus, the period of disruption of photosynthesis was short. After this period, the post-extinction flora was dominated by ferns for a substantial period of time.

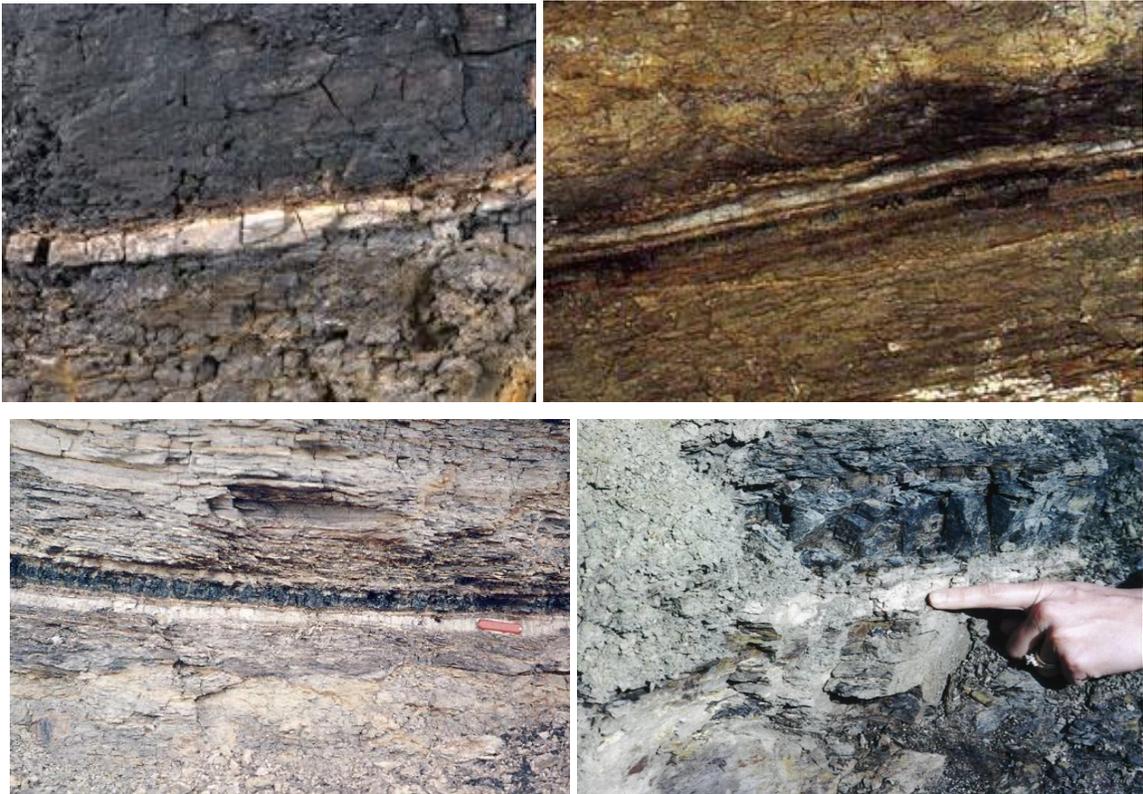


Fig. 1.3.2.8h. The Cretaceous-Paleogene boundary in sedimentary rocks from various locations. High concentrations of iridium are confined to the light thin clay layers.

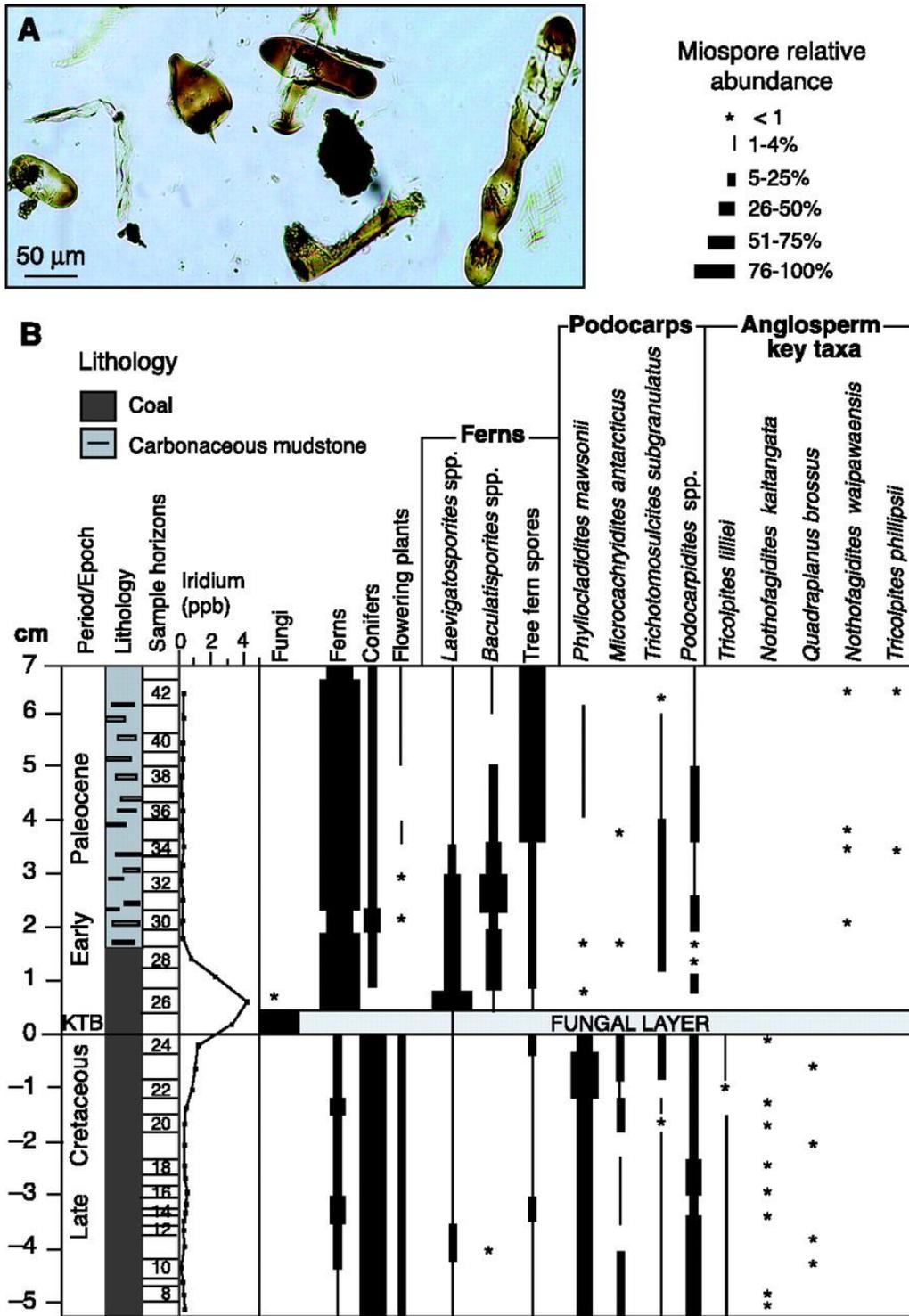


Fig. 1.3.2.8i. (A) Fungal spores and hyphae from the "fungal spike" layer at Moody Creek Mine, New Zealand. (B) Changes in Ir concentration and relative abundance of pollen and spores across the K-T boundary (*Science* 303, 1489, 2004). Similar changes occurred after some other extinctions (*Trends in Ecology and Evolution* 22, 548, 2007).

### Section 1.3.3. Contemporary life

All properties of extant life emerged in the course of its evolutionary origin. Diversity of living beings is hierarchical and consists of clusters of more or less discrete species whose size is distributed according to the power law, reflecting the dynamics of cladogenesis, with most of the modern species being produced by rather recent cladogeneses. Ranges of species reflect their ages, joint distributions of ranges of clades reflects their history, and the global biogeographical patterns reflect the history of vicariance and dispersal. Current environments are just a phase in permanent changes, and many ecosystems are quite young. Human activities, causing direct extermination, habitat destruction, pollution, invasions of exotic species and climate change already devastated the biota and may soon lead to even more disastrous consequences.

#### *1.3.3.1. Biodiversity*

Let us return from our journey back in time, and take a look at the contemporary life from the perspective of its evolutionary origin. The first question is: how is the character of extant biodiversity affected by past evolution? We already addressed this question in Chapter 1.1, and recognized suboptimality of phenotypes of individual species, and homology and hierarchical distributions of trait states in multiple species as principal footprints of past evolution. Here, we will go further and consider more subtle features of extant biodiversity that are due to specific properties of past evolution.

The most salient among these features is that different regions of the space of genotypes and phenotypes are populated extremely unevenly. Some regions, for example those that correspond to trilobites and dinosaurs (and, with no doubt, to countless feasible forms of life that never existed on Earth) are empty, although this does not necessarily mean that trilobites and dinosaurs would be unfit in the modern world. Other regions are populated by just one or very few extant species, such as those that correspond to ginkgo (Fig. 1.3.2.3d, amborella (Fig. 1.3.2.3i), horseshoe crabs, coelacanths, or monotremes (Fig. 1.3.3.1a). At the other extreme, there are densely populated regions, such as >1000 species of Hawaiian *Drosophila* (not shown) or ~1000 species of cichlids from the lake

Malawi (Fig. 1.3.3.1b). Lake Malawi cichlids diverged from their last common ancestor ~1 mya and form the cluster of diameter ~0.01 within the space of genotypes. Despite their diversity caused by adaptations to very different ecological niches, they share a lot of morphological traits that define them all as cichlids. An immense cluster of beetles (order Coleoptera, ~350,000 known and perhaps 5,000,000 extant species totally) is much less compact genetically, because their diversification began ~300 mya, but still occupies a well-defined place within the space of phenotypes (Fig. 1.3.3.1c).



Fig. 1.3.3.1a. (top left) *Limulus polyphemus*. Four extant species of horseshoe crabs (family Limulidae) diverged from their closest extant relatives, arachnids, over 450 mya. (top right) *Latimeria chalumnae*. Two extant species of coelacanths, *L. chalumnae* and *L. menadoensis*, diverged from their closest extant relatives, the 6 species of lungfishes, over 400 mya. (bottom) *Ornithorhynchus anatinus* (platypus, left) and *Tachyglossus aculeatus* (echidna, right) are among five extant species of monotremes, who diverged from their closest extant relatives, marsupials and placentals, over 150 mya. Species that belong to such isolated clusters are not necessarily living fossils, although, apparently, they do tend to be more conservative morphologically than members of populous clades.

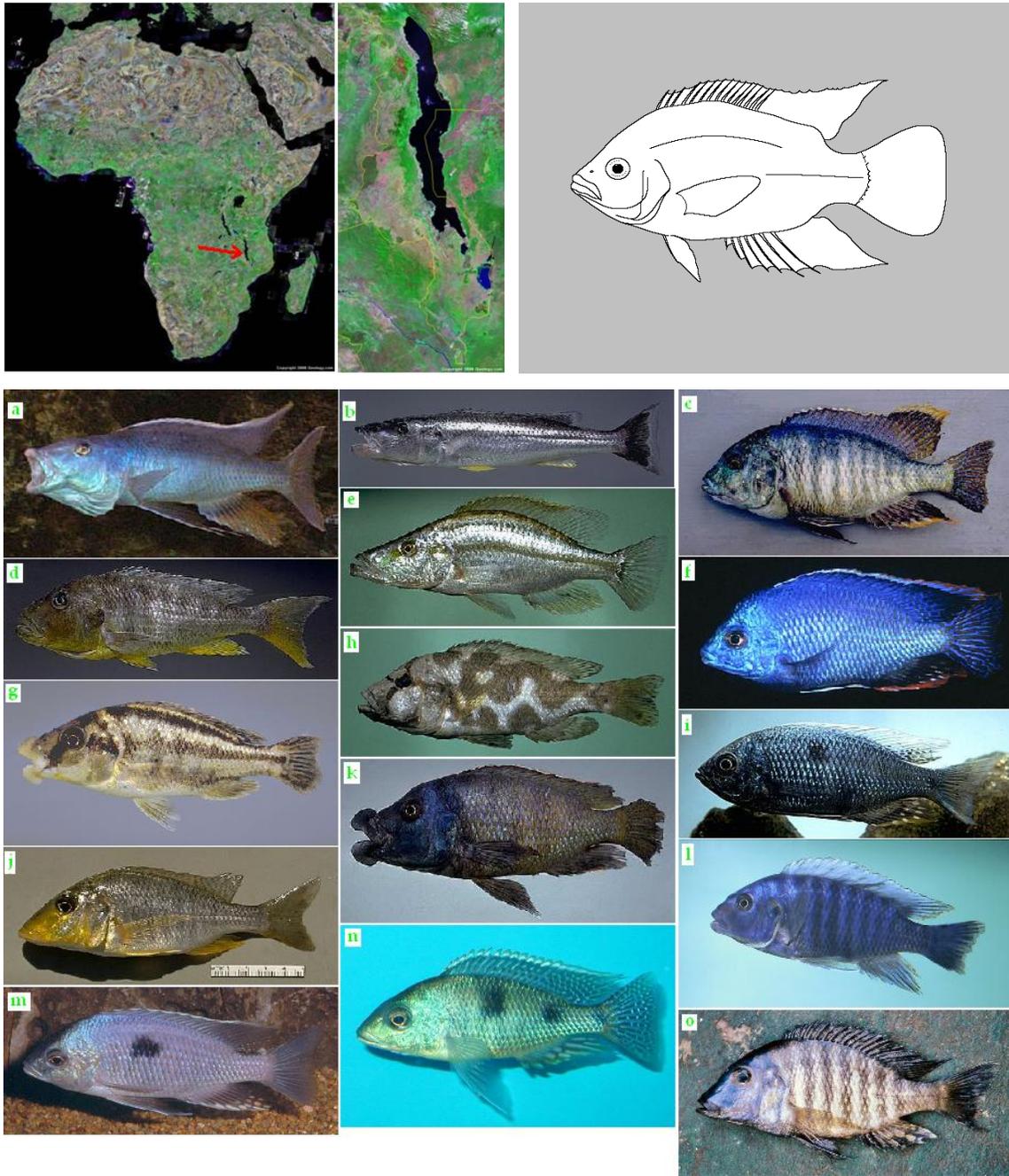


Fig. 1.3.3.1b. (top left) Lake Malawi, one of the Great African Rift lakes. (top right) The most salient morphological trait states that define a cichlid are broken lateral line and one (instead of two) nostrils on each side of the head; there are also many other cichlid-specific traits. (bottom) A sample of lake Malawi cichlids. a) *Champsocromis caeruleus*, a pursuit predator. b) *Rhamphochromis esox*. The species of *Rhamphochromis* are pursuit predators. c) *Trematocranus placodon* feeds principally on snails. d) *Buccochromis rhoadesii*. A predatory, fish-eating species. e) *Dimidiochromis compressiceps*, an ambush

predator that eats whole small fish. f) *Protomelas dejunctus* feeds on plankton and algae. g) *Cheilochromis euchilus* sucks out aquatic insects. h) *Nimbochromis livingstonii* is a predator that plays dead. i) *Copadichromis chrysonotus* feeds on zooplankton. j) *Taeniolethrinops praeorbitalis* digs small invertebrates from the sand. k) *Placidochromis milomo* harvests algae attached to hard substrates. l) *Petrotilapia tridentiger* combs loose tiny organisms from the strands of algae. m) *Copadichromis pleurostigma* feeds on zooplankton. n) *Tramitichromis intermedius* feeds on insect larvae and other soft invertebrates. o) *Lethrinops longipinnis* feeds mainly on chironomid larvae.



Fig. 1.3.3.1c. A tiny sample from the diversity of beetles.

This pattern obviously reflects a very uneven pace of cladogenesis in different lineages. Indeed, in terms of anagenesis, all extant species are equally old, as they are all descendants of LUCA. In contrast, in terms of cladogenesis the ages of extant species vary from 400 Ma and perhaps less to less than 10000 years. In fact, we will see in Chapter 2.6 that speciation is an ongoing process. The distribution of extant species by the number of their neighbors within the space of genotypes probably looks as in Fig. 1.3.3.1d. Certainly, most of species reside within densely populated regions of the space of genotypes, although there is a number of isolated clusters which contain only a small number of species (Fig. 1.3.3.1a).

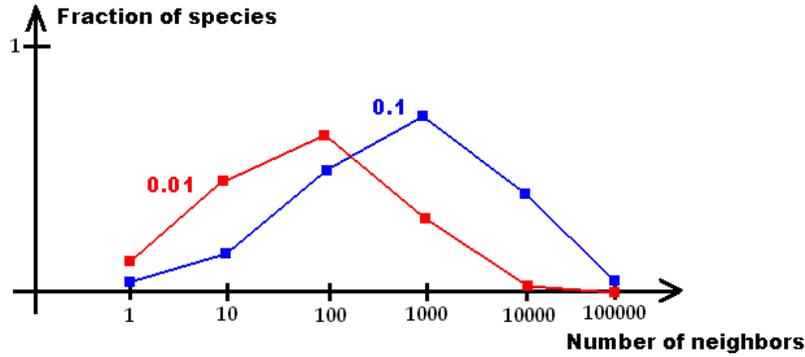


Fig. 1.3.3.1d. Distributions of the extant species by the number of their neighbors, within the space of genotypes, with genetic distances less than 0.01 and less than 0.1. I made these distributions up, because could not find the necessary data, but I am sure they look more or less like this.

Because evolution is primarily divergent (Section 1.1.1), pattern of occupancy of the space of genotypes by extant species reflects the age of their lineages, counting from the last cladogenesis. Because, very roughly, genetic distance of 0.01 accumulates in 1 Ma of independent evolution, extant biodiversity is dominated by species that originated less than ~10 mya. Indeed, after a cladogenesis, a lineage goes extinct in 10 Ma with probability >90%. As a result, the number of lineages whose descendants are represented among extant organism rapidly declines when we move deeper in the past (Fig. 1.3.3.1e). We can conclude that, despite the continuity of life since LUCA, there is a rapid turnover at the species level, due to continuous cladogenesis and extinction.

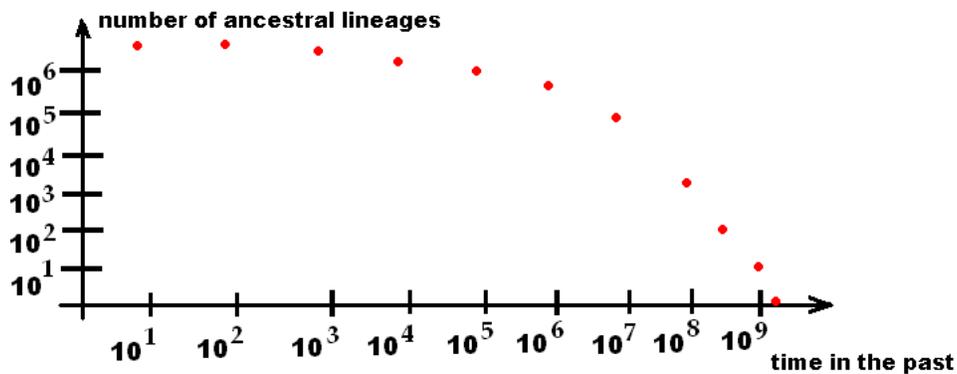


Fig. 1.3.3.1e. The number of lineages that existed at different moments in the past, which left some extant descendants. Again, this graph is only an approximation.

### 1.3.3.2. Biogeography

We already saw that distribution of species on the face of the Earth is strongly affected by their evolutionary histories (Sections 1.1.1.7, 1.1.2.5 and 1.1.2.6; Figs. 1.1.3.6e,f). Ranges of species change due to vicariance, dispersal, and local extinction, and these processes occur simultaneously with anagenesis and cladogenesis. The range of a species with limited dispersal often does not include all areas where it could thrive, as demonstrated by successive invasions. Generally, ranges of different species are more similar when the species are tightly related to each other. As a result, morphologically and ecologically similar species that share only a distant common ancestor may have very different ranges (Fig 1.3.3.2a).

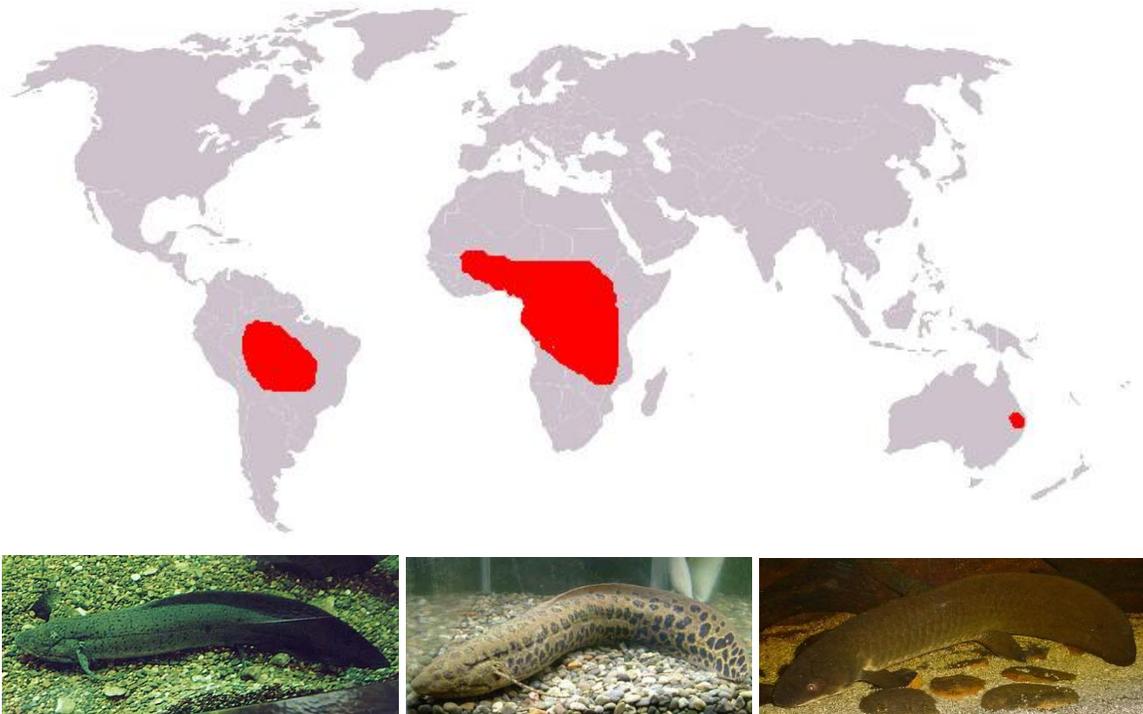


Fig. 1.3.3.2a. Ranges of the only six extant lungfishes: South American lungfish *Lepidosiren paradoxa* (left), four species of African lungfishes *Protopterus* (*P. annectens*, middle), and Australian lungfish *Neoceratodus forsteri* (right). The global distribution of extant lungfishes reflects geological processes that occurred during the last 400 Ma, as well as extinction of many members of this clade.

Similarity of ranges within a clade of tightly related species, such as members of a species flock (Section 1.1.2.5), reflects limited dispersal in the course of diversification of the clade and the lack of recent vicariant events in its area of endemism. In contrast, similarity between areas of endemism of distant clades, a phenomenon called provincialism, may reflect more distant geological history. Although the areas of endemism of different clades only rarely coincide exactly, the degree of their congruence is often rather high. Thus, the Earth could be subdivided into a number of biogeographical regions (provinces), whose boundaries separate areas of endemism of many different clades. These boundaries, due to ancient vicariant events and limited dispersal afterwards may still be fuzzy, because on geological times few barrier are capable to prevent dispersal completely (Fig. 1.3.3.2b).



Fig. 1.3.3.2b. Global biogeographical regions of terrestrial life, recognized on the basis of overall similarity of the biotas of different areas. Further subdivisions within these regions are also possible.

A famous example of a definite boundary between regions is Wallace line, which separates Oriental and Australian regions and areas of endemism of a number of terrestrial clades (Fig. 1.3.3.2c). This line corresponds to deep waters between Asian and Australian continental shelves. Thus, even when the ocean level dropped by over 100m

during glaciations, there were no land bridges across the Wallace line, and dispersal remained limited. We have seen that more recent vicariant events, such as those that separated Caribbean and Pacific marine biotas (Fig. 1.1.2.7a), leave a rather different footprint on the interrelationships of the biotas at the opposite sides of the barrier.

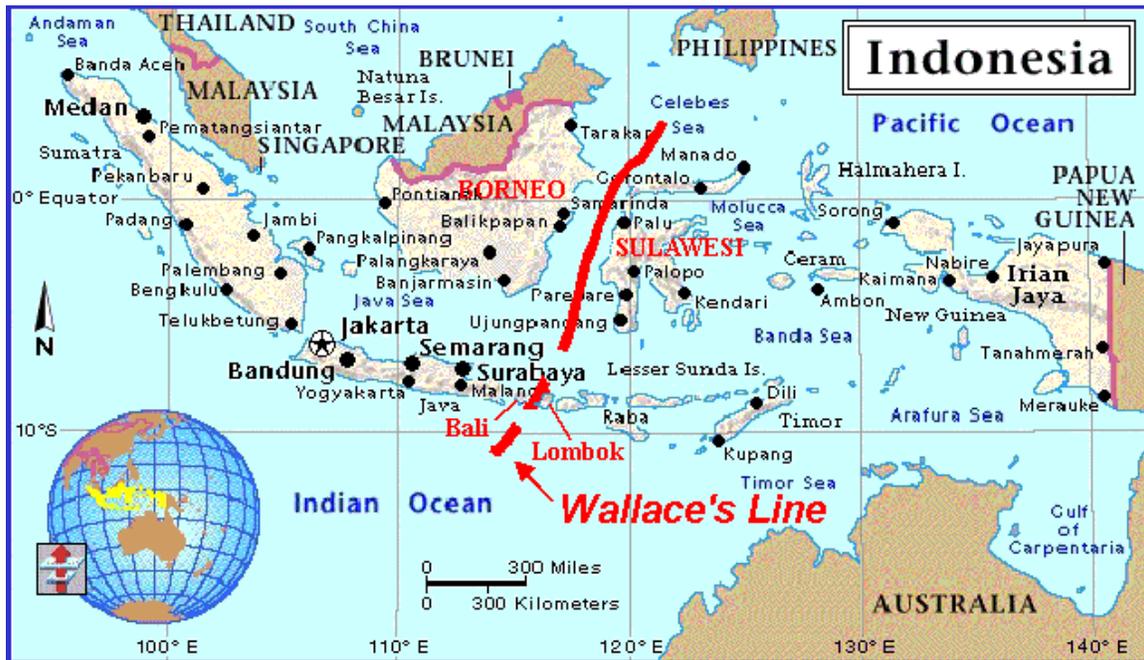


Fig. 1.3.3.2c. Wallace line.

Some salient patterns in distributions of extant species may be due to rather complex successions of events. For example, a striking similarity between many plant and animal species from Eastern Asia and Eastern North America is known since times of Carl Linneus. Analogously to the Caribbean and the Pacific marine biotas, Eastern Asia and Eastern North America floras contain rather similar species, that diverged over 10 mya, in over 100 clades (Fig. 1.3.3.2d). However, in contrast to the case of the Isthmus of Panama, Eastern Asian and Eastern North American species do not always form sister pairs, as more recent within-continent divergence also occurred in a number of cases. Disjunct Eastern Asian - Eastern North American distributions of many clades apparently is a relict of their wider distributions during the maximum development of the temperate forests in the Miocene. After this, local extinction of many elements of the temperate

flora in western North America and in Europe during the Pliocene and the Quaternary led to the present distributional pattern.

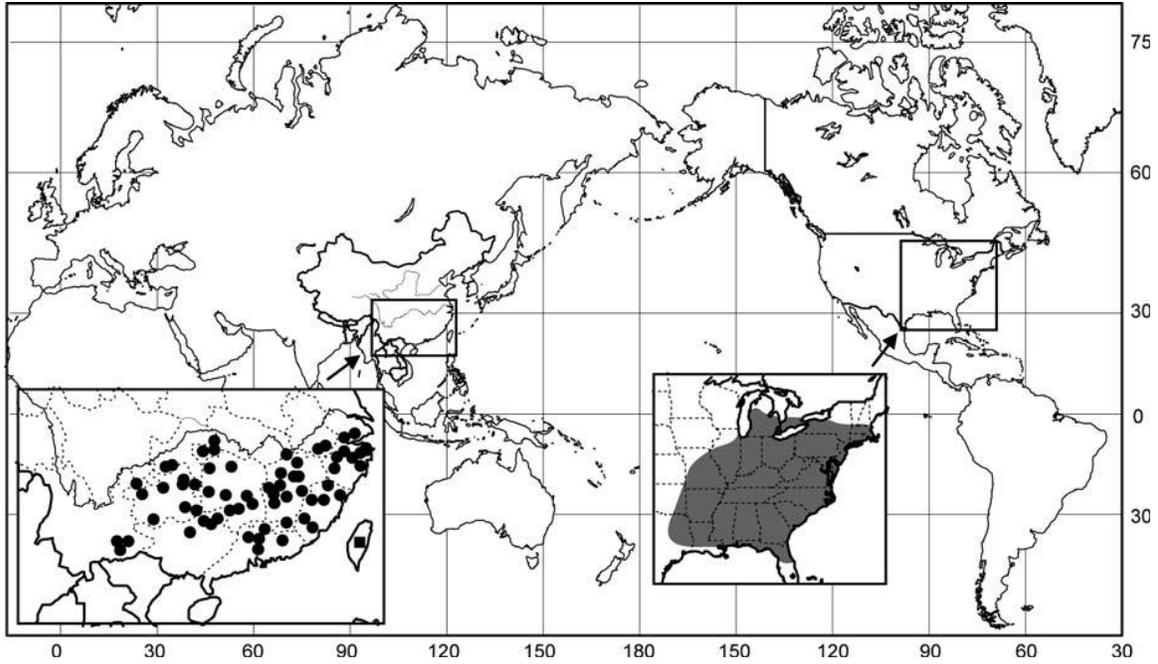


Fig. 1.3.3.2d. (top) Disjunct astern Asian - Eastern North American distribution of the plant genus *Sassafras* with two Asian and one American species. Two pairs of tightly related species from these areas: (middle) *Panax ginseng* (Asia) and *P. quinquefolius* (America), and (bottom) *Liriodendron chinense* (Asia) and *L. tulipifera* (America). (*Annual Review of Ecology and Systematics* 30, 421, 1999; *Plant Systematics and Evolution* 267, 191, 2007).

As any pattern which emerged in the process of slow, gradual changes, biogeographical distributions of species are rather vulnerable to disturbances, due to both extinction and introduction, deliberate or accidental, of exotic species. To a large extent, geography of life has already been changed irreversibly. There are thousands of exotic species of plants and animals that already became firmly established in new areas due to recent invasions, often with disastrous consequences to native biotas (Fig. 1.3.3.2d).



Fig. 1.3.3.2d. (left) *Lythrum salicaria* (Purple loosestrife), introduced to the northeastern U.S. and Canada in the 1800s, for ornamental and medicinal use. (center) *Boiga irregularis* (Brown tree snake), accidentally introduced from its native range in the South Pacific to Guam around 1950. (right) *Mnemiopsis leidyi*, a ctenophore accidentally introduced in the Black Sea around 1980.

### 1.3.3.3. Environments and ecosystems

Global environment was never stable in the past (Section 1.2.4), and the history of its changes provides the necessary context for understand the present conditions. The Pliocene-Quaternary Ice Age we live in begun 2.58 mya and led to establishment of permanent ice sheets over Antarctica and probably Greenland and fluctuating ice sheets

elsewhere. There were ~80 glacial cycles during this time, of durations between 40 and 100 Ka. During cold phases of these cycles (glacial periods), ice sheets covered large parts of Europe, Siberia, and North America. Warm phases (interglacial) were shorter than glacial periods. It is not entirely clear what led to these cycles, although Milankovich cycles, and changes in atmospheric composition and ocean currents were probably important. Dynamics of global temperature in the course of the last million of years were reconstructed with good confidence from data on  $\delta^{18}\text{O}$  (Fig. 1.2.4.1b) and  $\text{CO}_2$  concentration (Fig. 1.3.3.3a) in Antarctic ice.

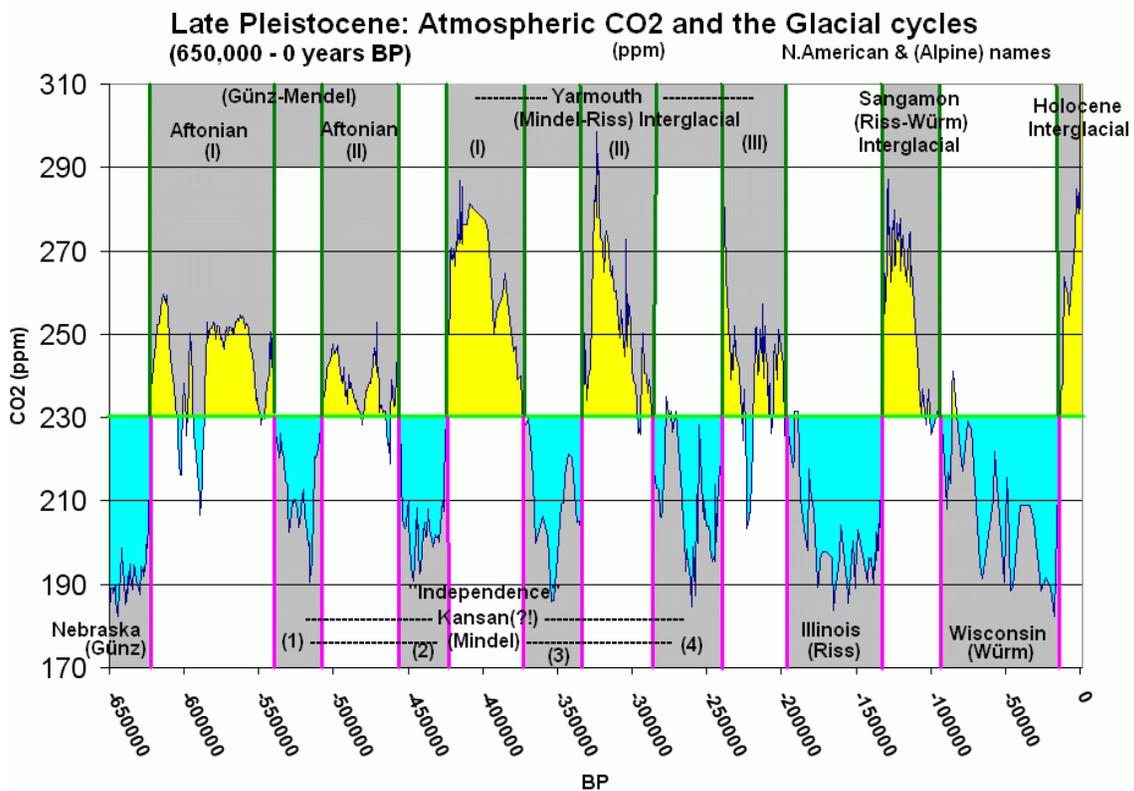


Fig. 1.3.3.3a. Glacial cycles during the last 0.65 Ma, as represented by atmospheric  $\text{CO}_2$  measured from ice cores ([http://en.wikipedia.org/wiki/Timeline\\_of\\_glaciation](http://en.wikipedia.org/wiki/Timeline_of_glaciation)).

The last glacial period started ~100,000 and ended ~12,000 years Before Present (BP). During that time, large areas were covered with ice sheets, polar deserts, tundras, and steppe-tundras (Fig. 1.3.3.3b). We are living in the interglacial, known as Holocene epoch (Fig. 1.2.4.5a) that followed the last glaciation. In the course of the Holocene,

climate was fairly stable (Fig. 1.2.4.1b), although in the last decades the global temperature begun to rise (Fig. 1.3.3.3c). This rise is probably caused primarily by the increased concentration of CO<sub>2</sub> in the atmosphere (Fig. 1.3.3.3c), due to human activities. Atmospheric concentration of CO<sub>2</sub> exceeded 2000 ppm during the Eocene (Fig. 1.2.4.4b), and the global temperature at that time was ~5C higher than currently (Fig. 1.2.4.1b), with no large ice sheets present anywhere.

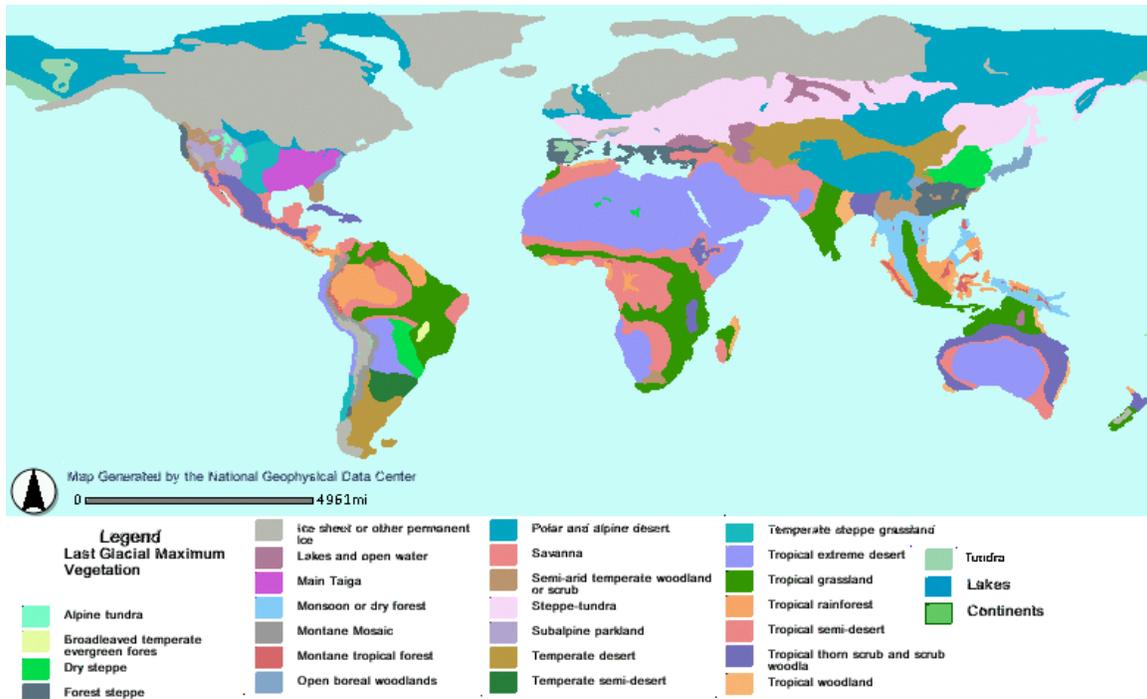


Fig. 1.3.3.3b. Map of vegetation during the last glacial maximum, ~18,000 years BP ([http://en.wikipedia.org/wiki/File:Last\\_glacial\\_vegetation\\_map.png](http://en.wikipedia.org/wiki/File:Last_glacial_vegetation_map.png)).

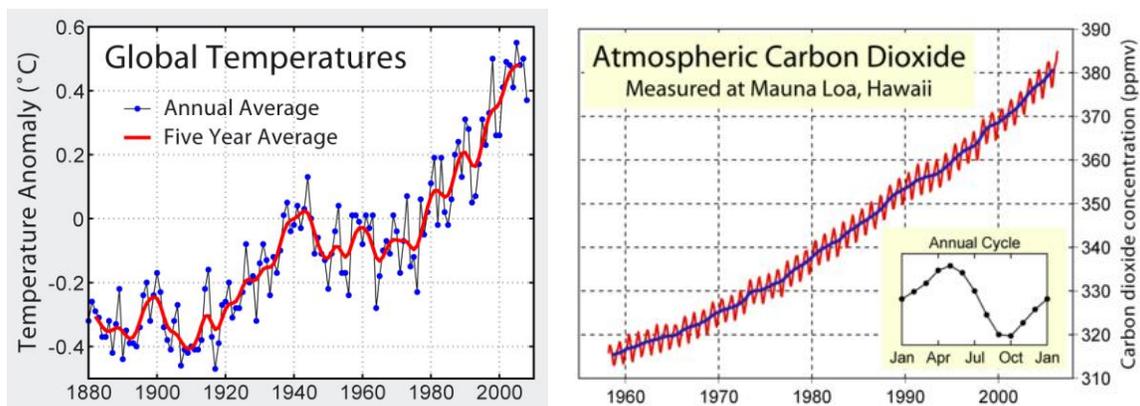


Fig. 1.3.3.3c. Recent dynamics of the global temperature and of the atmospheric concentration of CO<sub>2</sub> ([http://en.wikipedia.org/wiki/Global\\_warming](http://en.wikipedia.org/wiki/Global_warming)).

Obviously, ecosystems throughout the Globe experienced major changes of the abiotic conditions since the onset of the Holocene. This is especially the case for high latitudes in the Northern hemisphere, much of which were covered by ice, polar deserts and steppe-tundras until ~10,000 bp, indicating that the current ecosystems there are very young (Fig. 1.3.3.3d). This may be one of the reasons of a relatively small number of species and low productivity in high-latitude ecosystems, compared to that in the tropics.

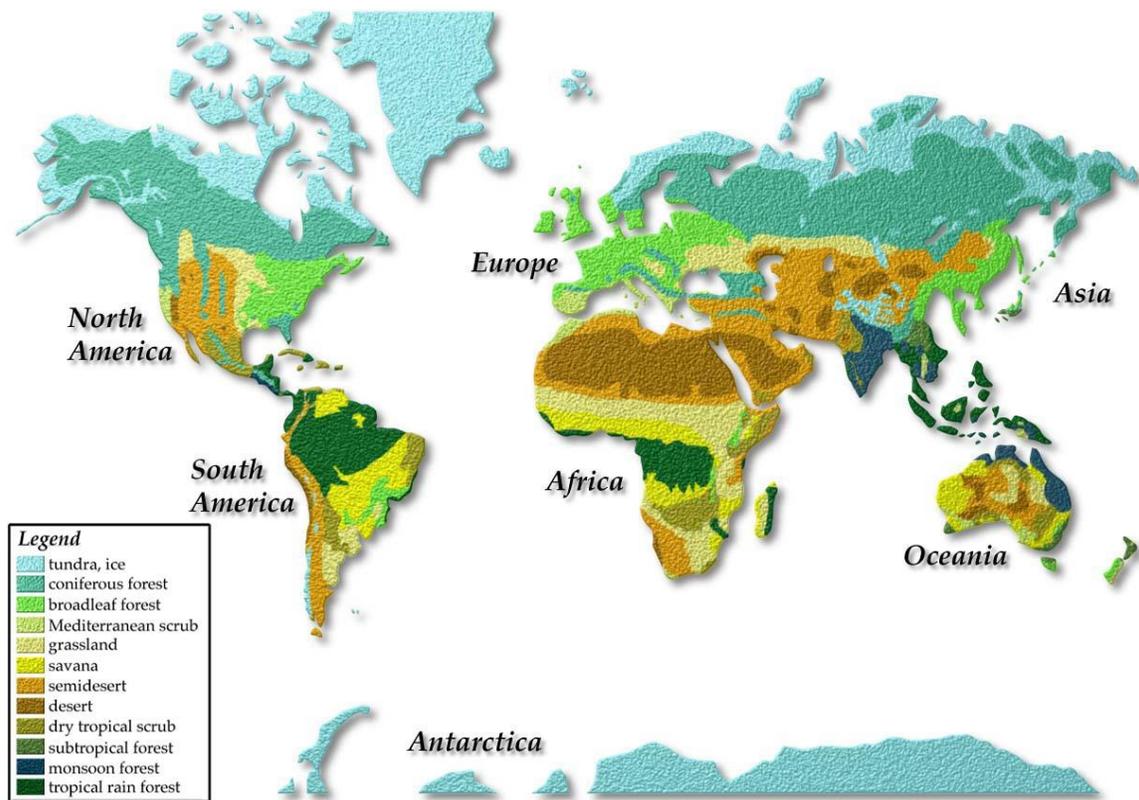


Fig. 1.3.3.3d. Map of the current World vegetation; compare to Fig. 1.3.3.3b (<http://www.miamisci.org/ecolinks/img/mapbiospherebig.jpg>).

However, tropical ecosystems were also not immune to the influences of recent climate changes. For example, a continuous 48,000-year-long paleoecological record from a Neotropical lower montane cloud forests (at elevations 1300-2000 m) reveals a

consistent forest presence and a glacial-period cooling of  $\sim 5^{\circ}$  to  $9^{\circ}\text{C}$ . After 30,000 years of compositional stability, a steady turnover of species marks the 8000-year-long transition from the last glacial period to Holocene conditions (Fig. 1.3.3.3e). Deep understanding the impact of past changes of the environment and evolution of species on ecosystems must be based on theoretical analysis and will be treated in Chapter 3.4.

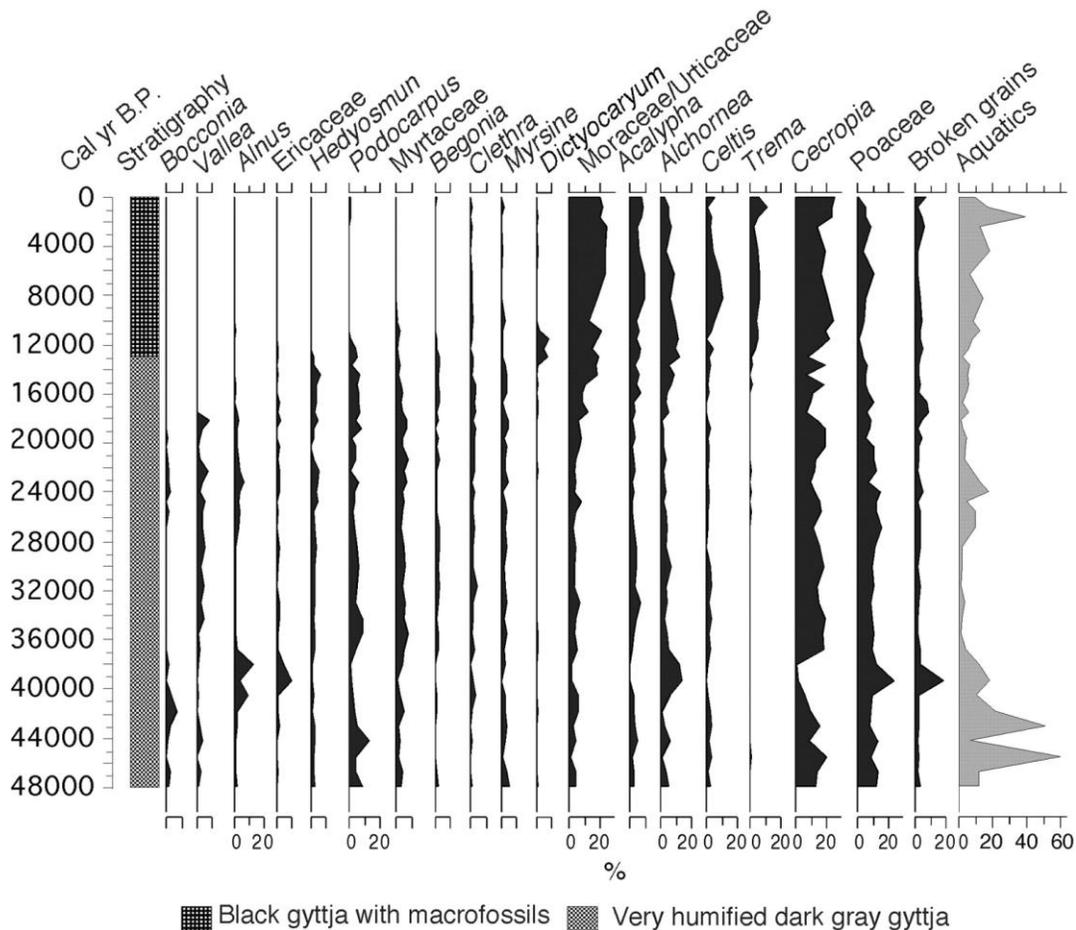


Fig. 1.3.3.3e. Percentage pollen diagram of selected taxa from Lago Consuelo forest, Peru. Taxa are ordered according to their apparent sensitivity to warming. Total taxa obtained from the site include 181 terrestrial pollen types, 4 aquatic pollen types, and 18 terrestrial fern and moss spore types (*Science* 303, 827, 2004).

#### 1.3.3.4. Ongoing mass extinction

We are living through a time of very rapid mass extinction. Initially, it mostly affected large animals (Fig. 1.3.3.4a). Fifty thousand years ago, ecosystems around the

globe were populated with large animals that are now extinct. In the course of the last 50,000 years, about 90 genera of mammals weighting over 44 kg went extinct. Only in Africa, megafauna mostly avoided extinction. It is plausible, but not certain, that prehistoric humans played the key role in this extinction, mostly due to hunting.

Recently, the impact of our species on the environment increased dramatically, due to industrialization and population growth. This increased the rate of extinction, not only due to hunting, but, more importantly, to habitat loss, pollution, and introduction of exotic species. The rate of the ongoing extinction, however, is not known precisely for the whole biodiversity. While extinction of a mammal or a bird will be documented with a high probability, many small species remain undescribed, especially in the tropics, and their extinction will go unnoticed. Between 1500 and 2009 CE, 875 extinctions have been documented by the International Union for Conservation of Nature and Natural Resources. However, the total number of extinctions during that time could be anything between 10,000 and 1,000,000 species. In the near future, climate change may become a major factor of extinction. Currently, a large fraction of species are endangered, *i. e.*, face a high risk of extinction in the near future. These include our closest relatives (Fig. 1.3.3.4b).

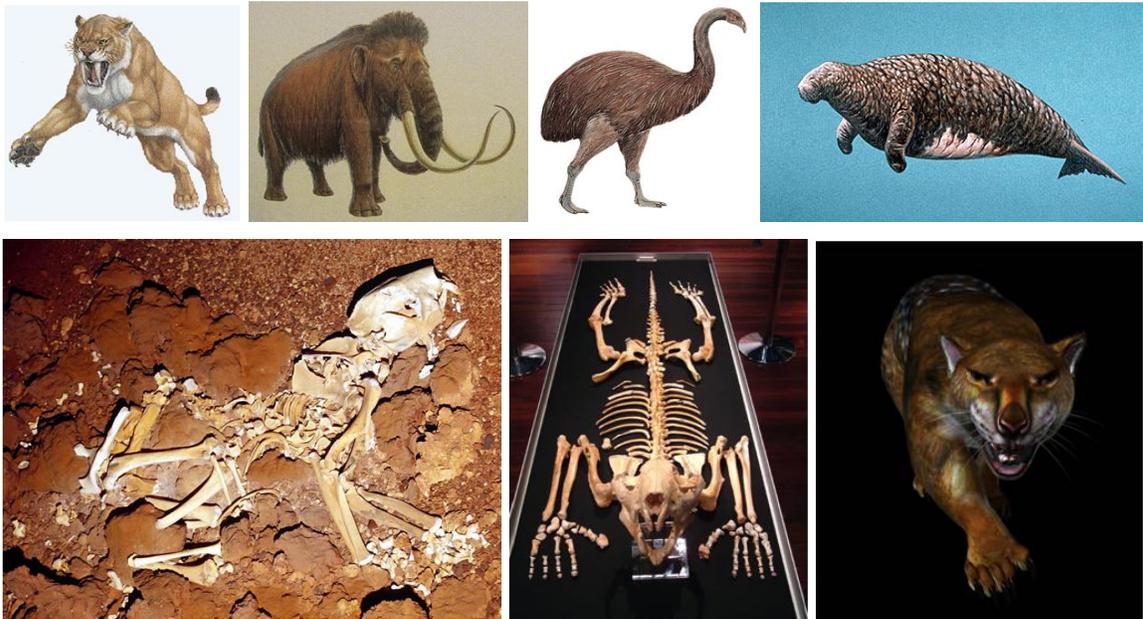




Fig. 1.3.3.4a. Some case of recent extinctions. (top, left to right) Several species of saber-toothed cats from the genus *Smilodon* all went extinct before 10 kya. Several species of mammoth, from the genus *Mammuthus* all went extinct before 3 kya. Ten species of *Moa* (family Diornithidae) all went extinct before 0.5 kya. Steller's sea cow *Hydrodamalis gigas*, discovered by Europeans in 1741 and hunted to extinction 27 years later. (middle row). Marsupial lion *Thylacoleo carnifex*, a member of extinct Australian megafauna, went extinct ~40 kya (bottom row, left to right). Other extinct marsupials, *Diprotodon optatum* (40 kya), *Palorchestes azael* (40 kya), *Zygomaturus trilobus* (20 kya), Tasmanian wolf *Thylacinus cynocephalus* (1936 CE) (*Annu. Rev. Ecol. Evol. Syst.* 37, 215, 2006).



Fig. 1.3.3.4b. Our closest living relatives, Bornean orangutan *Pongo pygmaeus* (~50,000 individuals in the wild), Sumatran orangutan *Pongo abelii* (~8,000), Western gorilla *Gorilla gorilla* (~350,000) Eastern gorilla *Gorilla beringei* (~15,000), Common chimpanzee *Pan troglodytes* (~150,000), and Bonobo *Pan paniscus* (~10,000) are all in danger of extinction in the XXI century. *Homo-Pongo* genetic distance 0.029; *Homo-Gorilla* is 0.017; and *Homo-Pan* is 0.013.

### History and perspectives

Like all branches of biology, paleontology is a rather young science. Famously, in 1726 a Swiss scholar Johann Jakob Scheuchzer described a fossil skeleton of a giant salamander as *Homo diluvii-testis*, assuming it to be remains of a human who drowned in

the Noah Flood. Only about a century later, the specimen was correctly interpreted by Georges Cuvier, who renamed it *Andrias scheuchzeri*. In Darwin's times, paleontology already was a full-fledged science, and its subsequent progress was enormous.

To a large extent, the progress in studies of fossils was due to old-fashioned discovery. Studies of the Cambrian got a major boost after Charles Doolittle Walcott found the Burgess Shale Lagerstätte in 1909. Ediacaran biota was discovered by Reg Sprigg in 1946. Of course, modern methods of analysis, including chemical methods that made it possible to identify biomarkers and physical methods used to study microfossils, are also very important. In 1980, applications of such methods allowed Luis and Walter Alvarez to propose a hypothesis, now almost universally accepted, that the KT extinction was caused by an extraterrestrial impact.

Since Darwin, direct paleontological studies of past evolution were complemented by indirect analyses based on morphology of extant species. These analyses played a major role in the early progress of evolutionary biology but, in retrospect, turned out to be remarkably prone to errors. Thus, introduction to molecular data was of key importance. Notably, in 1967 and 1975, Vincent Sarich, Mary-Claire King and Alan C. Wilson demonstrated that humans and chimpanzees are very close to each other genetically, implying their recent common ancestry. Modern phylogenetic methods and genome-level data led to tremendous progress since them, and with some important exceptions (Section 1.3.1.3), relationships among major clades of life has already been resolved. However, the exact driving forces of past evolution, both abiotic and biotic, often remain unclear. Still, it is now obvious that mass extinctions were due to drastic changes in abiotic conditions.

Some striking observations on the geographical distributions of plants and animals were made rather early. In 1716, a French Jesuit, Father Joseph Francis Lafitau, found American ginseng near Montreal, and recognized its similarity to Asian ginseng. Application of past evolution to studies of extant life were pioneered by Darwin and by Alfred Russel Wallace (1823-1913), a codiscoverer of evolution by natural selection, who described the boundary between the Oriental and Australian regions, which is now called the Wallace line. On a number of occasions, extant representatives of clades that were known only from the fossil record were unexpectedly encountered. In particular, a coelocanth *Latimeria chalumnae* was described in 1938 James Leonard Brierley Smith.

Today, evolutionary approaches permeate all biology, from creating murine models of human diseases to the analysis of invadability of ecosystems.

Perspectives. We can expect new fascinating discoveries, based on both direct and indirect data, to shed more light on details of the major evolutionary transitions in the past. However, it seems that the big picture has already been mostly revealed, and it is unlikely that too many statements made in this Chapter will need to be radically revised in the future. However, it is not clear how rapidly and to what extent the knowledge of the actual course of past evolution will translate into better understanding of its driving forces and mechanisms. Evolutionary perspective on extant biodiversity provides a solid basis for preserving what is still left of it, but whether the ongoing mass extinction will be stopped will depend on factors outside the domain of natural sciences.