1
MAJOR EVENTS IN THE HISTORY OF LIFE



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Cranium of Neandertal (Guattari 1) from Monte Circeo, Italy, approximately two-thirds natural size. (Photograph courtesy of R. Macchiarelli, Museo Nazionale Preistorico Etnografico, Rome.)

1.1 Early Life

1.1.1 Origin of Life

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Introduction

'All the organic beings which have ever lived on this Earth', wrote Charles Darwin in *On the Origin of Species by Means of Natural Selection*, 'may be descended from some one primordial form'. It is not known how this first ancestor came into being nor what its nature was. However, the presence of cyanobacteria-like microfossils in the 3.5 billion years old (Ga) Australian Apex sediments (Schopf 1993), deposited only a few million years after the end of the intense bombardment caused by the late accretion of planetesimals left over from the formation of the Solar System, demonstrates that the emergence and early diversification of life on Earth required no more than 500 million years. Together with the inclusions enriched in light isotopic carbon in 3.86 Ga samples from south-west Greenland (Mojzsis *et al.* 1996), these results show that a widespread, complex, and highly diversified Archaean microbiota was thriving soon after the Earth had cooled down and the influx of myriads of comets and asteroids had ceased.

It is unlikely that data on how life originated will be provided by the palaeontological record. There is no geological evidence of the environmental conditions on Earth at the time of the origin of life, nor any fossil register of the evolutionary processes that preceded the appearance of the first cells. Direct information is lacking not only on the composition of the terrestrial atmosphere during the period of the origin of life, but also on the temperature, ocean pH values, and other general and local environmental conditions which may or may not have been important for the emergence of living systems.

The lack of an all-embracing, generally agreed definition of life sometimes gives the impression that what is meant by its origin is defined in somewhat imprecise terms, and that several entirely different questions are often confused. For instance, until a few years ago the origin of the genetic code and of protein synthesis were considered synonymous with the appearance of life itself. This is no longer a dominant point of view; the discovery and development of the catalytic activity of RNA molecules has given considerable support to the idea of an 'RNA world'—a hypothetical stage, before the development of proteins and DNA genomes, during which alternative life forms based on ribozymes existed (Gesteland *et al.* 1999). This has led many to argue that the starting point for the history of life on Earth was the *de novo* emergence of the RNA world from a nucleotide-rich prebiotic soup. Others are more sceptical and believe that it lies in the origin of cryptic and largely unknown pre-RNA worlds. There is even a third group that favours the possibility that life began with the appearance of chemoautotrophic autocatalytic metabolic networks, lacking genetic material.

Despite the seemingly insurmountable obstacles surrounding the understanding of the origin of life (or perhaps because of them), there has been no shortage of discussion about how it took place. Not surprisingly, several alternative and even opposing suggestions have been made regarding how life emerged and what were the defining characteristics of the first organisms. While the classical version of the hypothesis of chemical evolution and primordial heterotrophy needs to be updated, it still provides the most useful framework for addressing the issue of emergence of life.

How can the origin of life be studied?

Of necessity, work on the origin of life should be regarded as enquiring and explanatory rather than definitive and conclusive. This does not imply that our theories and explanations can be dismissed as pure speculation, but rather that the issue should be addressed conjecturally, in an attempt to construct a coherent, non-teleological historical narrative (Kamminga 1991). It is unlikely that the origin of life will ever be described in full detail; at best a sketchy outline, consistent with conditions on the prebiotic Earth (such as its anoxic environment) and the physicochemical properties of the likely molecular precursors of living systems, will be constructed.

The attributes of the first living organisms are unknown. They were probably simpler than any cell now alive, and may have lacked not only protein-based catalysis, but perhaps even the familiar genetic macromolecules, with their ribose-phosphate backbones. It is possible that the only property they shared with extant organisms was the structural complementarity between monomeric subunits of replicative informational polymers, e.g. joining together a growing chain of residues in a sequence directed by preformed polymers. However, such ancestral polymers may not have involved nucleotides. Hence caution must be exercised in extrapo-

lating deep molecular phylogenies back into primordial times. Genome sequencing and analysis is becoming critical for understanding early cellular evolution, but it cannot be applied to events prior to the evolution of protein biosynthesis. Older stages are not yet amenable to this type of analysis, and the organisms at the base of universal phylogenies are cladistically ancient species, not primitive unmodified microbes.

Given the huge gap between the abiotic synthesis of biochemical monomers and the DNA/protein-based last common ancestor of all living systems, it is naive to attempt to describe the origin of life on the basis of available phylogenetic trees. Like a mangrove, the roots of universal evolutionary trees may be submerged in the muddy waters of a prebiotic broth—but how the transition from the non-living to the living took place is still unknown.

Heterotrophic or autotrophic origins of life?

Although the idea of life as an emergent feature of nature has been widespread since the nineteenth century, a major methodological breakthrough by A.I. Oparin and J.B.S. Haldane in the 1920s transformed the origin of life from a purely speculative issue to a workable research programme. This was based on the idea that the first life forms were the outcome of a slow, multistep process that began with the abiotic synthesis of organic compounds and the formation of a 'primitive soup'. There followed the formation of colloidal gel-like systems, from which anaerobic heterotrophs evolved that could take up surrounding organic compounds and use them directly for growth and reproduction.

Many of Oparin's original ideas have been superseded, but his hypothesis provided a conceptual framework for the development of this field. His proposal became widely accepted, not only because it is simpler to envision a heterotrophic organism originating from organic molecules of abiotic origin rather than from an autotroph, but also because laboratory experiments have shown how easy it is to produce a number of biochemical monomers under reducing conditions.

The first successful synthesis of organic compounds under plausible primordial conditions was accomplished by the action of electrical discharges acting for a week over a mixture of CH_4, NH_3, H_2, and H_2O; racemic mixtures of several proteinic amino acids were produced, as well as hydroxy acids, urea, and other organic molecules (Miller 1993). This was followed a few years later by the demonstration of rapid adenine synthesis by the aqueous polymerization of HCN. The potential role of HCN as a precursor in prebiotic chemistry is further supported by the discovery that the hydrolytic products of its polymers include amino acids, purines, and orotic acid (a biosynthetic precursor of uracil). A potential prebiotic route for the synthesis of cytosine in high yields is provided by the reaction of cyanoacetylene with urea, especially when the concentration of the latter is increased by simulating the conditions of an evaporating pond.

The ease with which amino acids, purines, and pyrimidines can form by reactions in a simple vessel strongly suggests that these molecules were components of the prebiotic broth. They would have been associated with many other compounds, such as urea and carboxylic acids, sugars formed by the non-enzymatic condensation of formaldehyde, a wide variety of aliphatic and aromatic hydrocarbons, alcohols, and branched and straight fatty acids, including some which are membrane-forming compounds. The list also includes several highly reactive derivatives of HCN, such as cyanamide (H_2NCN) and its dimer ($H_2NC(NH)NH–CN$), dicyanamide (NC–NH–CN), and cyanogen (NC–CN), which are known to catalyse polymerization reactions. Additional aspects of prebiotic chemistry have been reviewed by Miller (1993), Deamer and Fleischaker (1994), Chyba and McDonald (1995), and Brack (1998).

The synthesis of chemical constituents of contemporary organisms by non-enzymatic processes under laboratory conditions does not necessarily imply that they were either essential for the origin of life or available in the primitive environment. However, the significance of prebiotic simulation experiments is supported by the occurrence of a large array of protein and non-protein amino acids, carboxylic acids, purines, pyrimidines, hydrocarbons, and other molecules in the 4.6 Ga Murchison meteorite (a carbonaceous chondrite which also yields evidence of liquid water) (Miller 1993; Chyba and McDonald 1995). The presence of these compounds in the meteorite makes it plausible, but does not prove, that a similar synthesis took place on the primitive Earth—or is it simply a coincidence?

The evolutionary framework provided by Oparin's theory and methodology has allowed further development and refinement without losing the overall structure and internal coherence of his approach (Kamminga 1991). Several competing approaches to the study of the origin of life coexist today, including proposals for RNA or thioester worlds, for an extraterrestrial origin of the primitive soup's components, and for the role of submarine hot springs as sites for prebiotic chemistry (Chyba and McDonald 1995; de Duve 1995). All, however, are based on the assumption that abiotic organic compounds were a necessary precursor to the appearance of life.

Pyrite formation and the emergence of life

So far, the only serious rival to the heterotrophic theory stems from the work of Wächtershäuser (1988). Accord-

ing to this hypothesis, life began with the appearance of an autocatalytic two-dimensional chemolithotrophic metabolic system based on the formation of the highly insoluble mineral pyrite. Synthesis and polymerization of organic compounds took place on the surface of FeS and FeS_2 in environments that resemble those of deep-sea hydrothermal vents. Replication followed the appearance of non-organismal iron sulphide-based two-dimensional life, in which chemoautotrophic carbon fixation took place by a reductive citric acid cycle, or reverse Krebs cycle, of the type originally described for the photosynthetic green sulphur bacterium *Chlorobium limicola*. Molecular phylogenetic trees show that this mode of carbon fixation and its modifications (such as the reductive acetyl-CoA or the reductive malonyl-CoA pathways) are found in anaerobic archaebacteria and the most deeply divergent eubacteria, which has been interpreted as evidence of its primitive character (Maden 1995). But is the reverse Krebs cycle truly primordial?

The reaction $FeS + H_2S = FeS_2 + H_2$ is a very favourable one. It has an irreversible, highly exergonic (energy liberating) character with a standard free energy change $\Delta G^\circ = -9.23$ kcal/mol, which corresponds to a reduction potential $E^\circ = -620$ mV. Thus, the FeS/H_2S combination is a strong reducing agent, and has been shown to provide an efficient source of electrons for the reduction of organic compounds under mild conditions. Pyrite formation can produce molecular hydrogen, and reduce nitrate to ammonia, acetylene to ethylene, thioacetic acid to acetic acid, as well as more complex synthesis (Maden 1995), including peptide-bonds that result from the activation of amino acids with carbon monoxide and (Ni, Fe)S (Huber and Wächtershäuser 1998). Although pyrite-mediated CO_2 reduction to organic compounds has not been achieved, the fixation under plausible prebiotic conditions of carbon monoxide into activated acetic acid by a mixture of coprecipitated NiS/FeS has been reported (cf. Huber and Wächtershäuser 1998). However, in these experiments the reactions occur in an aqueous environment to which powdered pyrite has been added; they do not form a dense monolayer of ionically bound molecules or take place on the surface of pyrite.

None of the above experiments itself proves that both enzymes and nucleic acids are the evolutionary outcome of surface-bounded metabolism. In fact, the results are also compatible with a more general, modified model of the primitive soup in which pyrite formation is recognized as an important source of electrons for the reduction of organic compounds. It is thus possible that under certain geological conditions the FeS/H_2S combination could have reduced not only CO but also CO_2 released from molten magma in deep-sea vents, leading to biochemical monomers. Peptide synthesis, for instance, could have taken place in an iron and nickel sulphide system (Huber and Wächtershäuser 1998) involving amino acids formed by electrical discharges via a Miller-type synthesis. If the compounds synthesized by this process do not remain bound to the pyrite surface, but drift away into the surrounding aqueous environment, then they would become part of the prebiotic soup, not of a two-dimensional organism. Thus, the experimental results achieved so far with the FeS/H_2S combination are consistent with a heterotrophic origin of life.

The essential question in deciding between these two different theories is not whether pyrite-mediated organic synthesis can occur, but whether direct CO_2 reduction and synthesis of organic compounds can be achieved by a hypothetical two-dimensional living system that lacks genetic information. Proof of Wächtershäuser's hypothesis requires the demonstration of not only the tight coupling of the reactions necessary to drive autocatalytic CO_2 assimilitation via a reductive citric acid cycle, but also the interweaving of a network of homologous cycles which, it is assumed, led to all the anabolic pathways (Maden 1995).

Many original assumptions of the heterotrophic theory have been challenged by our current understanding of genetics, biochemistry, cell biology, and the basic molecular processes of living organisms. The view advocated here assumes that, even if the first living systems were endowed with minimum synthetic abilities, their maintenance and replication depended primarily on prebiotically synthesized organic compounds. An updated heterotrophic hypothesis assumes that the raw material for assembling the first self-maintaining, replicative chemical systems was the outcome of abiotic synthesis, while the energy required to drive the chemical reactions involved in growth and reproduction may have been provided by cyanamide, thioesters, glycine nitrile, or other high energy compounds (de Duve 1995; Lazcano and Miller 1996). This modified version of the classical theory of chemical evolution and primordial heterotrophy can be examined experimentally, and can be expected to generate additional lines of research.

Prebiotic chemistry and the 'primitive soup'

Although it is generally agreed that free oxygen was absent from the primitive Earth, there is no agreement on the composition of the primitive atmosphere; opinions vary from strongly reducing ($CH_4 + N_2$, $NH_3 + H_2O$, or $CO_2 + H_2 + N_2$) to neutral ($CO_2 + N_2 + H_2O$). In general, non-reducing atmospheric models are favoured by atmospheric chemists, while prebiotic chemists lean towards more reducing conditions, under which the abiotic syntheses of amino acids, purines, pyrimidines, and other compounds are very efficient.

The possibility that the primitive atmosphere was

non-reducing does not create insurmountable problems, since the primitive soup could still form. For instance, geological sources of hydrogen, such as pyrite, may have been available; in the presence of ferrous iron, a sulphide ion (SH^-) would have been converted to a disulphide ion (S^{2-}), thereby releasing molecular hydrogen (Maden 1995). It is also possible that the impacts of iron-rich asteroids enhanced the reducing conditions, and that cometary collisions created localized environments favouring organic synthesis. Based on what is known about prebiotic chemistry and meteorite composition, if the primitive Earth was non-reducing, then the organic compounds required must have been brought in by interplanetary dust particles, comets, and meteorites. Recent measurements suggest that a significant percentage of meteoritic amino acids and nucleobases could survive the high temperatures associated with frictional heating during atmospheric entry, and become part of the primitive broth (Glavin and Bada 1999).

This eclectic view, in which the prebiotic soup is formed by contributions from endogenous syntheses, extraterrestrial organic compounds delivered by comets and meteorites, and pyrite-mediated CO reduction, does not contradict the heterotrophic theory. Even if the ultimate source of the organic molecules required for the origin of life turns out to be comets and meteorites, recognition of their extraterrestrial origin is not a rehabilitation of panspermia (the hypothesis that life existed elsewhere in the universe and had been transferred from planet to planet, eventually gaining a foothold on Earth), but an acknowledgement of the role of collisions in shaping the primitive terrestrial environment.

The search for the primordial genetic polymers

There is no evidence of abiotically produced oligopeptides or oligonucleotides in the Murchison meteorite, but condensation reactions clearly took place in the primitive Earth. Synonymous terms like 'primitive soup', 'primordial broth', or 'Darwin's warm little pond' have led in some cases to major misunderstandings, including the simplistic image of a worldwide ocean, rich in self-replicating molecules and accompanied by all sorts of biochemical monomers. The term 'warm little pond', which has long been used for convenience, refers not necessarily to the entire ocean, but to parts of the hydrosphere where the accumulation and interaction of the products of prebiotic synthesis may have taken place. These include not only membrane-bound systems, but also oceanic sediments, intertidal zones, shallow ponds, freshwater lakes, lagoons undergoing wet-and-dry cycles, and eutectic environments (e.g. glacial ponds), where evaporation or other physicochemical mechanisms (such as the adherence of biochemical monomers to active surfaces) could have raised local concentrations and promoted polymerization.

It is difficult to estimate the rate of self-organization of these polymers into replicating systems, because the chemical steps are unknown. Whatever the time scale required for the appearance of an informational polymer, once formed it must have persisted at least long enough to allow its replication. If polymers formed by a slow addition of monomers, this process must have been rapid compared to rates of hydrolysis, especially if a considerable amount of genetic information was contained in the polymer. Self-replicating systems capable of undergoing Darwinian evolution must have emerged in a period shorter than the destruction rates of their components; even if the backbone of primitive genetic polymers was highly stable, the nitrogen bases themselves would decompose over long periods of time. In fact, the accumulation of all components of the primitive soup will be limited by destructive processes, including the pyrolysis of organic compounds in submarine vents. Large amounts of the entire Earth's oceans circulate through the ridge crests every 10 million years, facing temperatures of 350°C or more, and placing an upper limit to the time available for the origin and early diversification of life (Lazcano and Miller 1996).

The popular idea of a hot origin of life is founded largely on the basal position in molecular phylogenies of hyperthermophiles, which exhibit optimal growth temperatures of 80–110°C. Although this hypothesis is also consistent with the emergence of life on a turbulent, hot primitive Earth (which may or may not be true), it is merely an extrapolation of the growth temperature of extant thermophilic prokaryotes. Since most biochemicals decompose rather rapidly at temperatures of 100°C, prebiotic chemistry clearly supports a low-temperature origin of life. A high-temperature origin, under conditions such as those found in deep-sea vents, may be possible, but chemical stability arguments rule out any involvement of the purines, pyrimidines, sugar-phosphate backbone, or even most of the 20 amino acids used by life today: under such extreme conditions, their half-lives are a few seconds. Any theory arguing otherwise must explain not only how life originated under such conditions, but also how the evolutionary transition occurred from the hypothetical high temperature-resistant origin to extant biochemistry.

Bridge(s) to the RNA world

The primitive broth must have been a bewildering organic chemical wonderland in which a wide array of different molecules were constantly synthesized, destroyed, or incorporated into cycles of chemical transformations. Regardless of the complexity of the prebiotic environment, life could not have evolved in the absence

of a genetic replicating mechanism to guarantee the maintenance, stability, and diversification of its basic components under the action of natural selection.

The nature of the system that preceded the ubiquitous DNA-based genetic machinery of extant living systems is unknown, but it must have been endowed with some capacity for self-replication. There is experimental evidence for self-replication in some chemical systems which lack the familiar nucleic acid-like structure. These include replicative micelles and vesicles, and self-complementary molecules which result from the chemical reaction between an amino-adenosine derivative and a complex aromatic ester (cf. Orgel 1992). There are also prions, the infamous infectious agents associated with bovine spongiform encephalopathy (BSE, or 'mad cow disease') and several human neurodegenerative maladies, which may represent a case of phenotypic inheritance that propagate by changing the harmless conformation of a normal protein into an infectious isoform.

Although the above examples suggest that replication may be a widespread phenomenon, these systems do not exhibit heritability, i.e. they are considered autocatalytic but non-informational (Orgel 1992). Hence, they are probably not related to the origin of life. On the other hand, although the properties of RNA molecules make them an extremely attractive model for the origin of life, their existence in the prebiotic environment is unlikely. It is not clear that phosphate esters could have been involved in the first genetic material, and the self-condensation of formaldehyde (i.e. the formose reaction, which appears to be the only plausible route for the prebiotic synthesis of sugars) leads to a complex array of carbohydrates, of which ribose is a minor unstable component. Without phosphate and ribose, RNA molecules could not have formed in the primitive soup. Thus, it is possible that the RNA world itself was the end product of ancient metabolic pathways that evolved in unknown pre-RNA worlds, in which informational macromolecules with different backbones may have been endowed with catalytic activity, i.e. with phenotype and genotype also residing in the same molecules, so that the synthesis of neither protein nor related catalysts is necessary (Lazcano and Miller 1996).

The chemical nature of the first genetic polymers and the catalytic agents that may have formed the pre-RNA worlds are completely unknown and can only be surmised. Modified nucleic acid backbones have been synthesized, which either incorporate a different version of ribose or lack it altogether. Experiments on nucleic acid with hexoses instead of pentoses, and on pyranoses instead of furanose (Eschenmoser 1994), suggest that a wide variety of informational polymers is possible, even when restricted to sugar-phosphate backbones.

One possibility that has not been explored is that the backbone of the original informational macromolecules may have been atactic (e.g. disordered) kerogen-like polymers such as those formed in some prebiotic simulations. There are other possible substitutes for ribose, including open chain, flexible molecules that lack asymmetric carbons. One of the most interesting chemical models for a possible precursor to RNA involves the so-called peptide nucleic acids (PNAs), which have a protein-like backbone of achiral 2-amino-ethyl-glycine, to which nucleic acid bases are attached by an acetic acid (Nielsen 1993). Such molecules form very stable complementary duplexes, both with themselves and with nucleic acids. Although they lack ribose, their functional groups are basically the same as in RNA, so they may also be endowed with catalytic activity.

Although the identification of adenine, guanine, and uracil in the Murchison meteorite supports the idea that these bases were present in the primitive environment (Miller 1993; Chyba and McDonald 1995), it is probable that other heterocycles capable of forming non-standard hydrogen bonding were also available. The Watson–Crick base-pair geometry permits more than the four usual nucleobases, and simpler genetic polymers may not only have lacked the sugar-phosphate backbones, but may also have depended on alternative non-standard hydrogen bonding patterns. The search for experimental models of pre-RNA polymers will be rewarding but difficult; it requires the identification of potentially prebiotic components and the demonstration of their non-enzymatic template-dependent polymerization, as well as coherent descriptions of how they may have catalysed the transition to an RNA world.

Questions for future research

Even though considerable progress has been made in understanding the emergence and early evolution of life, major uncertainties remain. The chemistry of some prebiotic simulations is robust and supported by meteorite analyses, but the gap between these rudimentary experiments and the simplest extant cell is enormous. There is a range of issues relevant to the origin of life, many of which cut across different scientific fields. The geochemical environments under which prebiotic syntheses of biochemical monomers and their polymers could have taken place need to be characterized. Experimental systems to study polymer replication, sequestration of organic compounds, the energy sources that may have been employed by the first replicating systems, and the appearance of metabolic pathways all need to be developed.

The origin of the main features of the genetic code is not understood, but the discovery of the catalytic activity of RNA molecules and the development of novel RNA enzymes through *in vitro* evolution has given

considerable support to the idea that the primitive translation apparatus may have been shaped, at least in part, by interactions between amino acids of prebiotic origin and polyribonucleotides (Gesteland *et al*. 1999). If the current interpretation of the evolutionary significance of these and other properties of RNA molecules is correct, then one of the central issues that origin-of-life research must confront is the understanding of the processes that led from the primitive soup into RNA-based life forms. The search for simple organic replicating polymers will play a central role in this inquiry. Even if the appearance of life remains an elusive issue, redefining the questions that need to be addressed to understand how it took place is, in itself, an encouraging scientific achievement.

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1.1.2 Exploring for a Fossil Record of Extraterrestrial Life

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Introduction

While speculation about the possibility of life elsewhere in the Cosmos has been a persistent theme throughout the history of humankind, the last decade of the twentieth century has witnessed a number of important advances in our understanding of the nature and evolution of terrestrial life. These developments have opened up important new possibilities for the existence of living systems elsewhere in the Solar System (or beyond) and have spawned a new interdisciplinary science called 'astrobiology'—the study of the origin, evolution, distribution, and destiny of life in the Cosmos. This new discipline embraces the traditional field of exobiology, which focuses on the origin of life and early biosphere evolution, along with a newer sister discipline, exopalaeontology, which seeks evidence for a fossil record of ancient life or prebiotic chemistry in extraterrestrial materials, or from other planets in the Solar System.

An important legacy of the Apollo space missions was the development of a detailed cratering history for the moon. This led to the view that during early accretion, prior to ≈4.4 Ga, surface conditions on Earth were unfavourable for the origin of life (Chang 1994). As a consequence of frequent giant impacts, magma oceans could have been widespread over the Earth's surface, and volatile compounds, including water and the biogenic elements needed for life's origin, would have been lost to space. Models of early accretion suggest that during the interval 4.4–4.2 Ga impact rates and object sizes declined to a point where the water (and associated organics) delivered to the Earth by volatile-rich impactors (e.g. comets) was retained. A stable atmosphere and oceans probably developed during this time, providing the first suitable environments for prebiotic chemical evolution and the origin of life.

Models also suggest that early biosphere development overlapped with one or more late, giant impacts that were large enough to volatilize the oceans and perhaps sterilize surface environments (Sleep *et al.* 1989). Such events would have frustrated the development of the early biosphere and may have even required that life originate more than once. The most protected habitat during this early period would have been the deep subsurface.

Discoveries of ≈3.45 Ga cellular microfossils from cherts in volcanic sequences in Western Australia (Schopf 1993), and possible 3.86 Ga chemofossils (carbon isotopic signatures) from phosphate-rich metasediments in Greenland (Mojzsis *et al.* 1996) indicate that once the conditions necessary for life's origin were in place, life arose very quickly, perhaps in a few hundred million years or less. This observation significantly improves the possibility that life originated on Mars, or elsewhere in the Solar System where habitable zones of liquid surface water were more ephemeral features of early planetary evolution.

While recent discoveries in Precambrian palaeontology have pushed back the dates for the oldest fossils, molecular phylogenies have also provided important clues about the origin and early evolution of life on Earth, based on the historical record preserved in the genomes of living organisms. Comparisons of genetic sequences in 16S ribosomal RNA indicate that terrestrial life is subdivided into three major domains: the Archaea, the Bacteria, and the Eukarya. It is also apparent that the vast proportion of biodiversity on Earth is microbial. Higher forms of multicellular life appeared quite late in Earth history and make up only a tiny fraction of the total number of species. The deepest branching lineages in the RNA tree are high-temperature forms that utilize reduced inorganic substrates, like sulphur or hydrogen. This suggests that the last common ancestor of life on Earth was a high-temperature ('thermophilic') chemotroph, a view that is consistent with the higher rates of heat flow, volcanism, and frequent impacts that prevailed on the early Earth. However, the RNA tree may reveal little about life's origin (see Section 1.1.1). The thermophilic properties of the most deeply rooted lineages may simply be a legacy of late giant impacts that eliminated all but the highest temperature species.

Possible extant life on Mars and Europa

The discovery of an extensive subsurface biosphere on the Earth opened up exciting new possibilities for the existence of habitable zones elsewhere in the Solar System. On Earth, subsurface habitats harbour many species that are capable of synthesizing organic molecules from simple inorganic substrates. The subsurface is the most compelling environment for extant Martian life because of the possibility that a deep subsurface ground water system may exist at several kilometres depth (Carr 1996). In addition, results from the Galileo mission provide support for the existence of a subsurface ocean beneath the crust of Europa, one of Jupiter's moons. It is postulated that heating of the moon's interior by tidal friction could sustain a subcrustal ocean of liquid water, and sea floor hydrothermal systems (Belton *et al.* 1996). Indeed, the complexly fractured and largely uncratered surface of Europa (Fig. 1.1.2.1) indicates an active ice 'tectonics' involving the periodic upflow of ice-brines from beneath the Europan crust. It is possible that where water welled up from below, it carried life forms or prebiotic chemistry from the underlying ocean and incorporated these materials into surface ices. Terrestrial microbes are known to retain viability at subzero temperatures by exploiting thin films of brine on grain surfaces in permafrost soils. Could viable organisms be present within similar ice-brine environments on Europa? Viability arguments aside, ice could also provide a means for the prolonged cryopreservation of organic materials, accessible to robotic landers.

Exploring for an ancient Martian biosphere

The Viking lander missions showed the present surface environment of Mars to be unfavourable for life due to the absence of liquid water, intense UV radiation, and oxidizing soils. At the same time, images obtained from Mars orbit revealed the early planet to be more Earth-like, with a broad range of surface environments suitable for life. It is likely that habitable environments disappeared from the surface ≈3.8 Ga as Mars began to lose its atmosphere (Farmer and Des Marais 1999). If extant life exists on Mars today, it is likely to be in deep subsurface environments that will be inaccessible to robotic platforms. Deep subsurface drilling will likely require a human presence. However, if life once existed in surface environments, it is likely to have left behind a fossil record in ancient sediments now exposed at the surface. Such deposits could be accessed during the robotic phase of exploration. This simple concept underlies the basic rationale of the present Mars exploration programme.

Studies of the Precambrian fossil record on Earth, and of modern microbial systems that are analogues for those on the early Earth and Mars, provide a conceptual framework for guiding the search for a fossil record on Mars. An understanding of how preservation varies between different groups of microorganisms over extremes of the environment, and how postdepositional, diagenetic changes affect the long-term preservation of microbial biosignatures in rocks, is crucial (Farmer and Des Marais 1999). Such studies allow the formulation of

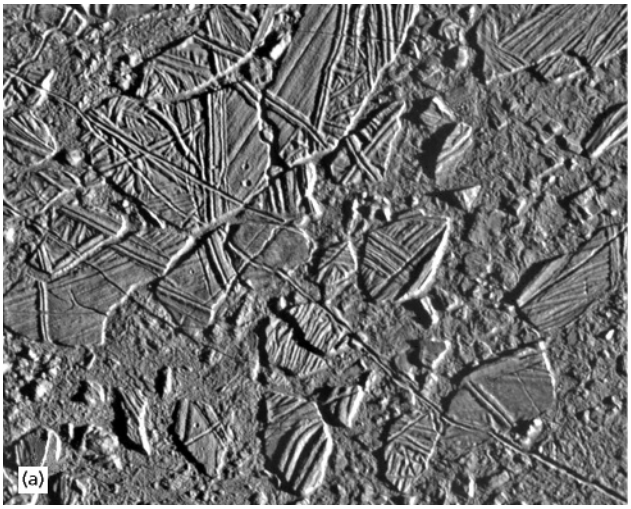




Fig. 1.1.2.1 (a) Galileo orbiter image of the surface of Europa, one of the moons of Jupiter. The surface crust is composed of water ice that has been fractured into irregular blocks. The fracture patterns suggest that the crust was mobilized by a layer of subsurface water which flowed up from below, filling fractures between blocks as they separated. Such observations support the view that Europa once had, and perhaps still has, a subcrustal ocean of liquid water that could sustain life or prebiotic chemistry. The smallest features visible in this image are about 20 m across. (b) Close-up of the surface of Europa showing a complex network of ridged fractures originally formed when plates of ice crust pulled apart. Many ridge segments were later offset along strike–slip faults. The large ridge in the lower right corner of the image is about 1 km across. (Photographs by courtesy of NASA.)

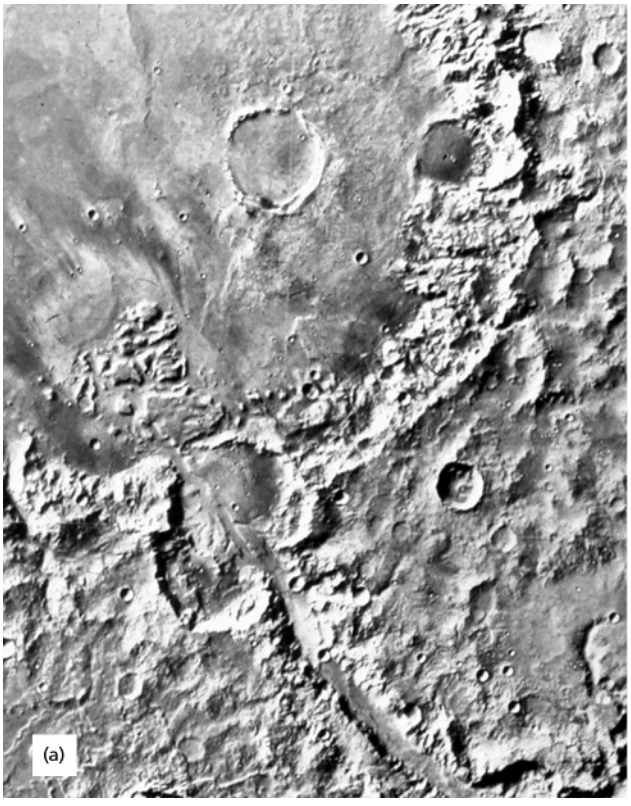
'rules' of preservation that help optimize strategies to explore for past life on Mars and other planetary bodies, such as Europa.

As with Earth-based palaeontology, site selection is crucial for the successful implementation of Mars missions designed to explore for past life. Preservation is a selective process that is strongly dependent upon the biogeological environment. Studies of microbial fossilization reveal that the rapid entombment of microorganisms and their by-products by fine-grained, clay-rich sediments and/or chemical precipitates is of singular importance in enhancing preservation. Favourable geological environments are those where microbial systems coexist with high rates of fine-grained detrital sedimentation, and/or aqueous mineral precipitation. Examples include rapidly mineralizing hydrothermal systems (below the upper temperature limit for life), terminal lake basins (where chemical sediments such as evaporites, fine-grained lacustrine sediments, and sublacustrine cold spring tufas are deposited), and mineralizing soils (e.g. hard-pans, including calcretes, ferracretes, and silcretes). Even if life did not develop on Mars, this exploration strategy is still important because the same sedimentary environments could preserve a record of prebiotic chemistry similar to that which spawned the development of life on Earth. This early prebiotic history has been lost from the terrestrial record.

Mars may preserve the most complete record of early events of planetary evolution anywhere in the Solar System. The 4.56 Ga age of Martian meteorite ALH 84001 (McKay *et al.* 1996) indicates that the ancient, heavily cratered highlands of Mars contain a crustal record extending back to the earliest period of planetary evolution. On Earth, comparably aged crustal sequences have been destroyed by tectonic cycling, metamorphism, weathering, and erosion. In contrast, Mars never developed a plate tectonic cycle and extensive water-mediated weathering and erosion was probably limited to the first billion years or so of the planet's history. Geomorphic features suggest that surface hydrological systems were active until near the end of heavy bombardment (≈3.8 Ga), after which time liquid water quickly disappeared from the surface, presumably as a result of the loss of the Martian atmosphere (Carr 1996).

The preservation of fossil biosignatures is favoured when organisms or their by-products are incorporated into low permeability sedimentary deposits (producing a closed chemical system during diagenesis) of stable mineralogy (promoting a prolonged residence time in the crust). Chemical sediments composed of silica, phosphate, and carbonate, along with fine-grained, clay-rich detrital sediments and water-deposited volcanic ash, are especially favourable lithologies for long-term preservation. This is illustrated by the fact that on Earth most of the Precambrian record is preserved in such lithologies.

Many potential sites for a fossil record have been



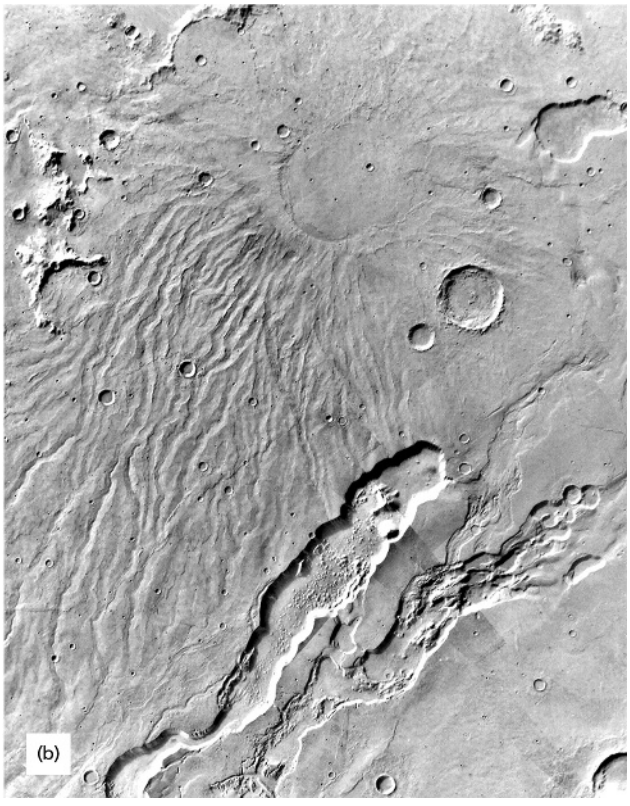


Fig. 1.1.2.2 (a) Gusev Crater, Mars. A large river canyon to the south (Ma'adim Vallis) drained into this ≈150 km diameter crater, depositing a delta where it entered the crater. Geological studies suggest a prolonged hydrological history for this region of Mars, with the Gusev Crater being the site of an ancient palaeolake system. (b) The slopes of Hadriaca Patera, an ancient Martian volcano, show channels radiating downslope, away from the caldera rim (caldera ≈75 km across). These small channels are interpreted to be the result of pyroclastic flows, the channels being subsequently enlarged by sapping flow. The basal slope of Hadriaca Patera was later eroded by outfloods of subsurface water which carved Dao Vallis, a large channel located near the bottom of the photograph (channel ≈45 km wide). The association of subsurface water and a heat source (the subsurface magma that produced the volcano) suggests the potential for sustained hydrothermal activity in this region. (Photographs by courtesy of NASA.)

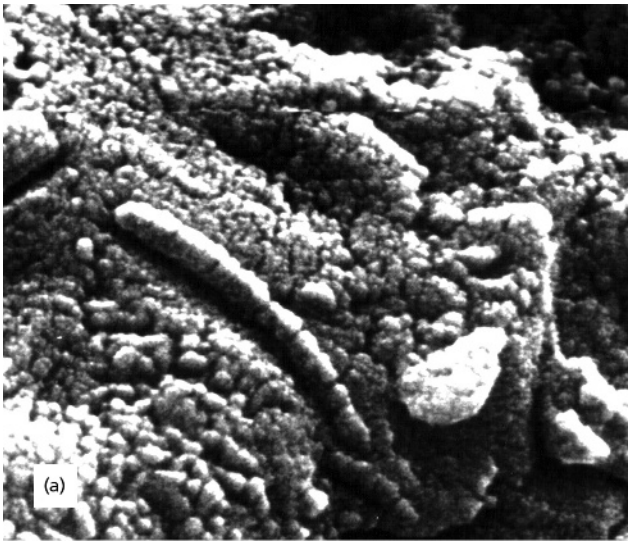
identified on Mars using orbital photographs obtained by Viking (e.g. Fig. 1.1.2.2). However, information about the mineralogical composition of the Martian surface is still lacking. Mineralogy provides important clues about the palaeoenvironment, information needed to determine the best sites for detailed surface exploration. An important exploration goal is to identify aqueous mineral assemblages (of the types that commonly capture and preserve fossil biosignatures) from orbit using spectral mapping methods prior to landed missions. In targeting sites for sample return, evaporative lake basins and hydrothermal sites are given a high priority. In terrestrial settings, the deposits formed in these environments frequently provide optimal conditions for preservation.

Putative signs of life in a Martian meteorite

The report of possible fossil signatures in Martian meteorite Allan Hills 84001 (McKay *et al.* 1996) generated an intense, ongoing debate over the usefulness of a variety of morphological, mineralogical, and geochemical data for detecting biosignatures in ancient rocks. Subsequent work by the broader scientific community indicates that the major lines of evidence used to support the biological hypothesis for ALH 84001 are more easily explained by inorganic processes.

Polycyclic aromatic hydrocarbons (PAHs), such as those found in ALH 84001, are not generally regarded as being diagnostic of life. In addition, it has been shown that a major fraction of the organic matter present in the meteorite exhibits radiocarbon activity, indicating that it originated through terrestrial contamination after reaching the Earth (Jull *et al.* 1998). Although a small fraction of remaining organic matter could be Martian, it has not yet been characterized.

A key test of the biological hypothesis for ALH 84001 is the formation temperature of the carbonates that



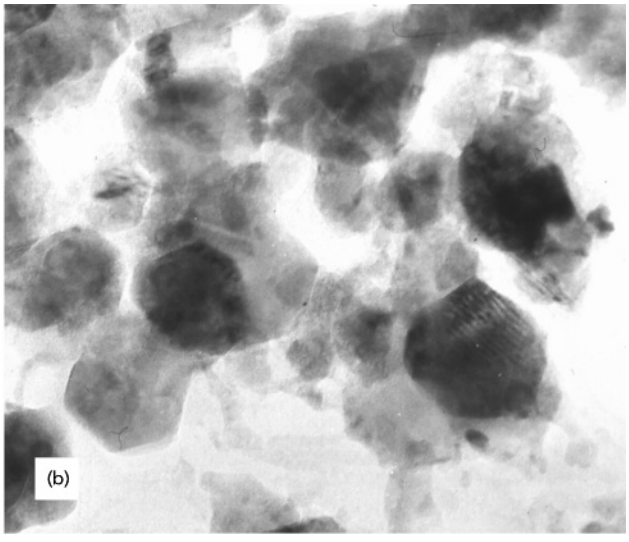


Fig. 1.1.2.3 (a) Scanning electron micrograph of nanostructures found on fracture surfaces of carbonate minerals in Martian meteorite, ALH 84001. The elongated structure in the centre of the image is ≈2 μm long and consists of a series of smaller segments each ≈0.1 μm wide. (b) Transmission electron micrograph showing small magnetite grains found within carbonate minerals of ALH 84001. The magnetite grains average 15–20 nm wide. Magnetite crystallites in ALH 84001 exhibit epitaxial relationships with the host carbonate grains and screw dislocations suggestive of vapour-phase deposition. (Photographs by courtesy of the Lunar Planetary Institute.)

contain the putative fossil evidence. Carbon and oxygen isotope measurements obtained for carbonates in the Alan Hills meteorite indicate a wide range of formation temperatures, the lowest falling within the range for life (<120°C). Because the carbonates experienced multiple shock events, each with highly localized effects, the spread of isotopic values is perhaps not surprising. However, the lowest temperature estimates are likely to be primary, having been least affected by shock metamorphism (Treiman and Romanek 1998).

Magnetite grains present in the rims of the ALH 84001 carbonates (Fig. 1.1.2.3b) were compared to intracellular magnetite crystals ('magnetosomes') formed by terrestrial magnetotactic bacteria. However, ultrastructural features (spiral defects) discovered in some of the ALH 84001 magnetites suggest that they were formed by vapour deposition at high temperatures. In addition, the ALH 84001 magnetites exhibit epitaxial growth relationships with the host carbonate, and are therefore unlikely to have formed within the cells of bacteria (Bradley *et al.* 1998).

Nanometre-scale morphologies having shapes similar to microbes were observed on some fracture surfaces of carbonates in the ALH 84001 meteorite (Fig. 1.1.2.3a). These were compared to terrestrial 'nanobacteria'. This is an informal term used to describe small (<0.1 μm) rods and spheroids found in rocks which resemble spores or resting stages of microorganisms (see Kirkland *et al.* 1999). At this observational scale, problems often arise in distinguishing biological structures from inorganic forms which originate by self-organizing crystal growth, or as artefacts created during the application of crystalline metal coatings used to prepare samples for scanning electron microscopy (SEM). The putative microfossils in the ALH 84001 meteorite have subsequently been explained by a combination of the above processes. At the nanometre scale, shape is clearly a poor criterion for biogenicity. In the absence of other types of compelling evidence, it is probably best to avoid the use of the term 'nanobacteria', and adopt instead a non-genetic descriptive term, like 'nanostructures', which does not imply an origin.

The apparent refutation of the biological hypothesis for the ALH 84001 meteorite leaves the question of Martian life unresolved. Answering this question is likely to require the careful *in situ* study of Martian samples that formed under aqueous conditions that were favourable for the rapid capture and long-term preservation of biosignatures. Given the difficulty of recognizing ancient microbial signatures in rocks, the return of samples to the Earth for analysis in specialized laboratories may be required for an adequate test of the life hypothesis. The careful re-examination of biological evidence for the ALH 84001 meteorite has improved the basis for interpreting the Precambrian record on Earth by establishing more rigorous standards for biogenicity in ancient materials. The broadly based effort has also helped to prepare the scientific community for a series of Mars sample return missions tentatively scheduled to begin in 2009.

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1.1.3 Life in the Archaean

R. BUICK

Introduction

When did life on Earth first appear? What were primordial organisms like? How and where did they live? Though these are age-old philosophical and theological questions, they also have scientific significance. Clearly, Earth's history would have been different if abundant, diverse life had arisen when the crust solidified, perhaps 4.5 billion years ago, rather than halfway through geological time, at the end of the Archaean (2.5 Ga).

To answer these questions empirically, palaeontological and geochemical relics of an Archaean biota are required, but finding such evidence can be difficult. Archaean rocks are rare because the exposed rock mass diminishes markedly with age due to erosion, burial, and subduction. Many that remain are poorly preserved because the probability of destructive deformation or metamorphism increases with age. However, in a few ancient cratons, relatively untraumatized Archaean supracrustal rocks still exist in reasonable abundance, permitting palaeobiological investigation of suitable facies. These consist mainly of kerogenous cherts and shales, banded ironstones, and carbonates of various compositions, but more exotic lithologies (sandstones, palaeosols, hydrothermal deposits) can also yield useful data.

As even the most pristine Archaean rocks have complex histories, their sedimentary environment, stratigraphic relationships, postdepositional evolution, and geochronology must be fully understood to ascertain whether any biological remains are indeed ancient and not younger contamination. However, these basic geological data are rarely available in many Archaean terrains. Furthermore, as early organisms were probably small, simple, and subtle in their environmental impact, the biogenicity of putative Archaean fossils is often ambiguous. More studies of modern microbes, their biogeochemical interactions, and their inorganic mimics are needed to resolve this issue. Perhaps most importantly, it is essential to approach Archaean palaeobiology from first principles, because the nature of the early fossil record is unpredictable, and to subject all data to severe scrutiny, because real discoveries are of such significance.

How are relics of Archaean life preserved?

Microfossils

The ideal form of Archaean palaeobiological evidence is the preserved remains of the organisms themselves (see Section 3.4.2). As no macrofossils have ever been found in rocks older than 2.1 Ga, the search for Archaean fossils has been largely conducted by microscopy. The most convincing are barely of Archaean age, ≈2.52 Ga from the Transvaal Supergroup of South Africa (Lanier 1986; Klein *et al.* 1987; Altermann and Schopf 1995). The assemblages (Fig. 1.1.3.1) contain solitary or paired ellipsoids (0.2–2.5 μm), solitary, paired or clustered spheroids (1.5–20 μm), solitary tubular filaments (diameter 0.5–3 μm) and interwoven mats of tubular filaments (diameter 10–30 μm), all composed of kerogen that is isotopically

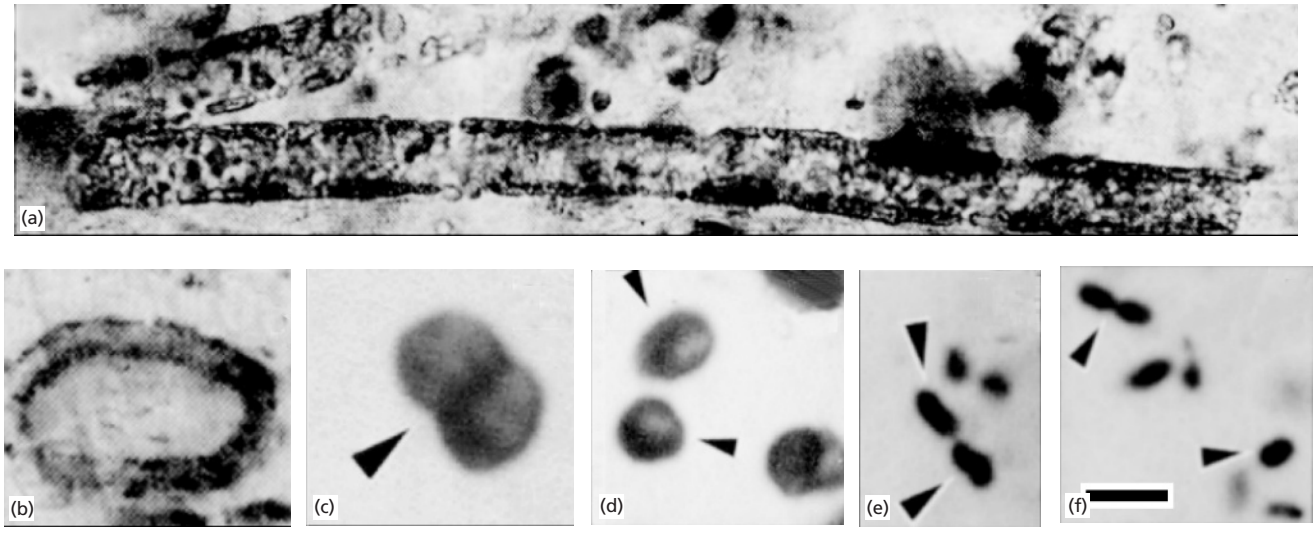


Fig. 1.1.3.1 Archaean microfossils from the 2.52 Ga Transvaal Supergroup, South Africa. (a) Filaments in longitudinal section. (b) Filament in cross-section. (c,d) Spheroids, paired and clustered. (e,f) Ellipsoids, solitary and paired. Bar = 18.7 µm for (a); 6.8 µm for (b); 1.8 µm for (c); 3.0 µm for (d) and (f); 2.5 µm for (e).(a,b, From Klein *et al.* 1987, with permission from Elsevier Science; c–f, from Lanier 1986.)

similar to younger biological carbon. These objects are undoubtedly syngenetic and compellingly biogenic, representing uncontroversial microfossils.

Older assemblages are more problematic. Very rare, poorly preserved, filamentous structures have been reported from the 2.72 Ga Tumbiana Formation of Australia (Schopf and Walter 1983), but it is not clear that these have an organic composition or a matting habit, both common characteristics of biogenic filaments. Numerous simple spheroidal and filamentous objects of carbonaceous composition have been described from the 3.45–3.25 Ga Swaziland Supergroup of South Africa, with perhaps the most lifelike from the Kromberg Formation (Walsh 1992). These hollow cylindrical filaments (diameter 1.5–5 µm) are composed of kerogen much finer in grain size than in the surrounding matrix, making an inorganic origin difficult to envisage. Filaments, some of which are spectacularly lifelike, have also been reported from North Pole, Australia, in the ≈3.46 Ga Warrawoona Group (Awramik *et al.* 1983). These, however, are probably younger contaminants. They are composed of brown kerogen, indicating lesser metamorphism than experienced by indigenous Warrawoona kerogen, which is black (as befits organic matter exposed to temperatures of ≈300°C). The fossiliferous sample was evidently collected on an exhumed unconformity between the early Archaean Warrawoona Group and the late Archaean (≈2.7 Ga) Fortescue Group, suggesting that they could have been emplaced in their host rock during deposition of the latter. Similarly, some of the septate filaments and clustered spheroids reported from cherts in the <3.46 Ga Apex Basalt, Australia (Schopf and Packer 1987), are dark brown—a colour incompatible with the greenschist metamorphic grade of the surrounding rocks. This suggests that these objects are either not organic or not indigenous, making their claimed status as the oldest known microfossils dubious.

Stromatolites

Many assemblages of stromatolites (laminated sedimentary structures accreted as a result of microbial growth, movement, or metabolism) are now known from Archaean rocks (see Section 4.1.2). Those of late Archaean age (<3.0 Ga) are generally regarded as biogenic (Fig. 1.1.3.2). However, the origin of older stromatolite-like structures is controversial. Based on a detailed structural analysis of three of the better-known occurrences, it has been argued that all those older than 3.2 Ga are in fact abiogenic evaporative precipitates, hydrothermal accretions, or deformational features (Lowe 1994). However, this study neglected the most thoroughly described, best illustrated, and most complex stromatolitic occurrence so far reported from the early Archaean, i.e. the bed of stratiform, pseudocolumnar, and semicolumnar structures from the Warrawoona Group (>3.46 Ga) at North Pole, Australia (Buick *et al.* 1981). These defy categorization as evaporative, hydrothermal, or deformational features, as they have

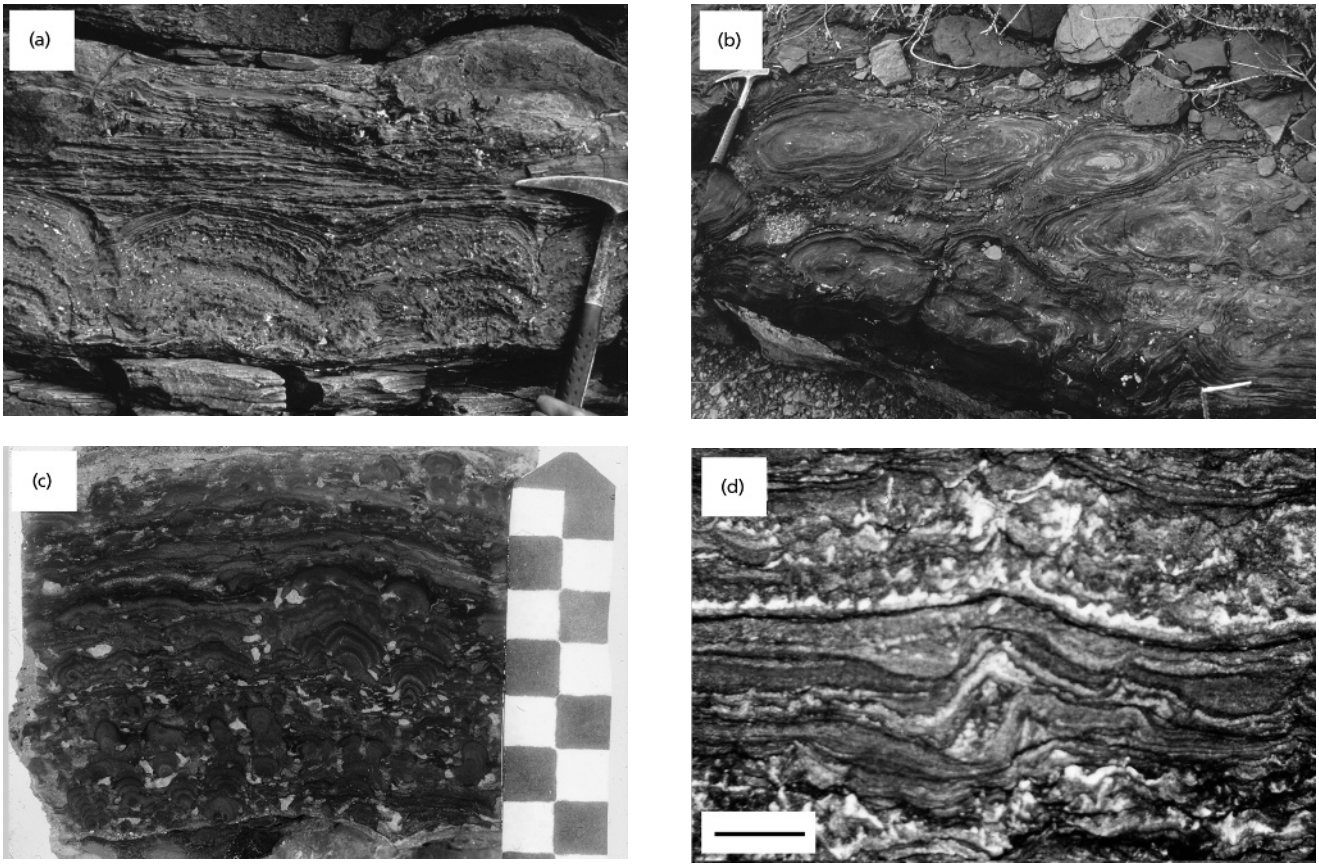


Fig. 1.1.3.2 Stromatolites from the 2.72 Ga Tumbiana Formation, Fortescue Group, Billadunna, Australia. (a) Cross-section of pseudocolumnar structures with fenestrae (white spots). (b) Plan view of domical crests of pseudocolumnar structures. (c) Cross-section slab of pseudocolumnar structures showing a finer order of flexure within the major structures and alternating light and dark laminae with interspersed fenestrae (white patches). (d) Thin-section of wrinkly microlaminae with cuspate palimpsests (white) after tufted clusters of microbial filaments. Scale in (c) is in centimetres. Bar =3.15 mm for (d).

several orders of lamination contorted into several orders of flexures, only moderate morphological inheritance, and lenses of desiccated fragments filling troughs between flexures (Fig. 1.1.3.3). Moreover, their kerogenous microlaminae, which thicken over flexures, suggest biological inhabitants. So, it is perhaps premature to dismiss all early Archaean stromatolites as abiogenic on the strength of a limited survey.

Mathematical models show that stromatolite-like structures with fractal growth-surface geometry can be produced inorganically by the interaction of sedimentation, precipitation, and gravitation (Grotzinger and Rothman 1996). If so, early in Earth's history when inorganic carbonate evidently precipitated voluminously on the sea floor and in the water column, such structures could have formed in abundance. However, at least some early Archaean stromatolites, including those from North Pole, do not possess self-similar growth surfaces and are quite irregular on several scales, so perhaps they are indeed biogenic. But clearly a biological origin cannot be assumed for such ancient structures without multiple lines of supporting evidence, preferably including microfossils indicating by their disposition or composition an active involvement in sedimentation.

Carbon isotopes

A more continuous record of Archaean biology is preserved in the carbon isotope ratios of sedimentary rocks. As autotrophy incorporates the light stable isotope of carbon (^{12}C) into newly synthesized organic matter in preference to the heavy isotope (^{13}C), any kerogen ultimately derived from autotrophic organisms will have a $\delta^{13}C_{org}$ value fractionated from that of the bulk Earth. Reflecting this biotic accumulation of ^{12}C, carbonate precipitated from water inhabited by autotrophs will be somewhat enriched in ^{13}C. So, on the modern Earth, $\delta^{13}C_{org}$ averages around –25‰ and marine $\delta^{13}C_{carb}$ is generally about 0‰, compared with a mantle value of about –5‰. This fractionation pattern can be traced back through the sedimentary record (Fig. 1.1.3.4b), with a few significant but temporary variations, to the end of

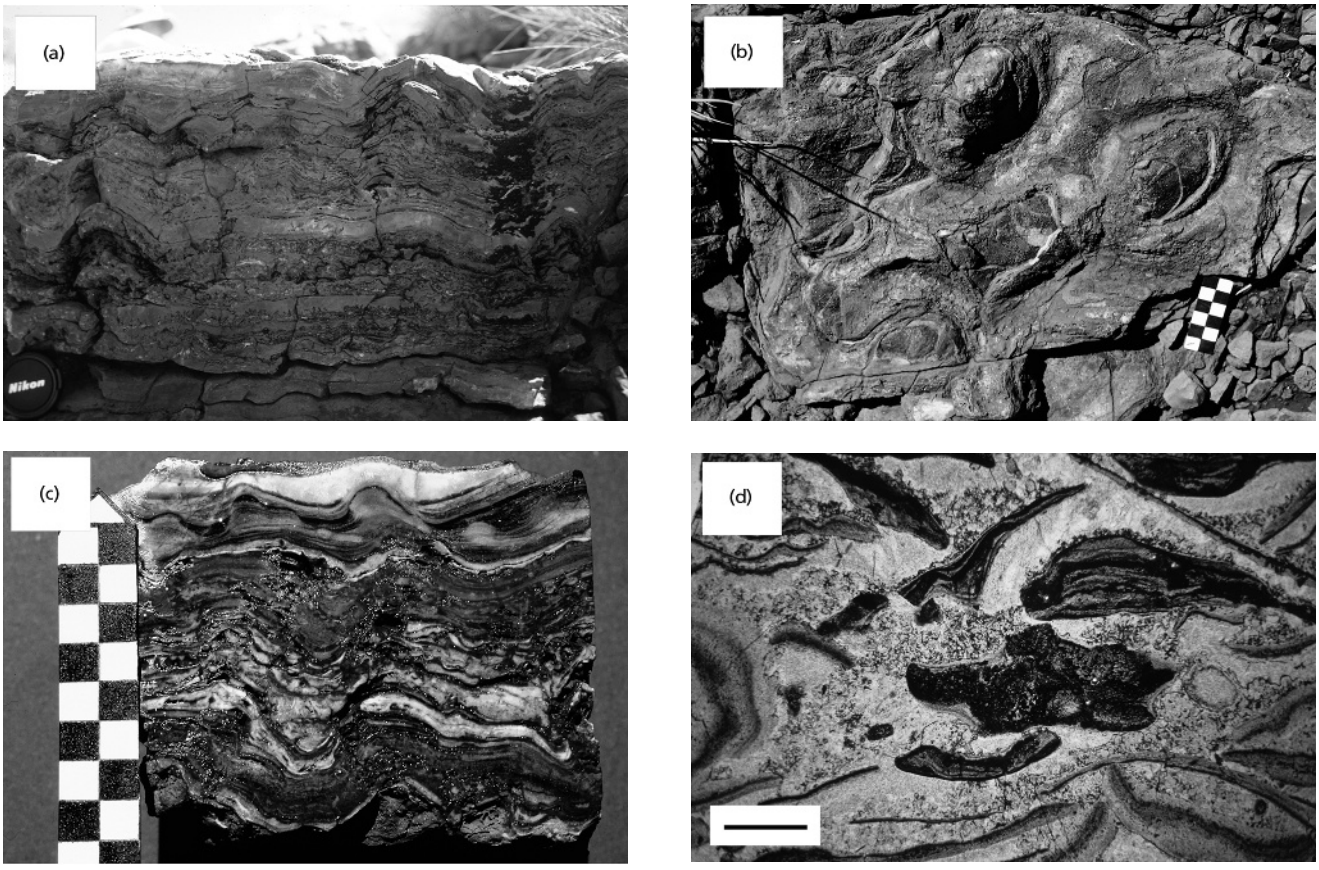


Fig. 1.1.3.3 Stromatolites from the >3.46 Ga Warrawoona Group, North Pole, Australia. (a) Cross-section of pseudocolumnar structures with flexures initiated at, and propagating to, different heights within the bed. (b) Plan view of domical crests to pseudocolumnar structures. (c) Cross-section slab of pseudocolumnar structures showing a finer order of flexure within the major structures and alternating light and dark laminae on several scales. (d) Thin-section of ripped-up curved intraclasts with wrinkly kerogenous microlaminae accumulated in a trough between pseudocolumns. Scale in (b) and (c) is in centimetres. Bar = 0.44 mm for (d).

the Archaean. The only major trend is a gradual increase in the difference between $\delta^{13}C_{org}$ and $\delta^{13}C_{carb}$, from –25‰ to –35‰, through the Proterozoic. When ^{13}C loss by thermal alteration during diagenesis and metamorphism is considered, this trend is enhanced, with corrected $\delta^{13}C_{org}$ values at the Archaean–Proterozoic boundary averaging around –40‰. Such a pattern indicates the persistence of autotrophic fractionation through time, with the trend possibly imposed by progressive growth in the amount of organic carbon buried in sedimentary rock, steadily removing more of the light isotope from biological availability.

The Archaean carbon isotope record is less simple. Back to 3.5 Ga, $\delta^{13}C_{carb}$ values for most low-grade metasedimentary rocks average close to 0‰, suggesting biological autotrophy (Schidlowski 1993). However, carbonates associated with banded ironstones are distinctly light (–3‰ to –10‰), probably due to precipitation from the suboxic depths of a stratified ocean rich in light bicarbonate derived from biological respiration. The only older sedimentary carbonates occur in highly metamorphosed terrains and it is contentious whether they are of sedimentary or metasomatic origin. Thus the isotopic record of carbonate carbon can be interpreted as showing clear evidence for life almost, but not quite, back to the beginning of the geological record. Organic carbon is consistent with such an interpretation. Archaean $\delta^{13}C_{org}$ values are generally about –30‰ which, after correction for metamorphic loss of light hydrocarbons, translates to original ratios nearer –40‰, similar to early Proterozoic values indicative of autotrophy. But before ≈3.5 Ga, the organic record, like its carbonate equivalent, is sparse, metamorphosed, and controversial.

Organic geochemistry

Organic geochemical analysis of Archaean sedimentary rocks was widely used in early attempts to determine the antiquity of life, but is now rather discredited. Most

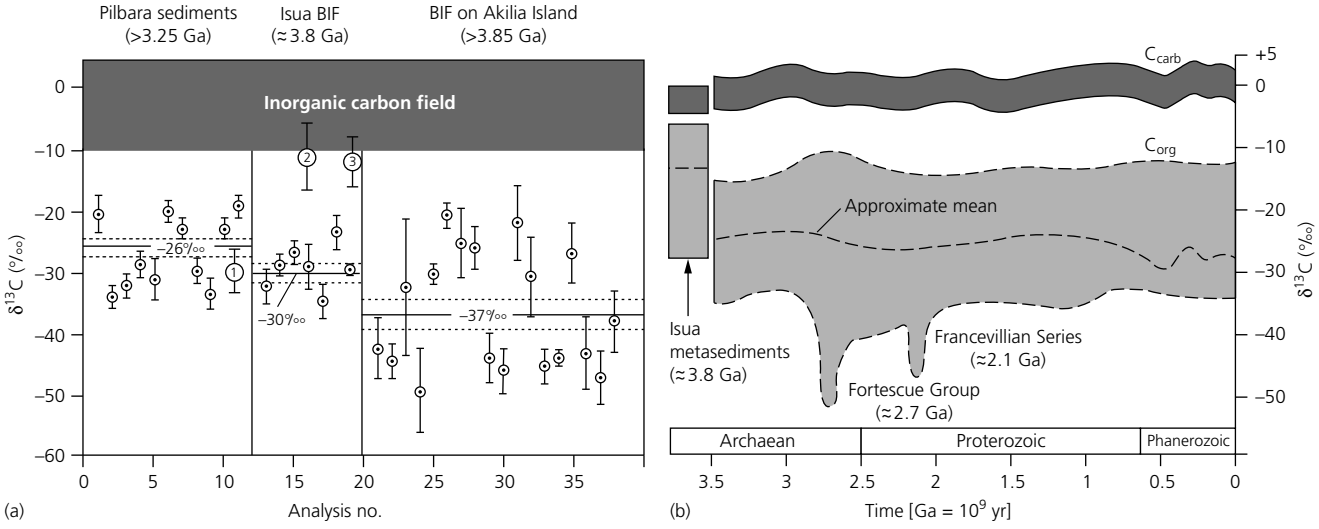


Fig. 1.1.3.4 Sedimentary carbon isotope values through time. (a) Ion-microprobe analyses of minute graphite inclusions within apatite crystals in several early Archaean iron-formations, including the Isua and Akilia, Greenland. Each analysis is marked by a ring with 1σ standard deviations indicated by vertical bars; numbered rings and bars represent whole-rock organic carbon values previously obtained; weighted means of data represented by solid lines with 2σ confidence interval marked by dotted lines; dark bar at top represents range of values for sedimentary carbonate. (b) Range of whole-rock organic carbon and carbonate values from 3.8 to 0 Ga. (a, Reprinted with permission from *Nature* (Mojzsis *et al*. 1996), copyright 1996 Macmillan Magazines Limited; b, from Schidlowski 1993.)

investigations concentrated on solvent extraction, searching for soluble organic compounds derived from distinctive biological molecules ('biomarkers'). These yielded *n*-alkanes, alkanoic acids, isoprenoid alkanes, porphyrins, and amino acids from rocks as old as the ≈3.4 Ga Swaziland Supergroup of southern Africa and even the >3.7 Ga Itsaq Gneiss of Greenland. However, all of these compounds were obtained at concentrations permitted by the permeability of their host rocks, allowing them to have migrated into the rock after deposition, and some of the chiral compounds were still optically active, which if indigeneous should have long since been racemized. Hence, these soluble compounds are now generally regarded as younger contamination (Hayes *et al*. 1983).

In attempts to overcome this problem, Archaean insoluble kerogen has been analysed by pyrolysis. This produced a variety of aliphatic, aromatic, and heterocyclic compounds, once thought to be indigenous degradation products of primordial organisms. However, irreversible contamination of kerogen by younger hydrocarbons can occur to such an extent that, without determination of yield proportions for all products (as in most Archaean studies), pyrolysis is ineffective in the search for early life (Hayes *et al*. 1983).

However, the discovery of Archaean oil and its degradational derivatives (Fig. 1.1.3.5) offers new opportunities for organic geochemical investigation of the early biota (Dutkiewicz *et al*. 1998). If the oil proves to come from biological sources, it should yield chemical fossils of the organisms from which it was derived. Although the known Archaean oil exists in minute quantities, it is sealed in fluid inclusions that have protected it from pollution since its entrapment. So, if modern contamination in the laboratory can be avoided (a difficult but perhaps not insurmountable problem), it may be possible to extract biomarkers that reveal something about the broad biological affinities of the precursor organisms, their metabolic pathways, and their habitat preference.

When did life first appear?

The oldest known rocks that could possibly contain relics of life are >3.7 Ga metasediments (upper amphibolite facies: >650°C with multiple deformations) in the Itsaq Gneiss Complex of Greenland. From these, many microfossils and biomarkers have been reported but all have been subsequently discounted. Evidently, at such high metamorphic grades, only isotopic geochemistry can provide satisfactory evidence of life, but even then its interpretation is not straightforward. Carbon isotope values are reset by metamorphism above greenschist facies, either by isotopic equilibration between kerogen and carbonates, or by expulsion of light hydrocarbons from kerogen. In such circumstances, premetamorphic isotopic ratios are hard to determine without comprehensive data on the abundance and isotopic composition of both organic and carbonate carbon, to assess equilibration, and on organic hydrogen/carbon ratios, to assess hydrocarbon loss (H/C declines as hydrocarbons

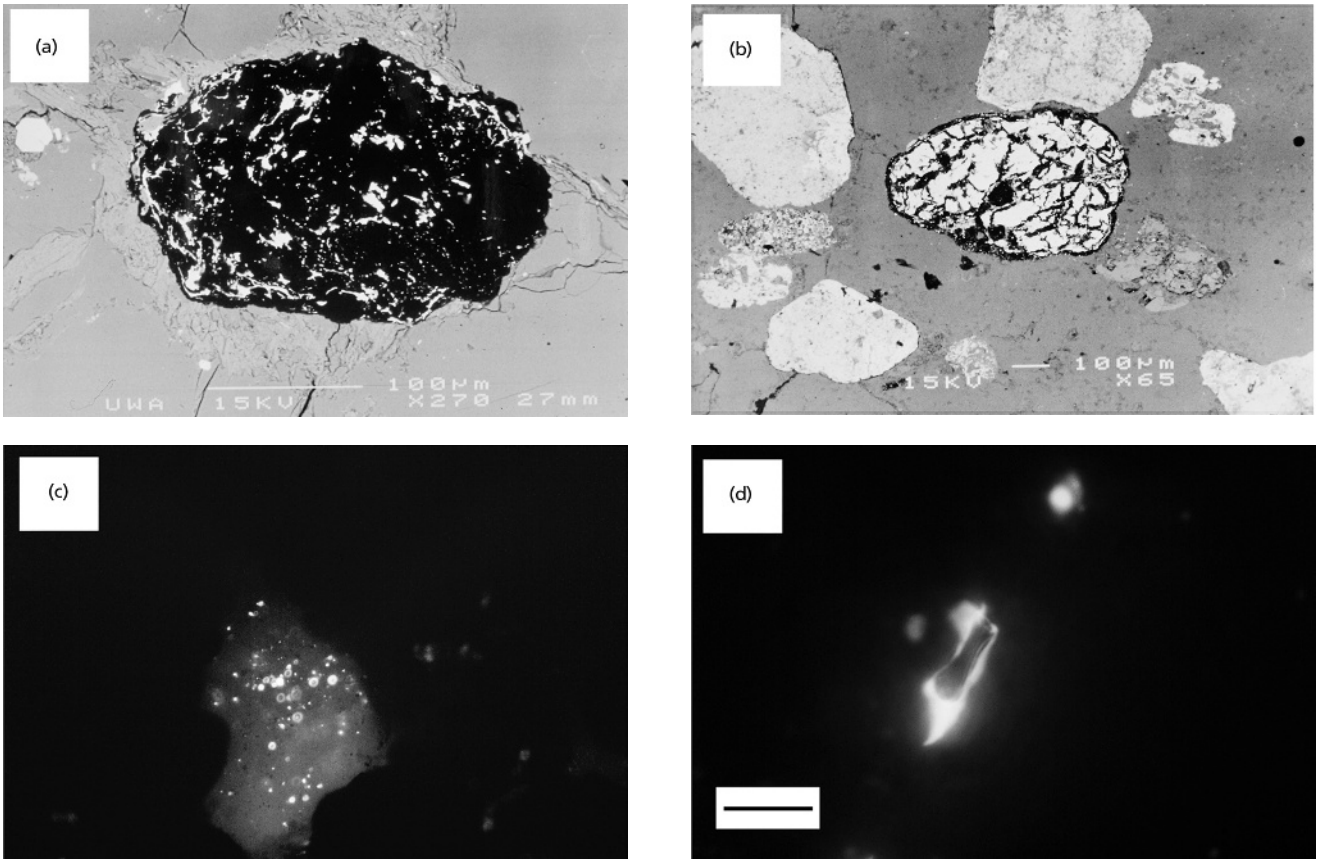


Fig. 1.1.3.5 Relics of Archaean petroleum. (a) SEM-backscattered electron (BSE) image of a bitumen nodule formed when migrating hydrocarbons were polymerized by radioactive uraninite (white), in the ≈ 2.85 Ga Elsburg Formation, Witwatersrand Supergroup, South Africa. (b) SEM–BSE image of radiogenic bitumen derived from fluid hydrocarbons infiltrating and coating a detrital uraninite grain (white), in the ≈ 3.25 Ga Mosquito Creek Formation, Australia. (c) UV-epifluorescence photo of fluorescent oil-bearing fluid inclusions in microfractures within a detrital quartz grain surrounded by black bitumen nodules, in the ≈ 2.85 Ga Elsburg Formation, Witwatersrand Supergroup, South Africa. (d) UV-epifluorescence photo of a complex oil-bearing fluid inclusion with an outer fluorescent rim of liquid oil (white) surrounding a clear gas bubble (grey), in the ≈ 2.85 Ga Elsburg Formation, Witwatersrand Supergroup, South Africa. Bar in (d) = 120 µm for (c), 10 µm for (d).

are expelled). Moreover, particularly ancient metamorphosed rocks pose special problems because abiogenic carbon could be present. Carbonaceous meteorites, primitive igneous rocks, and simulated prebiotic chemosyntheses all yield insoluble carbon with $\delta^{13}C_{org}$ values similar to metamorphosed biotic kerogen; significantly, the Itsaq metasediments were deposited at the end of an intense meteoritic bombardment. So, they might contain isotopically light carbon derived from mixed abiogenic sources which then suffered metamorphic homogenization, making it impossible to distinguish from an original biotic signature.

Whole-rock $\delta^{13}C_{org}$ values of Itsaq metasediments range from –5‰ to –28‰ (average –15‰) and it has been argued that these represent metamorphically reset photoautotrophic fractionations of biological origin (Schidlowski 1993). However, this interpretation is questionable because Itsaq $\delta^{13}C_{carb}$ values have undergone only limited resetting (their mean of –2‰ differs little from carbonates in unmetamorphosed Archaean ironstones), whereas $\delta^{13}C_{org}$ has a wide range. Moreover, ion microprobe analyses of minute graphite inclusions in apatite crystals from the Itsaq metamorphics (Mojzsis *et al*. 1996) produce markedly different isotopic results from the whole-rock studies (Fig. 1.1.3.4). These yield a unimodal population of values from Isua (>3.7 Ga) averaging –30‰ and a bimodal population from Akilia (>3.85 Ga) with a mean of –37‰ but distinct modes at –44‰ and –27‰ (Fig. 1.1.3.4a). However, it is uncertain whether these represent original isotopic signatures because there are no carbonate inclusions with which to compare them and no data allowing assessment of hydrocarbon loss. As the observed values were substantially affected by metamorphism, then the initial $\delta^{13}C_{org}$

values must have been even lighter. This would be hard to explain by biological processes other than methylotrophy which requires free oxygen (Hayes 1994), for which there is no evidence so early in Earth history. Furthermore, Rayleigh distillation of inorganic carbon during metamorphism (selective sequestration of a particular isotope in a closed system, thereby transforming the isotopic composition of the residue) could conceivably have produced graphite of the observed isotopic composition (Eiler *et al*. 1997). So, until similar data have been obtained by similar methods from similar Phanerozoic and Proterozoic rocks, perhaps judgement should be suspended on whether the carbonaceous inclusions in Greenland apatite are biogenic.

The next oldest rocks that might yield evidence of life are in the ≈3.52 Ga Coonterunah Group of Australia and Theespruit Formation of southern Africa. These have experienced mid-greenschist to lower-amphibolite facies metamorphism, about the grade where substantial isotopic resetting begins, and contain kerogen in quantities large enough to measure in whole-rock samples by conventional methods. The Theespruit Formation yields $\delta^{13}C_{org}$ values of –23‰ to –15‰ which might represent metamorphically reset autotrophic carbon, but without carbonates for comparison, such an origin remains conjecture. The Coonterunah Group contains sedimentary carbonate and kerogen, the former averaging about –2‰ and the latter about –24‰ (R. Buick and D.J. Des Marais, unpublished data). As their greenschist metamorphic grade probably did not severely affect isotopic ratios, the observed fractionation can be compared with those of younger Archaean and Proterozoic rocks and is consistent with an autotrophic origin. Thus, these rocks provide perhaps the oldest compelling evidence for life on Earth.

What were Archaean organisms like?

Archaean organisms were morphologically simple. Microfossils are spheroidal or ellipsoidal unicells that reproduced by binary fission, or filamentous chains of discoidal cells with or without cylindrical extracellular mucilaginous sheaths. As microbes are architecturally conservative, this does not necessarily imply minimal taxonomic diversity. In the modern world, a huge range of metabolic styles can lurk under the guise of a simple sphere or cylinder. So, taxonomic diversity may well have rivalled that of many modern microbial ecosystems.

Community structure was apparently also simple. Stromatolite microstructures are locally homogeneous, as are assemblages of undoubted microfossils. Benthic filaments could build mats, protecting individuals from desiccation, radiation, and erosion, and spheroids could grow in dense clusters, probably fulfilling a similar ecological function. Some mats influenced sedimentation, as bulbous, columnar, and branching stromatolites separated by mobile detrital sediment had appeared by the late Archaean.

Regardless of behaviour, organisms were small. Even late Archaean filaments were less than a few tenths of a millimetre long. Individual cells were apparently no larger than 20 μm. The thickness of the finest laminae in cherty stromatolites, where negligible compaction or recrystallization occurred, also gauges maximum cell size. Again 20 μm is the smallest measurement reported. Evidently, then, the biosphere was totally microbial.

From this, it might be inferred that the Archaean biota was also entirely prokaryotic. However, some eukaryotic algae have spheroidal vegetative cells as small as 2 μm, like those seen in the late Archaean. Although no fossils of demonstratively eukaryotic origin have ever been found in Archaean rocks, this may not mean much given the paucity of the record. A better record of the antiquity of eukaryotes may be revealed by biomarker studies.

How did Archaean organisms live?

Only a few of the many microbial metabolic strategies leave a detectable trace in the geological record. However, several of those that modulate biogeochemical cycles had already evolved by the late Archaean.

Photoautotrophy is the dominant form of carbon fixation on Earth today and thus controls the flow of energy through the biosphere. The process imparts a ≈25‰ isotopic fractionation between the carbon source and the organic product, varying somewhat according to the metabolic pathway, nutrient supply, carbon availability, and ambient temperature. Such a fractionation is evident in 3.52 Ga rocks of the Coonterunah Group. Coupled with the presence of structures in the 3.46 Ga Warrawoona Group that are best interpreted as stromatolites accreted by phototropic organisms, this strongly suggests that photoautotrophy had arisen by then. Further, there is presumptive isotopic evidence in the >3.7 Ga Itsaq metasediments for earlier establishment of this metabolic process, although the severity of the metamorphic overprint makes this interpretation equivocal.

Oxygenic photosynthesis is a form of photoautotrophy which is generally thought, on molecular phylogenetic grounds, to have arisen late in metabolic evolution. The only microbes that use this metabolic pathway are the cyanobacteria, some of which are morphologically distinctive. Though globular objects from the <3.46 Ga Apex Basalt have been interpreted as sheath-enclosed spheroidal colonies of cyanobacteria (Schopf and Packer 1987), these are either not fossils or not old. None of the well-preserved late Archaean microfossils is morphologically diagnostic of cyanobacteria;

all may be the remains of anoxygenic bacteria. It is not until ≈2.0 Ga that the first indisputable cyanobacterial fossils (*Eoentophysalis*) appear in the record.

Biological activity in environments lacking exogenous sources of reducing power provides indirect evidence for the advent of oxygenic photosynthesis (Buick 1992). In the 2.72 Ga Tumbiana Formation, Australia, a diverse stromatolite assemblage with palimpsests of phototropic filamentous microbes (Fig. 1.1.3.2) developed in sulphur-deficient lakes on flood basalts. Without allochthonous organic matter or hydrocarbons available, the local ecosystem was necessarily based on autotrophy. This must have been photosynthetic, because oxidized compounds for anaerobic respiration were evidently scarce. As the carbonate phase precipitating in the lakes was calcite rather than siderite, conditions were apparently not highly reducing, so molecular hydrogen was probably not abundant. Thus, anaerobic photosynthesis cannot have been the sole metabolic energy source powering the whole ecosystem and oxygenic photosynthesis must have been employed.

The same lake sediments have extremely light $\delta^{13}C_{org}$ values, –40‰ to –60‰, indicating that primary production was recycled by methanogenic and methylotrophic microbes (Hayes 1994). The former produce methane further depleted in ^{12}C, whereas the latter consume it. This also implies the existence of oxygenic photosynthesis, as methylotrophy requires molecular oxygen. These particular pathways probably prevailed because the local scarcity of oxidized substrates inhibited other forms of organic recycling (Buick 1992).

In modern marine environments, organic recycling is generally dominated by bacterial sulphate reduction. Though sulphate was abundantly available in some early Archaean evaporative environments, the very large (>20‰) whole-rock isotopic fractionations clearly indicative of this pathway are not obvious in the geological record until the early Proterozoic. As early as ≈3.4 Ga, however, micron-scale laser-ablation analyses of sedimentary pyrites reveal small but significant (10–15‰) $\delta^{34}S$ spreads. These may record microbial sulphate reduction where high ocean temperatures promoted high sulphate reduction rates, inducing negligible isotopic fractionations (Ohmoto *et al.* 1993). But the proposed temperature increase (30–40°C above present) is incompatible with the Archaean evaporite record, where relics of gypsum instead of anhydrite indicate rather cooler conditions. Moreover, biological sulphate reduction almost always produces large fractionations in experimental studies, regardless of reaction rate. So, until control studies using laser ablation on more modern biogenic pyrite formed under the proposed primordial conditions show similar isotopic spreads, the Archaean origin of bacterial sulphate reduction must remain speculative.

The early evolution of nitrogen metabolism is poorly known. The few available data suggest that $\delta^{15}N$ values of sedimentary organic matter, now +2‰ to +10‰, were lighter in the Archaean, down to –6‰ (Beaumont and Robert 1999). As the heavier modern values result from isotopic fractionation accompanying microbial denitrification of nitrate to molecular nitrogen, biological nitrification and denitrification were perhaps insignificant processes in suboxic Archaean environments. Regardless, biological nitrogen fixation must have already evolved because fixed inorganic nitrogen would have been scarce in such conditions.

Where did Archaean organisms live?

Contrary to popular belief, a wide environmental range is represented in the early geological record. By the end of the Archaean, life occupied many of these habitats, constraining the ecological tolerances of ancient organisms.

Benthic organisms flourished throughout the marine photic zone, indicated by the abundance of stromatolites in intertidal, shallow subtidal, and shelf settings. In the Transvaal Supergroup, South Africa, filamentous microbial mats grew at depths up to 50 m in an outer shelf to basin environment (Klein *et al.* 1987). Matting microbes could withstand considerable current energies, as Archaean stromatolites are frequently elongated with asymmetric ripples occupying intervening spaces. However, current activity was not a prerequisite for their existence, as cuspate stromatolites in the Transvaal Supergroup evidently grew below wave base under conditions of negligible water movement (Sumner 1997). Mat-forming organisms could tolerate a wide range of salinities, from normal marine through carbonate (Sumner 1997) to sulphate saturation (Buick *et al.* 1981), judging from the evaporite minerals precipitated during stromatolite formation.

Marine plankton was presumably also common, because basinal kerogenous shales are widespread and abundant. These have such high organic carbon contents (up to 165 mg/g), even after diagenetic and metamorphic decarbonation, that it is extremely unlikely that benthic production alone could have fixed so much carbon at such depths. However, no plausible microfossils have ever been found in Archaean shales.

Both benthic and planktic organisms also inhabited non-marine aqueous environments. Diverse stromatolites occur in lacustrine facies of the 2.72 Ga Tumbiana Formation, Australia, some interbedded with halite moulds indicating hypersaline conditions (Buick 1992). Their constructing microbes could withstand very high sedimentation rates as they incorporate thick lenses and laminae of volcanic ash, implying either rapid motility or high growth rates. Similar stromatolites occur in

similar settings in the Ventersdorp Supergroup, South Africa, which is of similar age. Lacustrine basinal shales associated with both of these stromatolite suites are highly kerogenous, so plankton evidently existed in non-marine water bodies as well as in the ocean.

It is unclear whether terrestrial surfaces were inhabited during the Archaean, as preservation is improbable in such settings. In the modern world, photosynthetic bacteria colonize rock and soil surfaces, especially in moist places, forming opportunistically viable crusts. Photosynthesizers also occupy pore spaces within rocks and soils as far as light penetrates. In the absence of an oxygenic atmosphere with an ozone shield, UV fluxes may have been too high for bacterial survival on exposed surfaces, but endolithic or soil-dwelling organisms might have thrived. Palaeosols in the 2.77 Ga Mt Roe Basalt, Australia, contain isotopically light kerogen which has been interpreted as the remains of terrestrial organisms (Rye 1998). However, the organic material is concentrated in fragments filling apparent erosion channels, so a terrestrial origin has yet to be demonstrated.

Phylogenetic studies of modern bacteria suggest that many of the most primitive organisms are thermophilic. However, it is difficult to determine whether the Archaean biota reflected this tendency. The marine oxygen isotope geothermometer—the most effective measure of palaeotemperatures in the later Phanerozoic—is unreliable if seawater $\delta^{18}O$ has evolved through time. Moreover, many Archaean cherts are hydrothermally silicified volcanogenic and evaporitic sediments, so their $\delta^{18}O$ values do not record ambient seawater temperatures. A better constraint is provided by evaporitic parageneses, in which the precipitation of either gypsum or anhydrite as the sulphate phase is governed by temperature. Voluminous evaporites, pseudomorphous after gypsum, are associated with the >3.46 Ga probable stromatolites at North Pole, Australia, indicating temperatures of ≈57°C if sea water had no NaCl, or less if sea water was saline. As halite moulds occur in other early Archaean sedimentary rocks, it seems likely that the earliest microbial communities evident in the fossil record were not dominated by thermophiles. So, as early as ≈3.5 Ga, the microbial world had evidently evolved beyond the state exemplified by the lowest branches of the tree of life.

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1.1.4 Late Proterozoic Biogeochemical Cycles

G.A. LOGAN and R.E. SUMMONS

Introduction

The Proterozoic Eon (2500–540 Ma) saw episodic increases in atmospheric oxygen, the evolution of multicellular life, and at its close, an enormous radiation of animal diversity. The rise of metazoans is marked by the Ediacara fauna (see Section 1.2.1), with body fossils evident in sediments as old as 594 Ma, i.e. the end of the last Varanger glaciation. Evidence for metazoan activity is also present in the trace fossil record. Simple burrows and traces indicate sediment processing, and hence the development of a through gut. Zooplankton have not yet been identified in sediments from this period but it seems likely that water column grazers would also have utilized a through gut. This evolutionary innovation is potentially important for the course of biogeochemical cycles; its first appearance provided a significant additional mechanism for reprocessing organic matter and nutrients found in phytoplankton and transferring the residues out of the photic zone down to the sea floor, in the form of fast-sinking faecal pellets. Furthermore, sediment agitation, or bioturbation related to metazoan feeding and movement, would have affected porewater chemistry and nutrient distribution in surface sediments, which, in turn, would have altered the composition of bacterial communities and early diagenesis (Aller 1982).

Sediments spanning the Neoproterozoic to Early Cambrian preserve several geochemical signals which appear to reflect these biological changes. These include a reordering of the $\delta^{13}C$ relationship between kerogen (insoluble organic matter) and co-occurring bitumen (organic matter soluble in organic solvents), a marked increase in the abundance of phosphorites, and a depletion in $\delta^{34}S$ of diagenetic pyrite. All these changes appear to be related to a major reorganization in biogeochemical cycles of carbon, phosphorus, and sulphur (Logan *et al.* 1995) and, as a consequence, in the distribution of these elements and their isotopes in the biosphere and geosphere. These geochemical signals are important because they record evidence of changing biological activity and environmental parameters independent of sediment lithologies and the occurrence of visible fossils.

Impact of animal activity on organic matter

The carbon isotopic composition of co-occurring kerogen and bitumen has been extensively studied in Phanerozoic and Proterozoic sediments, in the course of research to establish the origin and migration history of petroleum. Phanerozoic kerogen is enriched in ^{13}C relative to associated bitumen, unless contamination or hydrocarbon migration has affected the samples. Early studies of Proterozoic organic matter showed the reverse—unlike Phanerozoic material, the bitumen could be enriched in ^{13}C relative to associated kerogen in some samples. Based on experience with Phanerozoic organic matter, these data were originally dismissed as the result of migration contamination (Hoering 1965). This enigma has been resolved by recent developments in analytical techniques. The availability of gas chromatography-combustion-isotope ratio monitoring mass spectrometry (GC-C-IRMS) instruments has allowed the measurement of $\delta^{13}C$ compositions for individual compounds that comprise complex mixtures such as bitumen. When applied to Proterozoic sediments with reliable pedigrees, it was found that only certain compounds, specifically the *n*-alkanes, were enriched in ^{13}C relative to associated kerogen (Logan *et al.* 1995, 1997). Thus, the unusual isotopic relationship observed in Proterozoic kerogens indicates that Phanerozoic kerogens must be fundamentally different in make-up. A specific source of ^{13}C-enriched *n*-alkanes that is dissimilar to the bulk of original TOC (total organic carbon) is required to explain the difference. These compounds are generally derived from cell wall lipids and fat stores within plants and bacteria. To explain why Proterozoic bitumen, and *n*-alkanes in particular, could be selectively enriched in ^{13}C, a new model was developed (Logan *et al.* 1995).

As a consequence of isotopic fractionation in the pathways leading to their biosynthesis, lipids are depleted in ^{13}C relative to total cell carbon. They are also depleted relative to the proteins and carbohydrates comprising the bulk of carbon in those cells. Lipid moieties in Phanerozoic kerogen also tend to be depleted in ^{13}C relative to TOC even after burial, diagenesis, and petroleum generation. However, hydrocarbons can approach the $\delta^{13}C$ composition of the kerogen as hydrocarbon generation progresses (Eglinton 1994). Generally, the bulk of organic matter preserved in kerogen is thought to comprise the most recalcitrant products of photosynthetic activity. A major component has been identified chemically and microscopically as algaenan, an aliphatic biopolymer, which is thought to produce the bulk of *n*-alkanes that eventually find their way into petroleum.

Selective ^{13}C-enrichment occurs as a proportion of carbon is metabolically reprocessed through food chains in what is called 'heterotrophic enrichment' (Hayes 1993). This process leads to the organisms at higher trophic levels becoming increasingly enriched

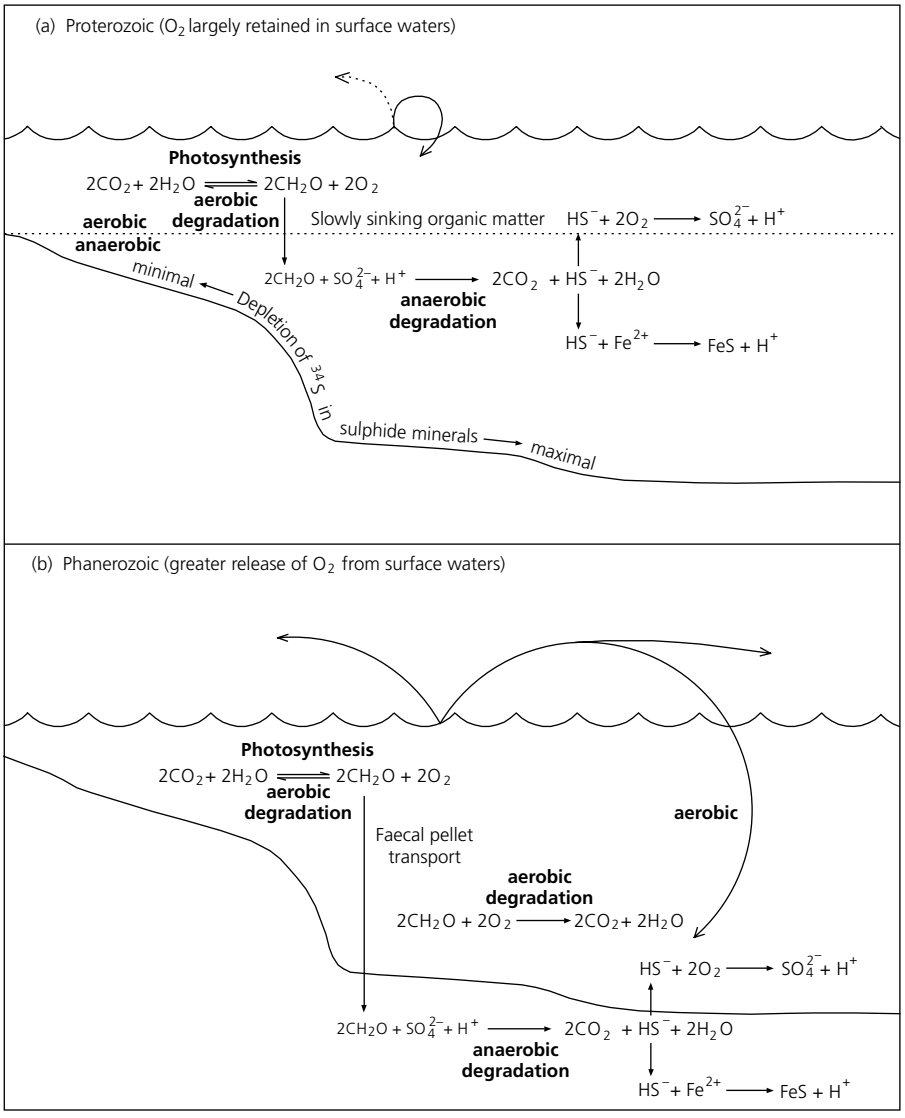


Fig. 1.1.4.1 (a) Slow-sinking organic matter is degraded in the upper water column and acts as an oxygen sink, leading to low oxygen levels in deeper waters. (b) Fast-sinking particles remove organic matter from the photic zone, increasing oxygen availability. This oxygen-enriched water ventilates deeper waters and forces anaerobic activity into the sediment pile.

in ^{13}C. An absence of grazing zooplankton during most of the Proterozoic would result in much photosynthetic organic carbon sinking more slowly through the water column (Logan *et al.* 1995). This organic matter, if not adsorbed on to fast-sinking mineral particles or confined within faecal pellets, would be more prone to bacterial reprocessing. This would lead to a relative enrichment of the preserved carbon in lipids derived from later stage heterotrophic bacteria. These lipids, enriched in ^{13}C, could have provided the source of *n*-alkanes in Proterozoic bitumen. This model incorporates a testable hypothesis. In Proterozoic shallow water environments, where sediment settling times were shorter, the bitumen fraction of TOC should not be as enriched relative to the kerogens as it would in sediments from deeper waters. This was shown to be the case in sediments from the Bitter Springs Formation (Logan *et al.* 1997).

Implications of the impact of animals on biogeochemical cycles

A significant proportion (in some cases up to 66%) of bioavailable carbon currently reaches the abyssal sea floor in the form of fast-sinking faecal pellets (e.g. Pilskaln and Honjo 1987). Accordingly, a number of significant observations follow from the hypothesis that the first arrival of coelomate metazoans introduced a new mechanism for removing phytoplankton debris from the photic zone. Oxygen concentrations within the surface ocean could only increase in proportion to organic carbon which escaped remineralization by removal from the photic zone (Fig. 1.1.4.1a). As the surface ocean oxygen sink, provided by decaying phytoplankton, decreased by more rapid transfer of labile organic matter to deeper waters, a net increase in oxygen availability in the photic zone occurred. In turn, down-

welling of these oxygen-enriched surface waters increased oxygen availability in the deeper ocean (Fig. 1.1.4.1b).

The repackaging of phytoplankton debris would also have affected the distribution of nutrients and trace elements in the water column and in the surface sediments. Phosphate is a vital nutrient for life and, along with nitrate, it limits biological production in the oceans. However, unlike nitrate, phosphate cannot be generated directly in an environment. Its distribution is linked to transport mechanisms, and to tectonic cycles and the weathering of granites (Cook 1992). This means that, over geological time periods, phosphorus is a limiting nutrient for primary productivity. Therefore, the observed switch from low levels of phosphorite formation during most of the Proterozoic, to massive and abundant phosphoritic sediments by Early Cambrian times (Cook 1992) is of great significance. The precipitation of phosphorus occurs under quite specific redox conditions, requiring aerobic environments in order to complex with iron hydroxides. Certain bacteria also fix phosphorus under aerobic conditions and consume it during periods of anoxia. This leads to a strong coupling between phosphorus and oxygen in the Phanerozoic (Van Cappellen and Ingall 1994). In the absence of fast-sinking particles, nutrients such as phosphorus and nitrate would have been recycled rapidly by decay within the photic zone maintaining a strong 'nutrient trap'. Any biological innovation which caused nutrient-rich primary organic matter to be rapidly removed from the photic zone would have broken this 'nutrient trap'. At the same time that oxygen availability was rising in deeper waters, phosphorus transfer also increased, and a labile supply of organic matter was added at the sediment–water interface.

Increased levels of labile, nutrient-rich organic matter at the sediment–water interface, coupled with increased oxygen availability within the lower water column, would have provided a stimulus to benthic communities (see Section 1.2.3). This organic matter would be a rich food source not only for benthic metazoans but also for sedimentary bacterial communities. This combination of bacterial activity and bioturbation directly affects porewater chemistry (Aller 1982). Injection of oxygen during bioturbation would have forced anaerobic bacteria deeper into the sediment pile and created more variable and fluctuating redox conditions close to the sediment–water interface.

Sulphate-reducing bacteria use seawater sulphate to oxidize organic matter; during this process the sulphide produced is depleted in ^{34}S relative to the sulphate used. In pure bacterial culture, depletions in ^{34}S range from 4 to 46‰, with an average of 18‰; in Phanerozoic marine sediments depletions range from 24 to 71‰, with an average of 51‰ (Canfield and Teske 1996). This means that sulphate-reducing bacteria are not solely responsible for the ^{34}S depletions seen in Phanerozoic sediments. It is currently hypothesized that sulphide-oxidizing bacteria may be responsible for the observed shift in the sulphate–sulphide isotopic relationship at some time prior to the Cambrian (Canfield and Teske 1996). Sulphide-oxidizing bacteria, such as *Beggiatoia* or *Thioploca*, have specific environmental tolerances and require both hydrogen sulphide and oxygen.

Proterozoic marine sulphides are generally enriched in ^{34}S compared with Phanerozoic sulphides (Canfield and Teske 1996). If sulphate supplies are limited during sulphate reduction, the isotopic composition of the total sulphide gradually approaches that of the starting sulphate. Therefore, if porewater sulphate is completely consumed, the isotopic composition of the sulphide produced will be the same as the starting material. Without bioturbation, Proterozoic porewaters would have become rapidly anoxic just below the sediment–water interface due to low oxygen concentrations and low levels of replenishment. Sulphate within porewaters would also not be replenished and $\delta^{34}S$ compositions of pyrite would approach that of coeval seawater sulphate as sulphate-reducing bacteria consumed sulphate at the expense of sedimentary organic matter. Evidence exists for a shift in the isotopic composition of some Proterozoic sulphides between 1.0 and 0.6 Ga, but a fundamental shift appears to occur around the Proterozoic–Cambrian boundary (Canfield and Teske 1996). This implies that a change in the supply of both oxygen and sulphide occurred in sediments around the boundary. A plausible explanation is that increased levels of bioturbation allowed greater mixing of porewaters and hence development of sulphide-oxidizing communities within marine sediments which, in turn, led to a general ^{34}S depletion in pyrite.

Conclusion

The major radiation of animals just prior to the Cambrian appears to be linked to contemporaneous changes in several geochemical signals. The advent of fast-sinking particles, such as faecal pellets, led to a change in the flux of labile carbon out of the photic zone, affecting oxygen availability throughout the water column. This new rapid transport of organic matter also affected its preservation by decreasing settling time, and thus reducing its availability to bacterial attack in the water column. Its nutrient-rich labile character would also have acted as a carbon and energy source for both benthic metazoan and bacterial communities. Increased oxygen concentrations in deeper waters, coupled with this enhanced food supply, stimulated bioturbation, which would have affected redox conditions close to the sediment–water interface. Changes in the redox condi-

tions impacted on sedimentary bacteria and on early diagenetic mineral precipitation, such as phosphorites and sulphides. The radiation of zooplankton and benthic metazoans had a profound effect on the environment, and this event is recorded in isotopic and other evidence of changes in biogeochemical cycles.

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1.2 The Cambrian Radiation

1.2.1 Metazoan Origins and Early Evolution

D.H. ERWIN

Introduction

The nature of the origin and early evolution of animals remains among the great conundrums of the history of life, despite incredible advances over the past decade. New fossil discoveries, a dramatically improved time scale, exciting new views of the relationships between major metazoan groups based on both molecular and morphological data, and a wealth of information from comparative studies of the developmental process have all contributed to our growing understanding of events during the late Neoproterozoic and earliest Cambrian (about 610–530 Ma).

Precise absolute age dating has recently provided the first reliable temporal framework for the evolution of early metazoans during the Neoproterozoic, the soft-bodied fossils of the Ediacaran assemblage, and the beginning of the Early Cambrian radiation. There is a continuing debate, however, over whether the origin of animals substantially predates their appearance in the fossil record. Such views have received impetus from molecular clock studies that may suggest a relatively early origin of the clade, relative to its appearance in the fossil record. An increasing diversity of molecular data has rejuvenated the issue of metazoan phylogeny, a once moribund field. The relative roles of environmental and developmental changes in precipitating the early phase of animal evolution are important areas of research.

Earliest history (?) of metazoans

The metazoan lineage diverged from a single-celled eukaryote, probably a choanoflagellate, about 1000 Ma, during the Proterozoic. This divergence occurred during a radiation of a number of higher eukaryotic groups, including plants and fungi, although there is considerable uncertainty about its timing. Reports of metazoans prior to about 610 Ma occur with some frequency, but none has been generally accepted by palaeontologists.

Given the significance that would be attached to undisputed pre-600 Ma metazoans, it is hardly surprising that such claims are subject to considerable scrutiny, and their proponents must advance substantial evidence in their favour. One difficulty is distinguishing possibly biogenic structures from inorganic structures, and metazoans from algae or other non-metazoan fossils. Some of these reports are intriguing, and evidence of metazoans before 600 Ma may yet appear.

Among claims for early metazoans are a group of narrow, seemingly annulated filaments from China, poorly dated to about 700–800 Ma, including *Sinosabellidites* and *Protoarenicola*. The lack of well-preserved structures and living analogues makes these difficult to assign to any group, algal or metazoan (Sun 1994). A variety of purported trace fossils has also been reported, including 1000 Ma worm burrows from India, several unusual forms from the Belt sequence of Wyoming (USA), and the supposed feeding trace *Brooksella canyonensis* from the 1000+ Ma Grand Canyon Series. None of these has yet been accepted as of metazoan origin. Other evidence which has been advanced to suggest the presence of metazoans prior to about 600 Ma includes molecular analyses (discussed below), possible faecal pellets (requiring an anus, and thus a relatively complex organism), and a decline in the diversity and abundance of stromatolites. Each of these lines of reasoning has become increasingly difficult to sustain (see also Section 3.4.2).

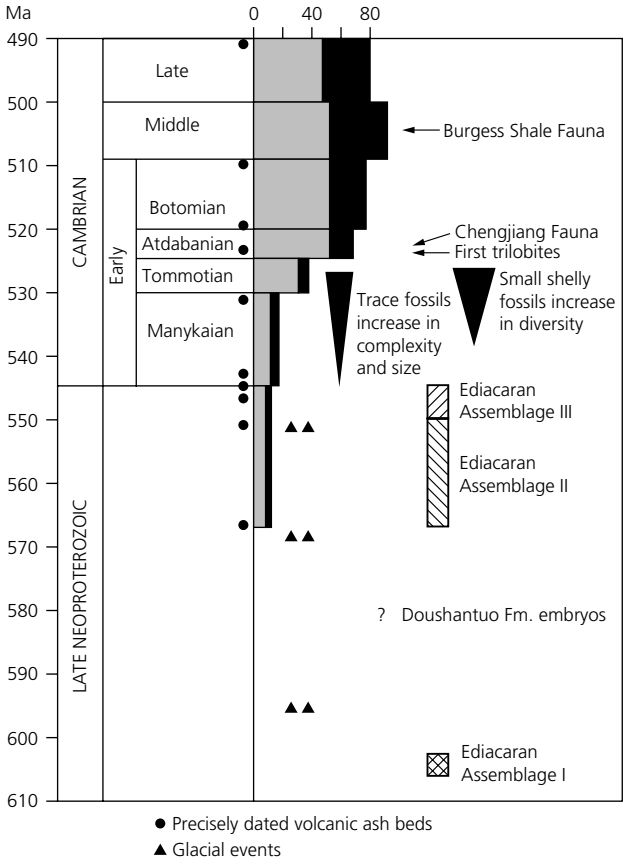


Fig. 1.2.1.1 Geological and biological events of the late Neoproterozoic and Cambrian, based on recent geochronological data. The grey and black boxes show the increasing diversity of marine metazoan orders and classes, respectively, based on data from Sepkoski (after Grotzinger *et al*. 1995). Ediacaran assemblages I, II, and III are of increasingly higher diversity and complexity. Assemblage I is known only from the Mackenzie Mountains of Canada.

Ediacaran metazoans

The late Neoproterozoic was an interval of substantial geological activity, including glaciations, rapid geochemical changes, and pervasive tectonic movements. Many workers have suggested that these events triggered the metazoan radiation. Establishing a causal connection, however, between the environmental changes and the biotic events remains difficult. Remarkable changes in carbon isotopes, often correlated with glacial sediments, suggest several discrete glacial episodes during this interval (Fig. 1.2.1.1; Kaufman *et al*. 1997). One of these, best recorded in the Windermere Supergroup of the Mackenzie Mountains of Canada, is dated to about 600 Ma and overlies a suite of simple discs and rings that may record the earliest assemblage of metazoans. Evidence of a possible second ice age occurs higher in the section following the initial diversification of the Ediacaran fauna (described below), but before the most diverse Ediacaran assemblage. These isotopic shifts suggest substantial changes in the carbon cycle, but the link to evolutionary innovations is unclear. Fortunately, since the unicellular fossils of this interval have limited biostratigraphic utility between different continental regions, the isotopic changes have proved to be of great value for correlation between regions (Kaufman *et al*. 1997).

The Ediacaran fossils form the most notable part of the late Neoproterozoic fossil record. First discovered in rocks from Namibia and Newfoundland, this assemblage of soft-bodied organisms was named for a locality in the Ediacaran Hills of South Australia and has now been recovered from more than 30 localities around the world. The Ediacaran fossils were initially assigned to the Cambrian, until overwhelming evidence demonstrated that they underlie the first skeletonized fossils. Until recently they were generally dated at 620–680 Ma, with the base of the Cambrian at 570–590 Ma. Thus a lengthy, unfossiliferous gap was believed to occur between the Ediacaran fossils and the radiation of skeletonized and other fossils at the base of the Cambrian. This gap has vanished with the application of high-precision dating of the mineral zircon, which incorpor-

ates uranium when it is formed during volcanic eruptions, and has allowed the development of a far more precise time scale for Neoproterozoic events than was previously available (see also Section 5.4.2).

The Ediacaran assemblage includes a spectrum of morphologies, many of which seem unfamiliar, even bizarre, to modern eyes. The earliest fossils are the simple discs from the Twitya Formation in the Mackenzie Mountains; although they have not been found in other areas, this assemblage has been characterized as Ediacaran Assemblage I (Narbonne *et al.* 1994). Dating to about the same time are trace fossils which may have faecal strings. This is importance evidence, for it suggests that a complete gut (with an anus) was present in these bilaterians. Sponges are known to have evolved by this time. The remaining localities of Ediacaran fossils are dated to the last 20 million years of the late Neoproterozoic. These successively more diverse assemblages include fronds as much as 1 m long, seemingly segmented forms, and discs.

The affinities of Ediacaran forms are unknown—or rather the affinities are well known to individual experts, each of whom has a different opinion. Some workers believe that the fossils form a single, monophyletic assemblage that has been described variously as an extinct animal-like clade, the Vendozoa, possibly photosynthetic or chemosynthetic (Seilacher 1992), as relatives of the Cnidaria, as lichens, or as protists. Other workers view the Ediacaran fossils as phylogenetically diverse, possibly including members of the Cnidaria, Annelida, Arthropoda, Mollusca, and even Echinodermata. The more diverse assemblages are known as Assemblage II, which is replaced by the high-diversity Assemblage III for the last few million years of the late Neoproterozoic. Clearly defined mouths are absent from Ediacarans (*Kimberella* may be an exception: Fedonkin and Waggoner 1997) and there are few useful characters for phylogenetic analysis. *Swartpuntia,* recently described from Namibia (Narbonne *et al.* 1997), is frond-like with multiple vanes attached to a central stalk, similar to *Pteridinium*. But it is also seemingly segmented, much like *Dickinsonia.* While the combination of characters is useful in linking two morphologically disparate groups, they also confound the issue of the overall affinities of the assemblage. The group including *Dickinsonia*, *Pteridinium*, and now *Swartpuntia* was characterized by Seilacher (1992) as having a unique quilted construction, much like an air mattress. The members of this group are probably more closely related to each other than to other Ediacaran fossils.

The rocks of the Kuibis and Schwarzrand subgroups in the southern Namibian desert have been the key to resolving the Neoproterozoic time scale. Hundreds of square kilometres of outcrop have yielded a detailed record of the sedimentological, geochemical, and palaeontological changes through the late Neoproterozoic. Of particular significance is a number of volcanic ash beds interbedded with Ediacaran fossils, trace fossils, and rocks amenable to stable isotope studies. The Namibian sections also contain the earliest skeletal fossils, the tube *Cloudina*, and other small shelly fossils. U/Pb dating of the mineral zircon has allowed geologists to place the biotic and environmental changes within a firm temporal framework. The diverse Ediacaran Assemblage III is younger than 549 Ma, and carbon isotope chemostratigraphy suggests that this is true globally (Grotzinger *et al.* 1995). Moreover, some of the Ediacaran fossils are as young as 543 Ma, essentially the same age as the Cambrian boundary as dated in Siberia and elsewhere. Thus the diverse Ediacaran fossils are far younger than previously believed, and there is no lengthy gap between the Ediacaran fossils and the onset of the Cambrian. Moreover, *Cloudina* and the other shelly fossils suggest an element of continuity with the growing diversity of shelly fossils during the overlying Manykaian Stage of the Early Cambrian (Grotzinger *et al.* 1995).

The preservation of the Ediacaran fossils is unusual and remains incompletely understood. Soft-bodied fossils are rarely preserved, but this assemblage has been found in both deep- and shallow-water settings, most commonly as sole marks on the bottom of event beds, indicating rapid deposition. That apparently soft-bodied organisms can survive these storm events without marked injury suggests that they were relatively tough. Some workers have also suggested that the sediment may have been stabilized by microbial mats, aiding preservation.

Many uncertainties about the preservational process remain. What is the meaning of the apparent disappearance of most Ediacaran fossils at the onset of the Cambrian? Fronds similar to *Swartpuntia* from Namibia have been found in Early Cambrian sediments from the Uratanna Formation, South Australia. These fronds occur in association with trace fossils indicative of the Early Cambrian, and demonstrate that the Ediacaran assemblage did not disappear in a mass extinction before the Cambrian, as has been suggested.

Given the phylogenetic quagmire presented by the Ediacaran fossils, the trace fossil record may provide the best potential for interpreting functional aspects, and thus complexity, of Neoproterozoic animals. Many palaeontologists have assumed that the animals that made the trace fossils (burrows and tracks preserved in sediment) were unrelated to the Ediacaran assemblage. On the other hand, the bilateral traces may have been produced by smaller and as yet undescribed Ediacaran fossils (Gehling 1991). The organisms that formed these horizontal to subhorizontal burrows must have had a head of sorts, were bilaterally symmetrical, and

evidently lacked limbs. Determining the diversity of late Neoproterozoic traces is difficult, and may have been seriously overestimated. Most late Neoproterozoic traces are rare, only 1–5 mm in diameter, and vertical burrows are largely lacking; bioturbation of the sediment is essentially unknown (Jensen 1997). Bilateral 'worms' seem to have produced most Neoproterozoic traces, probably with a hydrostatic skeleton. In contrast, trace fossils increase rapidly in diversity, size, and complexity in the Early Cambrian, further confirming the magnitude of the Early Cambrian radiation.

Trace and body fossils have now been augmented by an exciting new source of information about late Neoproterozoic animals. Phosphorites of the Doushantuo Formation (≈580–570 Ma) in southern China preserve, in exquisite three-dimensional detail, early metazoan embryos and a host of algae (Xiao *et al.* 1998). The embryos have undergone several cleavages and include stereoblastulae (a solid ball of cells resulting from early cleavage), indicating the presence of differentiated cell lines and fairly complex development. Since they may be older than all Ediacaran fossils except the discs from the Mackenzie Mountains of Canada, they represent the oldest known metazoan body fossils, but their affinities are unclear. They are probably embryos of cnidarians or bilaterians, and some developmental biologists have argued that they represent protostomes, but they may be embryos of Ediacaran animals. The Doushantuo discovery opens up an extremely promising avenue for future research as it suggests that the early developmental history of metazoans may be directly available to palaeontological inquiry. It also demonstrates that most of the major lineages of algae were present by 570 Ma.

Recent geochronological work has yielded several other important results (Fig. 1.2.1.1). The addition of the lengthy Manykaian Stage to the Early Cambrian, below the Tommotian Stage, came about through the decision to place the base of the Cambrian at the first occurrence of the trace fossil *Treptichnus pedum* in a section in Newfoundland. Thus the recognized Precambrian–Cambrian boundary no longer coincides with the onset of the classic Cambrian radiation at the base of the Tommotian Stage. More importantly, since the redefinition of the boundary, numerous assemblages of small shelly fossils have been found in sediments of Manykaian age in Mongolia (Brasier *et al.* 1996) and Siberia (Knoll *et al.* 1995), extending the small shelly fossils below their original occurrence in the Tommotian (see also Section 1.2.2). The diversity, size, and complexity of trace fossils also increases during the same interval (Jensen 1997). Thus, as more sections are studied in detail, what appeared earlier to be the rapid appearance of these small shelly fossils at the base of the Tommotian sections in Siberia is revealed to be a far more gradual appearance. Finally, the Early Cambrian now accounts for 33 million years of the Cambrian, with only 20 million years for the Middle and Upper Cambrian.

Dating the divergence

When did animals originate? This is not as simple a question as it first appears. When any two groups diverge they will be morphologically similar. With time, accumulated morphological changes distinguish the two lineages. Although the earliest indisputable animal fossils date to 580–560 Ma, the divergence of the metazoan clade from its sister clade must precede this. The critical question is by how much. One approach to the problem is the analysis of slowly evolving gene sequences. It is important to remember, however, the difference between molecular and morphological estimates of divergence dates. Molecular data will allow the timing of divergence of two lineages into distinct species to be estimated, but these species are unlikely to be morphologically distinct. The morphologies which characterize the major clades of animals evolved some time after their divergence. Given the uncertainties of fossil preservation, the earliest organisms with the new morphology are unlikely to be preserved and recovered by palaeontologists. Thus morphological estimates are based on when these distinctive forms appear in the fossil record. The extreme example of this difference is provided by a host of soft-bodied clades which must have diverged from other phyla before the Cambrian radiation, yet are not found in the fossil record.

Molecular estimates of divergence times depend upon a 'molecular clock', based upon the assumption that substitution rates within particular genes are sufficiently regular to allow the branching of two lineages to be dated by comparing molecular sequences (see Section 5.3.6). The clock hypothesis followed from the recognition that many changes in DNA are evolutionarily neutral (and thus not removed by selection). Thus, if the DNA (or, often, RNA) has been sequenced from the same gene in two lineages, and the rates of substitution for the gene can be determined, the date of divergence can be calculated. Many techniques have been developed to test the various assumptions of the molecular clock, and to identify the circumstances in which it can be useful.

But the molecular clock is inherently limited by several factors. First, substitution rates are not regular, and may vary widely between lineages, even for the same gene. For very distant events, such as the metazoan divergence, multiple substitutions have occurred and must be corrected for. Other assumptions must be made about the pattern of rate substitution. Finally, the substitution rates must be calibrated by using a well-dated divergence event from the fossil record. If the calibration event is older than the divergence being estimated with the molecular clock (an interpolated calibration date),

the clock date is more likely to be reliable than if the calibration event is younger (an extrapolated calibration date). This is because dramatic changes in substitution rates, as happen during evolutionary radiations, are more difficult to detect with extrapolated calibrations.

The first attempt at a molecular clock estimate for the divergence of animal phyla dates to 1981, but a more recent, comprehensive analysis (Wray *et al.* 1996) has triggered considerable additional work. A large dataset and more sophisticated analytical techniques lent credence to the results; seven genes were analysed, and a consensus estimate for the divergence of protostomes and deuterostomes was about 1200 Ma, and 1000 Ma for the echinoderm–chordate split. Other workers have attacked the methods used, altered the selection of genes and taxa, and recalibrated the substitution rates. Estimated divergences for the protostome–deuterostome split range between 1500 Ma and 670 Ma!

While all of these results are significantly older than estimates based on the fossil record, their inconsistency is a cause for significant concern. The results do not necessarily require a very early divergence of metazoa. Recall the assumption of rate uniformity inherent in the use of the molecular clock. Greatly increased rates of substitution during evolutionary bursts could also explain the data, for they would violate the assumptions of the clock and make more recent divergences appear older. Recognizing such bursts requires very careful analyses for differences in relative substitution rates between lineages. Such tests have yet to be performed, and thus the reliability of molecular divergence estimates remains uncertain. If, however, the molecular clock estimates are substantially correct and the major metazoan lineages diverged long before the Cambrian radiation, then lineage divergence, and perhaps even the acquisition of some characteristic aspects of particular clades, may have been effectively decoupled from the Cambrian radiation. This in no way reduces the morphological innovations and ecological significance of the radiation. It does, however, strengthen arguments that a change in the physical or biological environment was responsible for the correlated radiation of so many lineages, from unicellular acritarchs to metazoa.

Branches of the tree

Important advances in understanding the relationships between the major clades of animals have been made in the past decade, spurred by a wealth of new molecular data, detailed morphological and ultrastructural studies, and input from comparative molecular developmental biology. Further, the application of rigorous methods of phylogenetic analysis has provided a standard framework for analysing and comparing datasets. While metazoan phylogeny is far from resolved, the field has been revolutionized since the release of the first robust molecular results in 1988.

A consensus metazoan phylogeny from about 10 years ago is shown in Fig. 1.2.1.2(a), and a synthesis of recent

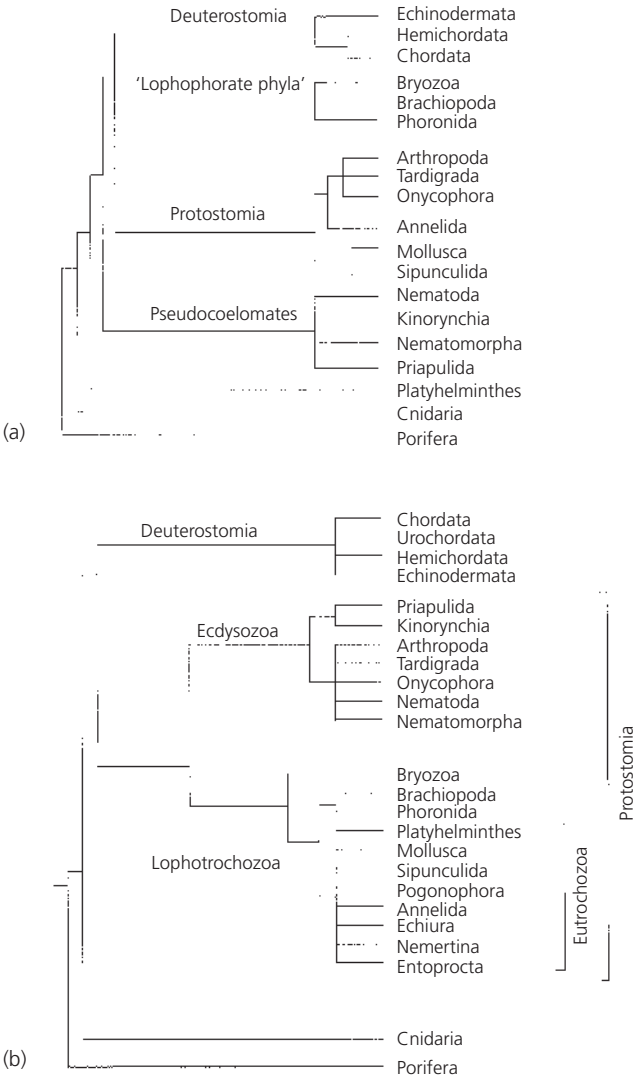


Fig. 1.2.1.2 (a) Consensus metazoan phylogeny before the introduction of recent molecular data and new methods of analysis. The pseudocoelomate phyla diverge before the protostome–deuterostome split, the lophophorate phyla are neither protostomes nor deuterostomes, and arthropods are shown as being more closely related to annelids than molluscs. This figure represents a common American view of metazoan phylogeny; other very different phylogenies were common elsewhere, particularly in Europe, but all differ from (b). (b) Metazoan phylogeny, based on recent analyses of 18S ribosomal DNA, and supported by a variety of developmental data. The pseudocoelomate phyla lie within the protostomes, and the protostomes are divided into two large clades, the Ecdysozoa and Lophotrochozoa. Arthropods are related to a variety of other moulting animals, but are not closely related to either molluscs or annelids. (Based on Aguinaldo *et al.* 1997 and references therein.)

results from 18S ribosomal (r)DNA in Fig. 1.2.1.2(b) (Aguinaldo *et al*. 1997). Several differences are apparent. The clades previously known as the pseudocoelomates, a variety of groups with very simple morphology, have vanished from their position between the cnidarians and the protostome–deuterostome split. Most, if not all, of these groups have greater affinities to protostome clades than to each other. The platyhelminthes (flatworms), a very simple group of worms lacking an anus, may, however, be polyphyletic. The traditional placement of them as a sister group to all higher metazoans may be partly correct, while other flatworms belong within the protostomes (Fig. 1.2.1.2b). The lophophorates (brachiopods, phoronids, and bryozoans) are no longer a jumble of protostome and deuterostome features, but lie at the base of the new clade Lophotrochozoa, one of two major clades within the protostomes. For years invertebrate biologists have debated whether arthropods were more closely related to annelids or molluscs. New moecular data, supported by some developmental inforlmation, suggests that the arthropods are part of the other major basal protostome clade, a group of moulting animals, the Ecdysozoa.

This new topology is likely to be modified as research continues. The data from 18S rDNA analyses may be biased by the particular taxa sampled, uncertainties in aligning the sequences for comparison, and differences in the rates of substitution. It is unlikely that any single gene will ever provide a highly robust phylogenetic framework. New sources of phylogenetic information include other highly conserved nuclear genes, data from gene order and rearrangement, and gene duplications. If the topology shown in Fig. 1.2.1.2(b) is largely correct, a very different evolutionary history is suggested than in Fig. 1.2.1.2(a). A number of features previously considered to have evolved only once, including the coelom and segmentation, clearly evolved multiple times. The steady increase in morphological complexity inherent in Fig. 1.2.1.2(a) has been replaced in Fig. 1.2.1.2(b) by a scenario in which numerous lineages have evidently undergone considerable morphological simplification. Evaluating the relationships of many groups within the Ecdysozoa and Lophotrochozoa continues to be difficult, probably reflecting slow rates of molecular change relative to those of morphological divergence. It is unlikely that genes changed rapidly during an evolutionary radiation and then slowed down to preserve the pattern of change. Resolution of these internal nodes is likely to come from a combination of molecular, developmental, and ultrastructural data.

Developmental innovations

Although the morphologies of nematode worms, flies, and mice seem to have little in common, developmental biologists have recently discovered deep similarities in the genes that control development in these three groups (see Section 2.2.1). The genes controlling the formation of eyes, limbs, the heart, the head, and segmentation are shared between all protostomes and deuterostomes. Thus, these genes, if not necessarily their specific functions, must have been present in their common ancestor. This discovery was entirely unexpected, and the depth of the developmental similarities between different body plans remains unclear. Although the genetic pathways for limb formation, for example, are shared by mice and flies, this does not necessarily mean that these genes produced limbs in the last common ancestor. The genes may have been used for a related purpose and co-opted independently in each lineage. Although this seems unlikely, similar cases are known. Thus when genes are conserved (sequence similarity) this does not necessarily imply that they have the same function. Conversely, even if related genes do have the same function, it may not necessarily have been preserved from the common ancestor of the two lineages (Valentine *et al*. 1999).

In those cases where function has been preserved, developmental information provides a means of reconstructing much of the development and morphology of lineages that diverged during the Cambrian radiation. This opens up another new avenue for understanding the early evolution of animals and reveals that developmental biologists and palaeontologists have both been approaching the same question from different perspectives.

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1.2.2 Significance of Early Shells

S. CONWAY MORRIS

Introduction

The crack of the skier's leg or the smashing open by the thrush of a snail's shell epitomize our sense of the skeleton: integral to the organism, of obvious functional significance, yet potentially vulnerable. To the palaeontologist they represent our principal source of evidence. Yet many animals are soft-bodied (or with skeletons so delicate as to have a minimal preservation potential), while amongst 'robust' skeletons there is a wide spectrum of resistance against postmortem destruction. Prior to about 550 Ma fossil skeletons are almost entirely absent, at least in the familiar manifestation of shells, conchs, carapaces, spicules, and sclerites. Whether or not the Cambrian 'explosion' is a 'real' evolutionary event, as against a breaching of taphonomic thresholds that ended a protracted and cryptic history of animal evolution, remains controversial. Nevertheless, the diversity of skeletons does take a quantum leap at the beginning of the Cambrian.

In the oldest generally accepted mineralized animal skeletons, those of the Ediacaran-age (Fig. 1.2.2.1) taxon *Cloudina* (Fig. 1.2.2.2), there is evidence for a high organic content that gave the tube wall flexibility. *Cloudina* itself has received considerable attention (Grant 1990), but only recently have other biomineralized taxa been recognized (see Grotzinger *et al.* 1995). All these fossils, mostly simple tubes, occur in carbonates and the role of clastic sediments as a potential source of information is yet to be evaluated. So too do the even earlier stages of biomineralization, of which there is no effective record. Most probably the initial degree of mineralization was very light: one might conceive, for example, of isolated calcareous granules embedded in an organic matrix.

In the Lower Cambrian there was a pronounced episode of sedimentary phosphatization, a by-product of which was, in selected areas and horizons, widespread replacement of calcareous skeletons by diagenetic phosphates. It is clear, however, that there is a bias towards the preservation of smaller fossils, probably because of a preference for the processes of phosphatization to occur in microcavities. For example, there is an abundance of phosphatized molluscs and other cap-like forms of millimetric size. These fossils are readily released by digestion of carbonates in weak acid. The ease of this method means that 'crack-out' collection from comparable sediments is less popular, but significantly it reveals order-of-magnitude larger fossils. Similarly, minute sclerites are often favoured as sites of diagenetic phosphatization, even though the original animals with a scleritome composed of several thousand sclerites were much larger. In those skeletons with a high organic content, as inferred from crumpling and other distortion (Fig. 1.2.2.3a), phosphatic replacement ensures survival in fossils that otherwise would probably have a low preservation potential. Many of the Lower Cambrian groups with primary phosphatic skeletons are either of enigmatic phyletic status, such as mobergellans (Fig. 1.2.2.3b) and tommotiids (Fig. 1.2.2.3c), or belong to groups such as hadimopanellids (Fig. 1.2.2.3d) and protoconodonts whose modern representatives (i.e. priapulids and chaetognaths, respectively) show no comparable biomineralization. In this sense, there has been a subsequent shift in utilization of phosphate to the vertebrates.

Metazoan phylogeny

Although it is a palaeontological truism that skeletons appear abruptly at the beginning of the Cambrian, a number of staging posts can be identified. For example, while not unequivocally confirmed, it is likely that *Cloudina* (Fig. 1.2.2.2) is effectively confined to Ediacaran-age strata. In contrast, echinoderms appear not to make a debut until the middle Atdabanian. Precise U/Pb zircon dates place the age of the Vendian–Cambrian boundary at ≈ 550 Ma, but the timing of the stratigraphic slices that define correlatable units of the

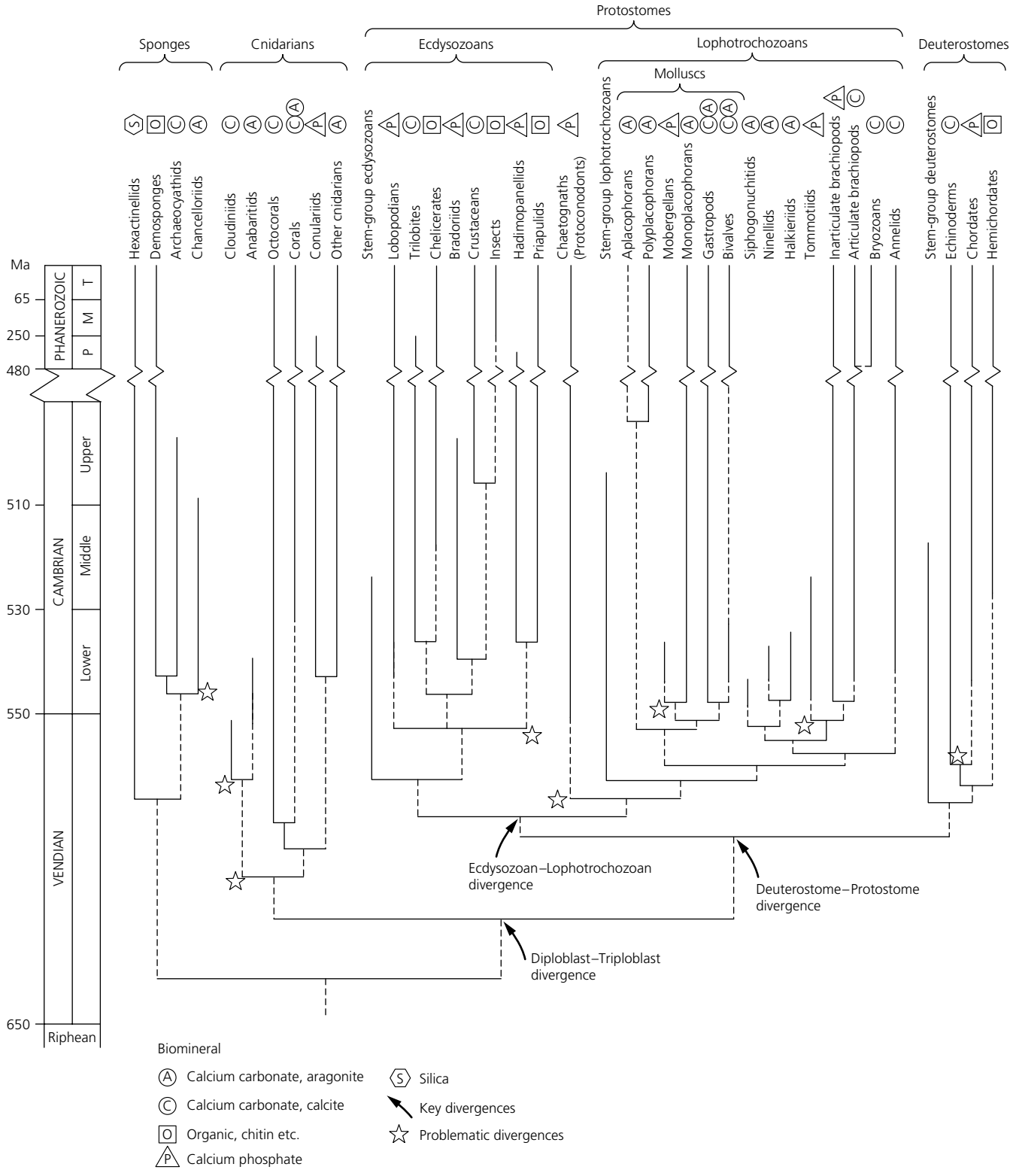


Fig. 1.2.2.1 Outline phylogeny of the Metazoa, emphasizing the distribution of biominerals. Only the principal biominerals are indicated, and subsidiary occurrences such as calcium sulphate in the statoconia of scyphozoans or ferric phosphate in holothurians (see Lowenstam and Weiner 1989) are not included. Many aspects of this phylogeny, which is based on multiple lines of evidence from anatomy, palaeontology, and molecular biology, remain controversial. The divergences that are especially questionable are indicated with a star. Inferred, or ghost, ranges are depicted with dashed lines, but the exact geological ages of the divergences are only indicative.

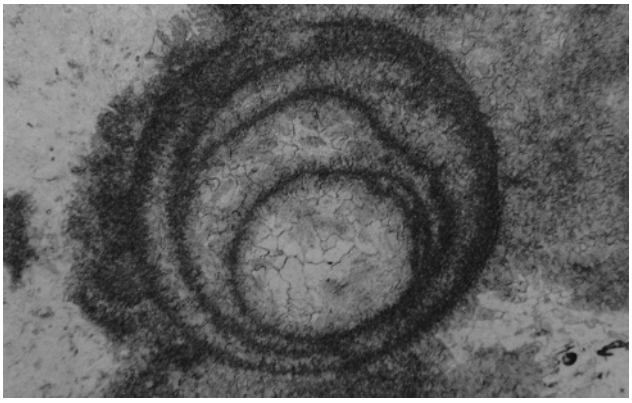
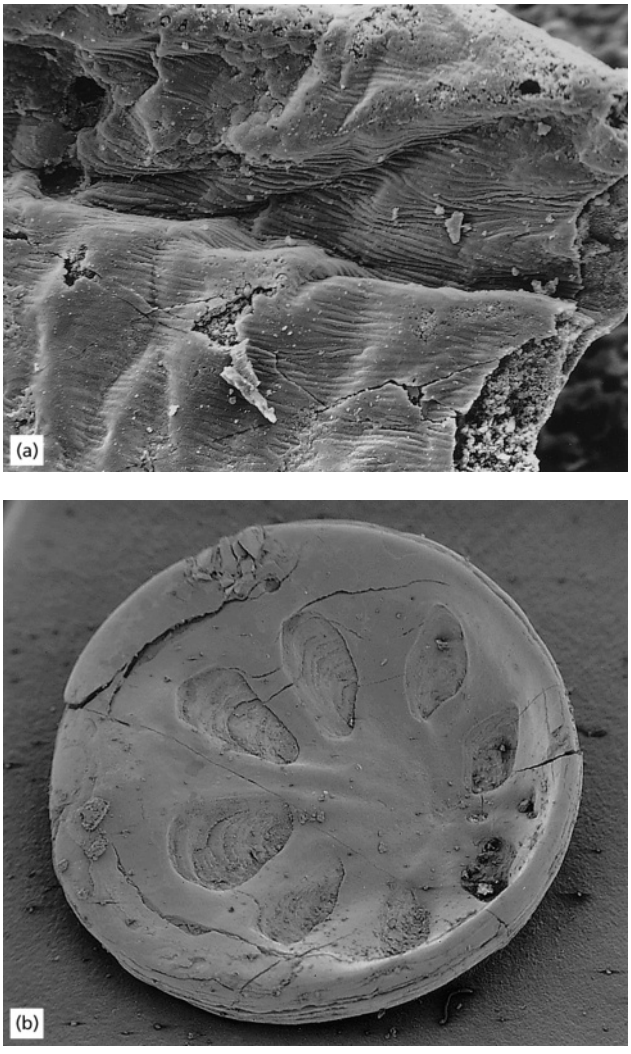


Fig. 1.2.2.2 *Cloudina*, transverse section of tube, subsurface Ediacaran, Ara Formation, Oman, ×32. (Reproduced with permission from Conway Morris, S., Mattes, B.W. and Chen, M. (1990) *Am. J. Sci.* **290A,** 245–260; Fig. 4.16.)



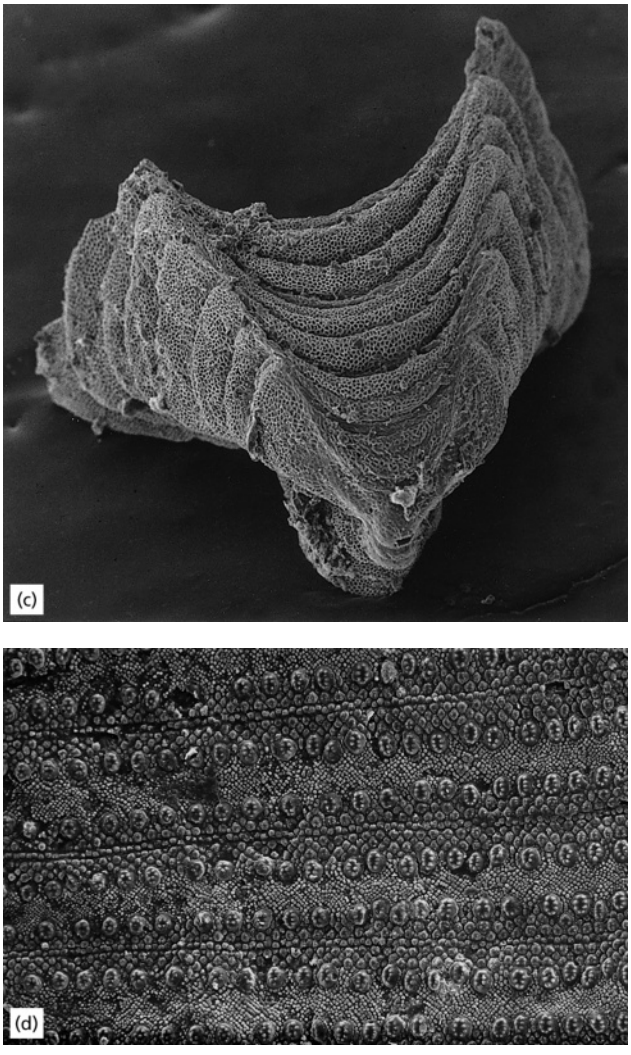


Fig. 1.2.2.3 (a) Detail of surface of the conulariid (carinachitid) *Carinachites*, to show folding of originally organic-rich skeleton, Lower Cambrian, Hongchunping Formation, Shaanxi, China, ×540. (Reproduced with permission from Conway Morris, S. and Chen, M. (1992) *J. Paleont.* **66,** 384–406; Fig. 9.15.) (b) The mobergellan *Discinella*, in ventral view to show the prominent muscle scars, Lower Cambrian, New York, ×22. (Reproduced with permission from Conway Morris, S. and Chapman, A.J. (1997) *J. Paleont.* **71,** 968–985; Fig. 10.1.) (c) The tommotiid *Paterimitra*, isolated sclerite, Lower Cambrian, Ajax Limestone, South Australia, ×112. (Reproduced with permission from Bengtson, S., Conway Morris, S., Cooper, B.J., Jell, P.A. and Runnegar, B.N. (1990) *Mem. Ass. aust. Palaeont.* **9,** 1–364; Fig. 92B.) (d) Latex cast of articulated array of hadimopanellid sclerites from *Palaeoscolex*, Lower Ordovician, Shineton Shale, England, ×225. (Reproduced with permission from Conway Morris, S. (1997) *Zool. J. Linn. Soc.* **119,** 69–82; Fig. 1.)

Vendian and Cambrian are less constrained. So too is the actual precision of stratigraphic correlations, although on the basis of chemostratigraphy sponge spicules from Mongolia appear to be of Ediacaran-equivalent age (Brasier *et al.* 1997), a discovery concordant with similar-aged soft-bodied fossils of sponges (Gehling and Rigby 1996). The principal episode of animal biomineralization occupied an interval of about 20 million years as presently dated (530–550 Ma). Nor was this the final word in skeletal development. Subsequently some groups appear to have lost the ability to mineralize. For example, in the halkieriid–wiwaxiid clade (Conway Morris and Peel 1995) the former group had robust calcareous (probably aragonitic) sclerites, whereas in the wiwaxiids the sclerite wall was organic. Even though a consensus on metazoan phylogeny is not available, it is unlikely that any configuration (Fig. 1.2.2.1) would conclude that biomineralization was monophyletic. The range of biominerals involved, notably silica, calcium carbonate (as both aragonite and calcite), and phosphate, also points to polyphyly (Fig. 1.2.2.1). Little is known about how the organic templates initiate and control crystal growth. It is at least clear that glycoproteins and acidic proteins (rich in aspartic acid) are important (Addadi and Weiner 1985), but so in some circumstances may be phospholipids and glycosaminoglycans. The recognition that different proteins control aragonite and calcite precipitation in the same animal (Belcher *et al.* 1996) can be contrasted, for example, with surprising evidence from diatoms (Kröger *et al.* 1994) which indicates that the structural protein involved with silica precipitation may be employed in other groups to form carbonate biominerals. Even less is known about the genes for biomineralization, but so far as our understanding of molecular evolution goes we might predict that genes and their protein products are co-opted on a multiple basis. It will not be surprising if the requirements for template construction lead to convergence and that unrelated genes are drawn upon for the necessary deployment.

Extrinsic and intrinsic factors

Implicit in this view, and inherent in any scheme of metazoan phylogeny (Fig. 1.2.2.1), is that not only is biomineralization polyphyletic but it is also opportunistic. It has been argued that such an opportunity could only arise, or at least be facilitated, as a response to changing ocean chemistry. This finds a direct resonance with the proposed correlation between an abundance of sedimentary phosphates, the inference of elevated phosphorus levels in sea water, and a supposed excess of phosphatic skeletons in contrast to the remainder of the Phanerozoic. The last item, however, finds little support from the fossil record. Nevertheless, in the case of calcium carbonate, and specifically the polymorphs calcite and aragonite, there is some evidence of a correlation with seawater chemistry (Harper *et al.* 1997). What would be less likely, at least in the case of animals, is that changes in seawater chemistry actually initiated the Cambrian 'explosion' of biomineralization.

It seems more probable that the primary motor for the widespread appearance of skeletons was ecological, and of paramount importance was protection against predatory attack. There is little evidence that early predators enjoyed the benefits of beweaponed biomineralization. Apart from the phosphatic teeth of the chaetognathous protoconodonts, such evidence as we presently have (principally from Burgess Shale-type faunas; Conway Morris 1998) is that prey last saw the light of day in the gullets of priapulids as well as the limbs and jaws of arthropods, none of which was actually mineralized. Direct evidence for predation is relatively limited and includes gut contents, boreholes, and coprolites. The arrangement of skeletons is, however, suggestive. These include the cataphract skeletons, most notably of the halkieriids, which combine flexibility and protection. Many other Cambrian fossils are cap-like or bivalved, and would have given some protection against durophagy. So too would the spicular arrangement of the sponges, chancelloriids, and octocorals. This is not to deny other functions to skeletons. The argument for support and muscle insertion has some force, yet most animals lacking mineralized skeletons still remained functionally uncompromised.

Skeleton space

There are perhaps two approaches to classifying these early skeletons. One is to consider which Cambrian groups possess biominerals, what is their composition and microstructure, and what range of functions they encompass. The second approach is more synthetic, and makes no necessary reference to phylogeny. One such (Thomas and Reif 1993) is based on a code of skeletal types, e.g. rigid, cones, imbricate, and their combinatorial associations (Fig. 1.2.2.4). In this way a matrix of occurrences can be completed, with the further discrimination of relative frequencies. Almost every skeletal variation has been tried and, more significantly, in many cases the 'invention' of a particular arrangement is blatantly polyphyletic (Fig. 1.2.2.4a). It is also possible to begin to investigate how this matrix was filled during the Vendian–Cambrian diversifications. So far as the Vendian is concerned, very few types are readily identifiable, notably tubes of *Cloudina* (Fig. 1.2.2.2) and sponge spicules. The succeeding basal interval of the Cambrian (Nemakit–Daldyn or Manykay Stage) is also skeletally depauperate, with mostly tubes, shell-like taxa, and protoconodont teeth. Thereafter, however, the

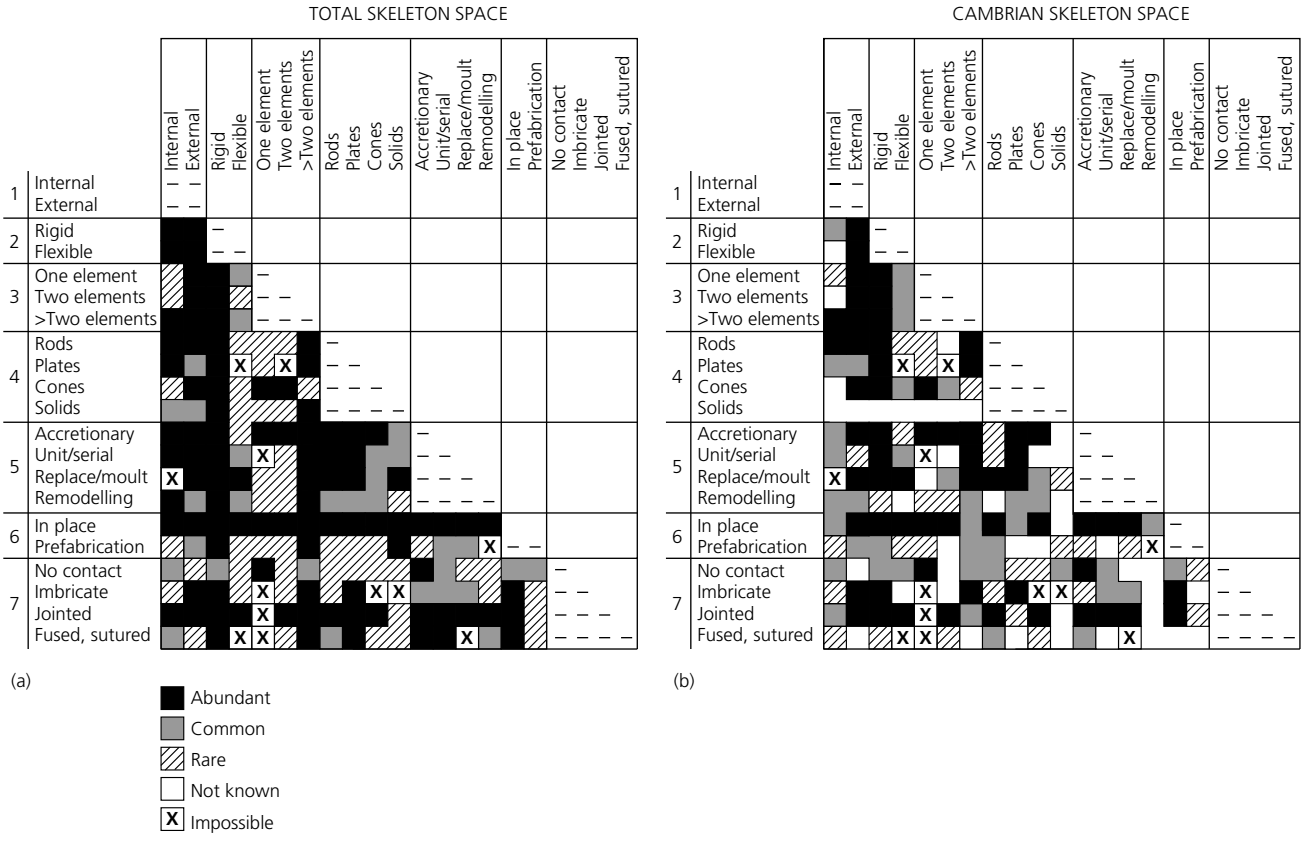


Fig. 1.2.2.4 A depiction of 'skeleton space' whereby a matrix is defined by 21 variables, divided into seven categories, which together define 186 possible pairs of character combinations. Of these a few are functionally impossible, a few others are potentially possible but have not been recognized, and the remainder are variably abundant (rare, common, abundant). (a) Total skeleton space. (Redrawn from Fig. 12 of Thomas and Reif 1993.) (b) Cambrian skeleton space. (Data based on Thomas, R.D.K. and Reif, W.-E. (1991) In: N. Schmidt-Kittler and K. Vogel (eds). *Constructional morphology and evolution*, pp. 283–294.)

'barrel' of skeleton design fills quickly, and Fig. 1.2.2.4(b) attempts to show the situation by the end of the Middle Cambrian. Comparing the two matrices (Fig. 1.2.2.4a,b) it is evident that the post-Cambrian expansion into the known totality of skeleton space was relatively modest, and was most notable in the category of 'solids', i.e. structures such as vertebrate teeth/bones and belemnites.

Taxonomic distribution

In terms of this heading it is convenient to divide the topic into two somewhat artificial sections, relating, respectively, to those groups which are taxonomically 'uncontroversial' vs. those that are more enigmatic. The ultimate aim is to accommodate all these data into a coherent scheme of metazoan phylogeny (Fig. 1.2.2.1). Readers of the future may wish to compare the entries between this *Palaeobiology II* and, say, *Palaeobiology VII* !

By general consensus the most primitive metazoans are sponges. Siliceous spicules of presumed hexactinellids have been identified from Ediacaran-age strata of Mongolia (Brasier *et al.* 1997) and south-central China. The Cambrian record of sponge spicules is more complete, and articulated arrays are well known from Burgess Shale-type faunas. Sponges were also the first major group to form massive calcareous skeletons. These are the archaeocyathids, some of which formed highly integrated skeletons related to an aquiferous system. Much more controversial are the chancelloriids, known from rosettes of hollow sclerites whose growth pattern resembles that of the sachitids and the halkieriids (see below). The chancelloriid body, however, was sponge-like, consisting of a bag-like structure attached to the sea floor with the rosettes scattered over the integument.

The Ediacaran–Cambrian record of cnidarians is rather less satisfactory. The tubes of *Cloudina* (Fig. 1.2.2.2) were conceivably inhabited by some sort of polyp. Structures identified as spicules are also claimed to occur in the Ediacaran frond-like fossils, such as *Charniodiscus*,

whose position as pennatulacean anthozoans seems moderately secure. Nevertheless, the presumed pennatulacean *Thaumaptilon*, from the Middle Cambrian Burgess Shale (Conway Morris 1998), lacks evidence for spicules. In contrast isolated octocoral spicules have been identified with some confidence in the Cambrian. The Cambrian record of corals is unsatisfactory, but putative examples of rugosans and tabulates are recorded. Convincing examples of early conulariids (Fig. 1.2.2.3a) suggest a connection to the scyphozoans, specifically the chitinous tube which in some living taxa houses the polyp which buds in a process known as strobilation. The Cambrian examples, referred to as carinachitids and hexanguloconulariids, appear to have been composed of phosphate minerals, albeit with a liberal addition of organic matter. Their overall form and especially the pronounced tetraradial symmetry are consistent with a cnidarian relationship. What may be a related form is known as *Punctatus*, and this provides a series of remarkable insights into Cambrian ontogeny because it is possible to trace its development, which is direct, from a prehatched embryo to an adult tube (Bengtson and Yue 1997).

In the Cambrian a variety of protostome phyla are well represented in the skeletal assemblages. These include the familiar arthropods, especially trilobites and bradoriids, the brachiopods (inarticulate and articulate), and molluscs. The last group is dominated by cap-shaped fossils, ostensibly monoplacophorans. Also identified in Early Cambrian assemblages are gastropods, rostroconchs, and bivalves. Cephalopods and chitons do not appear in the fossil record until the Upper Cambrian. The monoplacophorans are diverse, but their phylogeny is controversial (Peel 1991). Problems of analysis are compounded by a welter of cap-like objects, of which only a few ultimately may prove relevant to understanding the early evolution of molluscs. Whether or not the first molluscs were segmented, on which hangs a potentially key role for the chitons and certain aplacophorans, has been extensively but inconclusively debated. Skeletal remains, by themselves, are unlikely to resolve this issue.

Brachiopods are conspicuous in Cambrian assemblages, but here too the story is far from simple. Inarticulates probably predate articulates stratigraphically, but their interrelationships are obscure. Some inarticulate groups, notably the kutorginiids and mickwitziids, have unusual morphologies. The former have been identified, tentatively, as intermediates between the inarticulates and articulates. Mickwitziids are notable for their large shell size and complex microstructures: are they actually brachiopods? Other groups are yet more enigmatic. Helpfully labelled the 'pseudobrachiopods', this group of apparently bivalved shells are best known from South Australia, but also have representatives in China. The valves are deeply convex, have protuberances and corresponding recesses suitable for articulation, and areas for muscle insertion. Nevertheless, the best-known taxon *Apistoconcha siphonalis* (Fig. 1.2.2.5a) is peculiar in having margins between the opposing valves that are far from congruent. One suggestion is that the 'gaps' were filled with smaller plates; another possibility looks towards a halkieriid-like model (see below).

The arthropod record is dominated by the calcareous skeletons of trilobites. In certain groups, such as the burlingiids, the exoskeleton is conspicuously thin, whilst in the related naraoiids there is no mineralization. Amongst the bradoriids, which have traditionally been placed amongst the ostracods but are now regarded as a distinctive group, some taxa have phosphatic valves. As with any group discussed here a coherent discussion of biomineralization can only be achieved in the context of an agreed phylogeny (Fig. 1.2.2.1). For arthropods morphological character analysis has provided a series of cladograms. These, however, show various discrepancies with data from molecular biology, which in turn throw doubt on the phylogenetic reality of such concepts as the Atelocerata (= myriapods + insects). It is also clear from the Burgess Shale-type faunas (Conway Morris 1998) that the great majority of arthropods lacked cuticular mineralization. Moreover, in the stem-group lobopodians the bosses and spines that characterize the 'armoured' varieties are either heavily cuticularized (e.g. *Hallucigenia*) or, in the case of *Microdictyon*, are composed of a reticulate disc of phosphate. Whilst a defensive role for this structure is generally agreed, the reasons for phosphatic biomineralization in *Microdictyon* are not known.

Amongst the deuterostomes there are only mineralized remains of echinoderms, although the organic tubes of hemichordates are also recognized. The unique structure of the stereom skeleton of echinoderms permits easy identification of isolated ossicles. Rarer examples of articulated material, typically preserved in obrution deposits, reveals a bewildering array of groups, including 'eocrinoids', helicoplacoids, solutans, cinctans and ctenocystoids. The origin of the stereom tissue is obscure, but one might speculate that it was preceded by a mesodermal zone of collagenous fibrils that acted as a template. In the Burgess Shale animal *Echmatocrinus*, which has been interpreted as a primitive crinoid, the thin plates that coat the surface would be interpreted as a reduced stereom. An alternative proposal, however, places *Echmatocrinus* in the anthozoan cnidarians. The early phylogeny of chordates remains very controversial. Unequivocal chordate biominerals do not occur until the Middle Cambrian if, that is, the phosphatic elements of the paraconodonts (Müller and Hinz-Schallreuter 1998) are correctly identified as the teeth-like precursors of those seen in the euconodonts, or if the fragmentary remains of the Upper Cambrian *Anatolepis* are accepted as the earliest fish scales.

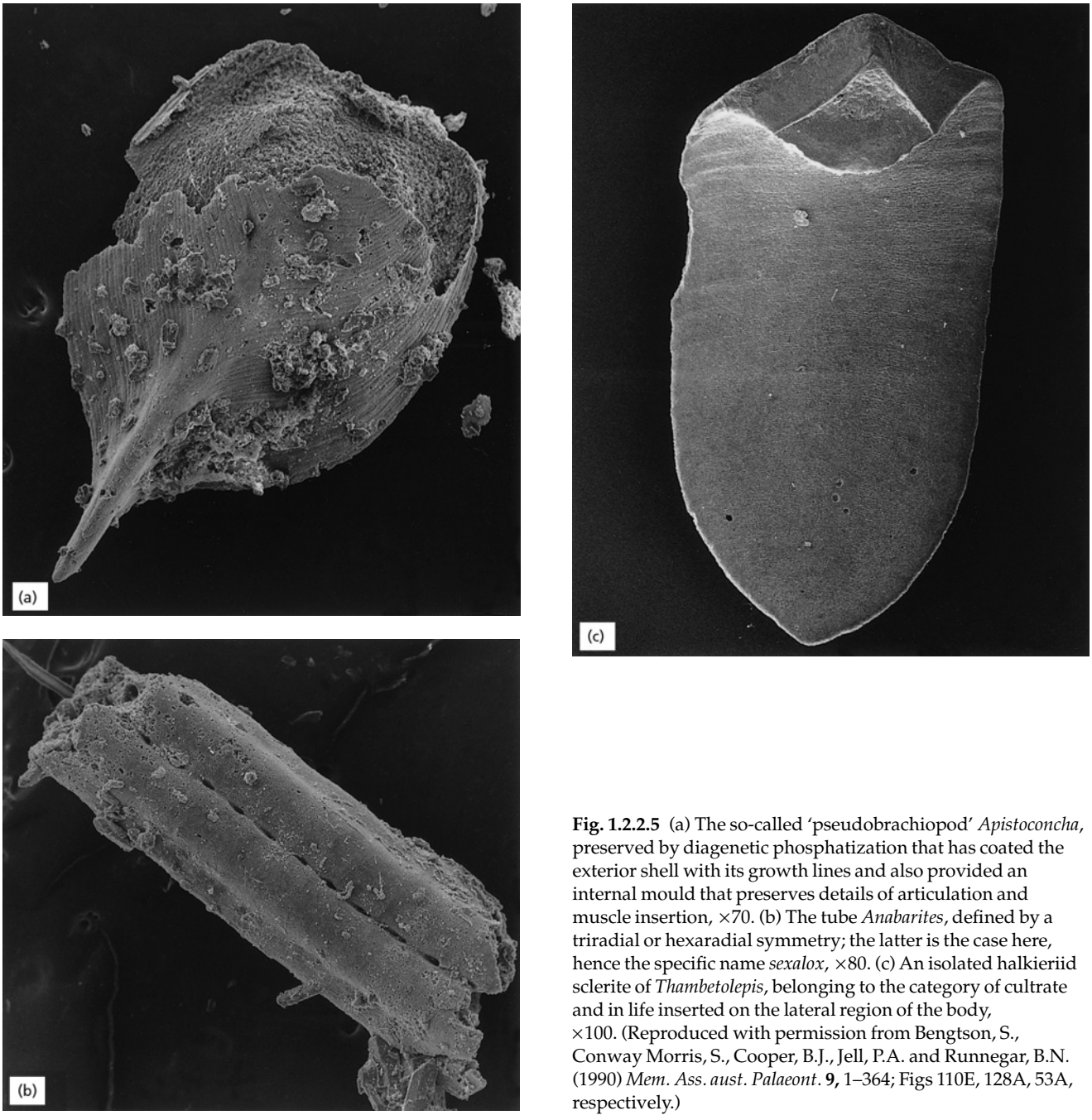


Fig. 1.2.2.5 (a) The so-called 'pseudobrachiopod' *Apistoconcha*, preserved by diagenetic phosphatization that has coated the exterior shell with its growth lines and also provided an internal mould that preserves details of articulation and muscle insertion, ×70. (b) The tube *Anabarites*, defined by a triradial or hexaradial symmetry; the latter is the case here, hence the specific name *sexalox*, ×80. (c) An isolated halkieriid sclerite of *Thambetolepis*, belonging to the category of cultrate and in life inserted on the lateral region of the body, ×100. (Reproduced with permission from Bengtson, S., Conway Morris, S., Cooper, B.J., Jell, P.A. and Runnegar, B.N. (1990) *Mem. Ass. aust. Palaeont.* **9,** 1–364; Figs 110E, 128A, 53A, respectively.)

Enigmatic taxa

Early Cambrian skeletal faunas are well known for their large number of enigmatic taxa, and many Cambrian taxa remain refractory to analysis. This area is best considered in terms of two categories: tubes and scleritomes. The former are a conspicuous component of many Early Cambrian assemblages. Some are simple and are composed either of calcium carbonate (e.g. coleolids), or phosphatic minerals (e.g. hyolithellids). It is likely that they were built by an annelidan-grade organism, but no direct proof is available. Tubes with three- or six-fold symmetries are known as anabaritids (Fig. 1.2.2.5b). A tenuous link has been proposed between the anabaritids and various Ediacaran fossils, most notably *Tribrachidium*, which also display a three-fold symmetry and may be cnidarian (Fig. 1.2.2.1).

In none of these cases is there unequivocal evidence for an operculum, although a possible instance in an anabaritid from central China is on record. Amongst the various proposals for the function of the phosphatic mobergellans (Fig. 1.2.2.3b), that of an operculum

receives some support. The interior displays prominent muscle scars arranged about a plane of bilateral symmetry. Their microstructure varies, and in a species from south-west Mongolia the equivalent structures consist of a plaque containing an array of radiating fibres. The hypothesis that mobergellans represent an operculum suffers some problems in as much as corresponding tubes have not been recognized. One possibility is that, for some reason, the tube was much more lightly mineralized than the phosphatic disc. An alternative is that mobergellans were either univalved, in a manner reminiscent of monoplacophorans, or even bivalved.

The importance of scleritomes in the Cambrian has become increasingly clear in recent years. Two notable breakthroughs concern the halkieriids (Fig. 1.2.2.5c) and the hadimopanellids. Prior to the discovery of *Halkieria evangelista* from the Sirius Passet Lagerstätte in North Greenland (Conway Morris and Peel 1995), reconstructions of halkieriids largely relied on comparisons with articulated material of *Wiwaxia corrugata*. The Greenland material demonstrates a slug-like animal with a sclerite composed of 2000 sclerites and, more surprisingly, a prominent shell at either end of the body. This cataphract arrangement is consistent with a protective role, while the shells in addition may have acted, respectively, as a platform for muscle insertions (anterior) and a covering for a respiratory chamber possibly housing ctenidia (posterior). The biomineral employed was probably aragonite, but there is a clear dichotomy of secretory styles in *Halkieria* between the interpolation of sclerites, which remain at a fixed size, as against growth along an accretionary margin in either shell. Halkieriid sclerites had already been widely recognized as isolated fossils, but the recognition of the *in situ* shells has promoted a reconsideration of various cap-like shells, isolated in acid-etched residues, as possibly being derived from halkieriid-like skeletons.

The clear similarities between siphogonuchitid and ninellid (Fig. 1.2.2.1) (and perhaps sachitid) sclerites and those of halkieriids also invites application of a scleritome model. In the case of the siphogonuchitids, the scleritome, which has yet to be recognized in an articulated form, may have been more primitive in having only two main types of sclerite and a shell composed of sclerites embedded in a ground-mass. In the less well-known ninellids, and possibly sachitids (which some workers suggest are related to the chancelloriids), the sclerite complement may have been more uniform. Finally, in some related groups the sclerites may have either been lost or become unmineralized, whereas the terminal shells remained mineralized. Such might apply to *Oikozetes* from the Burgess Shale, and possibly the 'pseudobrachiopods' (Fig. 1.2.2.5a) (Parkhaev 1998), both of which are known from two distinct types of shell.

The halkieriids (and wiwaxids) have also been given a wider significance as potentially occupying a key position in early protostome evolution (Conway Morris and Peel 1995). As well as having a generalized and possibly superficial similarity to the chitons and aplacophorans, widely believed to resemble primitive molluscs, there are more specific similarities to the brachiopods and annelids. The implications for this hypothesis are yet to be explored (or refuted), but whatever the origins of the bivalved brachiopods, the two valves never derived from a single plate which developed a median zone of weakness, as was the case in bivalves and the juliid gastropods, as well as ostracods and other bivalved arthropods. Brachiopods lack a ligament and each valve must have been derived from separate growth centre.

Hadimopanellid sclerites were first recognized in 1977, and in the absence of articulated material speculation on their affinities was virtually unconstrained: even chordates were proffered as a possibility. It was, however, clear that the most probable function was as a dermal armour. Recognition of phosphatized pieces of cuticle, discovery of exceptionally preserved material in Ordovician nodules, and re-examination of the type species of *Palaeoscolex* (*P. piscatorum*) revealed that the sclerites formed a closely packed cuticular array (Fig. 1.2.2.3d). It is now clear that hadimopanellids are effectively synonymous with the palaeoscolecidans (which include the Burgess Shale taxon *Louisella*), and that they are either priapulid worms or very closely related. Living priapulids have complex cuticular structures, but these are unmineralized and seem to have no close similarities to those found in the Cambrian. The diversity of Cambrian priapulids is incompletely surveyed. *Cricocosmia* from the Chengjiang Lagerstätte, in which the trunk bears two rows of prominent boss-like sclerites, is a reminder that other enigmatic skeletal material in the Cambrian may yet find a home in the priapulids.

Concerning other skeletal remains that almost certainly were arranged in a scleritome, the two principal groups are the cambroclaves and tommotiids. The former are calcareous, and small arrays reveal a tightly integrated scleritome (Fig. 1.2.2.6a). A more primitive state may have consisted of a scleritome with nail-like sclerites scattered over an integument. As with a number of other Cambrian groups, the taxonomic limits of the cambroclaves are fuzzy. Most probably the paracarinachitids belong here, but their proposed assignment to the chitons is highly questionable. The wider affinities of the cambroclaves are not known.

The tommotiids, despite being comparatively well understood, still defy a secure phyletic placement. The original mineralogy was phosphatic, and the sclerites show a wide variation of form encompassing taxa such as *Paterimitra* (Fig. 1.2.2.3c), *Eccentrotheca*, *Lapworthella* (Fig. 1.2.2.6b), *Micrina*, *Dailyatia*, *Camenella*, and *Tann-*

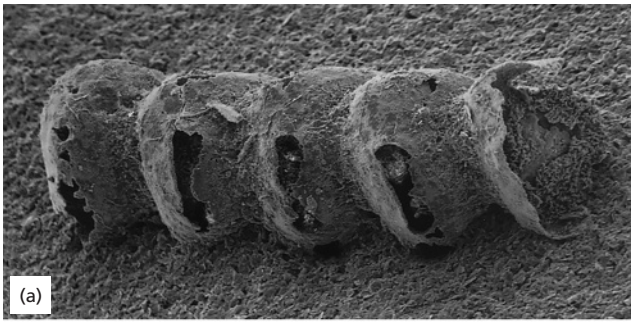




Fig. 1.2.2.6 (a) An articulated array of the cambroclave *Deltaclavus*, Lower Cambrian, Shuijingtuo Formation, Hubei, China, ×100. (Reproduced with permission from Conway Morris, S. and Chen, M. (1991) *Palaeontology* **34,** 357–397; Fig. 9c.) (b) An isolated sclerite of the tommotiid *Lapworthella*, Lower Cambrian, New York, ×270.

uolina. In the last two genera there is evidence of two sclerite morphs, whereas the scleritome of *Dailyatia* was apparently more complex. Left and right morphs point to a bilaterally symmetrical animal. Yet in *Lapworthella* such distinctions are not possible despite well-ordered patterns of sculpture, whilst *Eccentrotheca* can only be described as disorganized (the specific name *guano* was not given lightly). Even more confusingly *Micrina* has what appears to be articulatory teeth, but no counterpart against which to articulate. Tommotiids may, of course, be polyphyletic. Taxa such as *Tannuolina* and *Micrina* bear striking similarities to brachiopods, yet may be convergent. Discovery of the tommotiid scleritome is eagerly awaited.

Future work

Although the skeletal record provides important insights, taken alone it will remain incomplete if not misleading. Exceptional preservation in the form of Burgess Shale-type faunas and early phosphatization (including Orsten assemblages) will provide the main drivers of enquiry. As molecular biology has contributed to the framework of metazoan phylogeny, so too will it underpin our understanding of the processes of biomineralization. In these ways we will not only gain additional insights into the Cambrian 'explosion' but also unravel those evolutionary trajectories that led, ultimately, to the femur of a skier and the shell of a garden snail.

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1.2.3 Cambrian Food Webs

N.J. BUTTERFIELD

Introduction

Food webs are descriptions of who eats whom within a community, thereby tracking energy flow through the system and, to an important degree, characterizing its ecological structure. Clearly any palaeoecological analysis would be greatly served by a detailed accounting of its food web. Nowhere is this more so than in the Early Cambrian when, following approximately three billion years of relatively simple microbially dominated ecologies, large energetic animals were suddenly thrust into the equation. Whatever its ultimate causes, this Cambrian 'explosion' of metazoans necessarily involved a revolution in new types of feeding strategies and a fundamental expansion of ecological interactions. The Proterozoic–Phanerozoic transition thus stands as a unique interval witnessing the construction of modern-style food webs, and their myriad and mutual feedback effects on the environment and biogeochemical cycling. Is it possible to track that development?

All trophic structures are based ultimately on a source of primary productivity which, in the present context, can be considered as that provided by marine photosynthesis. Very simplistically, the energy captured in this process travels up a food chain via herbivores to primary, secondary, and even tertiary carnivores, and is returned to the system via respiration. With an average transfer efficiency of <10% between trophic levels, it is not surprising that food chains leading to large carnivores are characteristically short (typically comprising three or four links; Pimm *et al.* 1991), and that most of the biomass and metabolism of an ecosystem is concentrated near the base of the trophic pyramid. In the real world, of course, most prey have multiple predators and most predators have multiple prey; thus, the overall pattern of metabolic exchange in most communities appears as a reticulate web rather than a simple chain. Moreover, when omnivores, mixotrophs, detritivores, parasites, and other forms that defy simple trophic categorization are included in the equation, as well as a range of *indirect* effects (where the direct effects of one species on another alters the abundance of a third; Menge 1995), the system can become enormously complex. One potential advantage in considering the trophic structure of Early Cambrian communities is that it might represent a stage where the system was still simple. Alpha-level diversity appears to have been relatively low, and many of the complicating effects of scale and specialization are likely to have been limited or absent.

Reconstructing Cambrian trophic structures

Ancient food web analysis faces the fundamental problem of postmortem information loss. Taphonomic processes inevitably produce a fossil assemblage that only dimly mirrors the life assemblage from which it was drawn, and there is the obvious difficulty of determining trophic behaviour solely from fossil morphology. Because most organisms in most environments lack a mineralized skeleton, the exceptional preservation of non-mineralizing organisms necessarily becomes a focus of any detailed palaeoecological analysis (Conway Morris 1986). Within this context, trophic structure can be addressed through a combination of: (1) gut-content analysis; (2) functional morphology, with habit being inferred from mechanical optimality and modern analogues; (3) fossil associations that point to particular trophic relationships; (4) trace fossil analysis, including assessment of coprolite contents and various feeding traces; (5) addition by inference, or a 'fleshing out' of the community based on the recognition of coevolved characteristics (e.g. defensive adaptations imply the presence of predators); (6) inference from phylogeny; and (7) theoretical assessment of food webs.

In level-bottom environments, the most comprehensive palaeoecological analysis has been carried out on the Middle Cambrian Burgess Shale (Conway Morris 1986), but even here there is little direct evidence of trophic linkage. Although the alimentary canals of a number of taxa are preserved, identifiable contents are

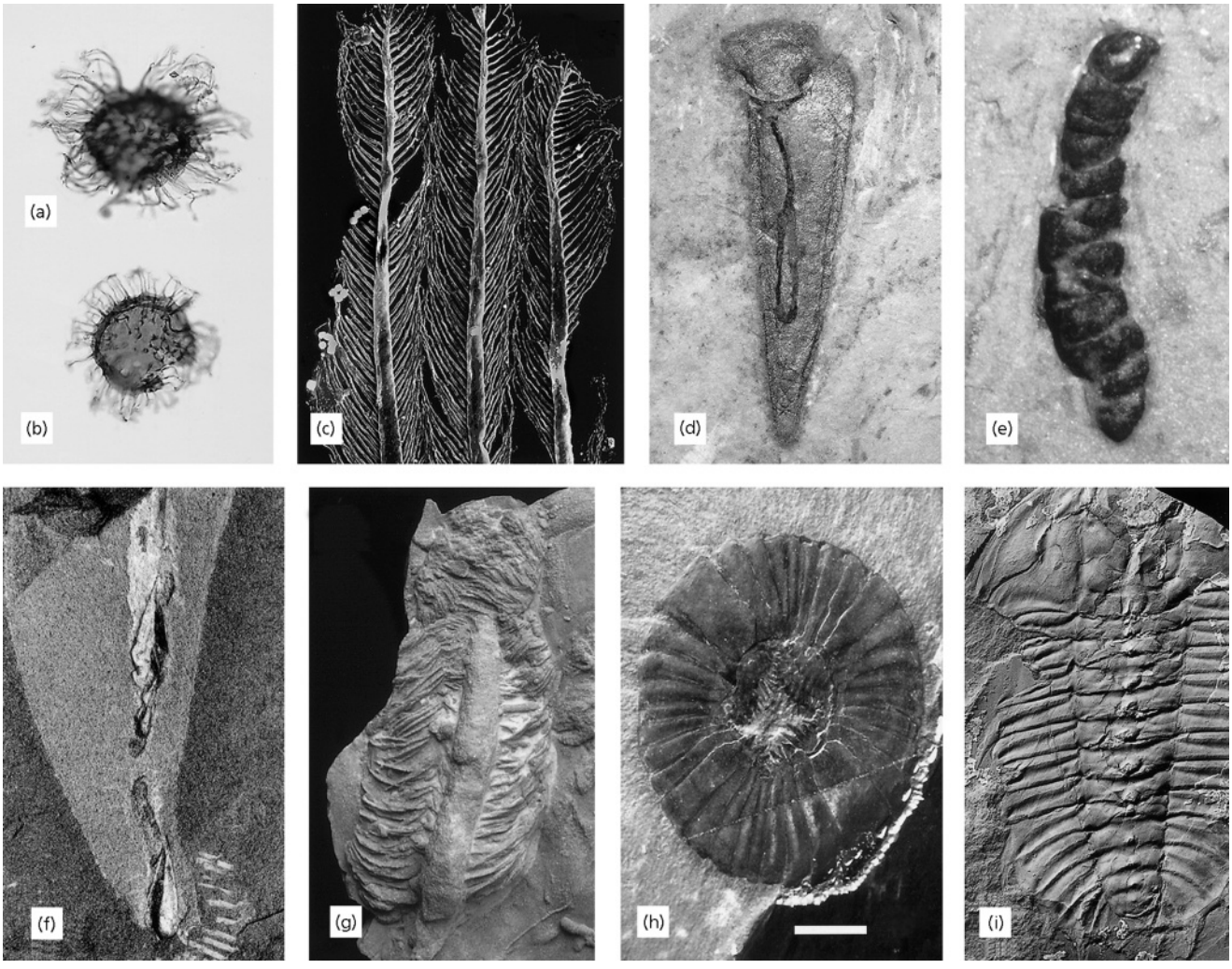


Fig. 1.2.3.1 Representatives of various Early and Middle Cambrian trophic levels. Together these can be arranged as a food chain of up to six tiers, e.g. phytoplankton primary producer (acritarch) → zooplankton herbivore (filter-feeding arthropod) → benthic suspension feeder, possibly a primary carnivore (hyolithid) → benthic secondary carnivore (priapulid) → benthic, possibly tertiary, carnivore (trilobite) → nektonic top predator (anomalocaridid). (a & b) Typical Cambrian acritarchs with a spinose or acanthomorphic ornament, Lower Cambrian, Topiggane Formation, Spitsbergen (courtesy of A.H. Knoll). (c) Arthropod filter apparatus, upper Lower Cambrian, Mount Cap Formation, NW Canada. (d) Hyolithid with simple, sediment-free, phosphatized gut, Middle Cambrian, Mount Cap Formation. (e) Phosphatized faecal string, Middle Cambrian, Mount Cap Formation. (f) Posterior part of priapulid worm *Ottoia* with ingested whole hyolithids, Middle Cambrian, Burgess Shale, SW Canada (courtesy of S. Conway Morris). (g) Hunting trace of arthropod and its prey, an infaunal 'worm', Lower Cambrian, Mickwitzia Sandstone, Sweden (courtesy of S. Jensen). (h) Mouth apparatus of an anomalocaridid, Middle Cambrian, Burgess Shale. (i) Trilobite with non-fatal bite-mark (upper left), Middle Cambrian, Stephen Formation, SW Canada (courtesy of D.M. Rudkin). Scale bar in (h) represents approximately 20 µm for (a) and (b); 10 µm for (c); 2 mm for (d); 1 mm for (e); 5 mm for (f); 10 mm for (g), (h) and (i).

sparse: the gut of the large arthropod *Sidneyia* has been shown to include the remains of a hyolithid, a small trilobite, and comminuted shelly material (possibly bradoriids), whereas the priapulid worm *Ottoia* clearly ingested whole, live hyolithids (Fig. 1.2.3.1f) and may also have engaged in cannibalism. At a slightly lower level of confidence, functional morphology supplemented by phylogenetic inference provides a reasonable measure of trophic status. Thus, acritarchs and algae represent primary productivity in the Burgess Shale community; sponges, chancelloriids, brachiopods, stalked echinoderms, and sea-pen-like forms were engaged in sessile filter-feeding or suspension feeding; the arthropod *Odaraia* was a nektonic suspension-feeder; and various trilobites, chaetognath-like forms, and anomalocaridids were probably carnivores. An association of the lobopo-

dian *Aysheaia* with sponges suggests that it may have been parasitic on them. The remainder (and majority) of the Burgess Shale forms remain poorly resolved trophically, but most likely represent various types of grazers and detritivores.

A detailed quantitative analysis revealed that the Phyllopod Bed community (the erstwhile principal unit of the Burgess Shale) contained most of the trophic habits seen in modern marine communities, though perhaps extending only to the level of primary carnivores (Conway Morris 1986).

Taphonomic bias of course applies to any fossil assemblage, and in the Phyllopod Bed it appears to favour relatively large benthic metazoans: zooplankton and nekton are rare, as are meiofauna and truly soft-bodied forms lacking a recalcitrant cuticle; sedimentary trace fossils are entirely absent. If the dearth of these forms is artefactual, as appears to be the case, then it may be more useful to look at early metazoan ecosystems in a more qualitative way—what trophic interactions can be discerned for the Early to Middle Cambrian as a whole? Discovery of Early Cambrian filter-feeding zooplankton (Fig. 1.2.3.1c), for example, reveals an early and sophisticated metazoan exploitation of the water column; a hyolithid preserved with a simple, sediment-free gut (Fig. 1.2.3.1d) establishes a suspension-feeding habit for these common but enigmatic Cambrian fossils; diverse coprolites (e.g. Fig. 1.2.3.1e)—some containing acritarchs, others comminuted lingulid shells—record the activities of vagrant herbivores and prey-selective carnivores; centimetre-scale vertical burrows packed with skeletal debris are interpreted as the stomach contents of shell-breaking cnidarians (Alpert and Moore 1975); borings, particularly in brachiopod valves, indicate specialized adaptations for penetrating shelled prey (Conway; Morris and Bengtson 1994); intersecting trace fossils suggest that arthropods actively hunted infaunal 'worms' (Fig. 1.2.3.1g; Jensen 1990); and healed injuries on trilobites (Fig. 1.2.3.1i) point to the presence of a large biting predator (often suggested to be an anomalocaridid, although it is difficult to envisage how the *Peytoia* mouthpiece (Fig. 1.2.3.1h) might have effected these particular bites). Taken together, these disparate data point to the likelihood that some Early Cambrian food chains extended to five or six tiers (Fig. 1.2.3.1), and included an overall range of fates and behaviours similar to that in modern food webs. The principal difference between the trophic structures of the Early to Middle Cambrian and Recent would seem to be one of intensity and increasing *breadth* of food webs (as opposed to *length* of food chains). This in turn is likely to be a consequence of increased alpha-level diversity and long-term escalation.

Early evolution of food webs

The simple identification of who eats whom, of course, reveals little about the dynamics of a food web, especially during the evolution of new behavioural repertoires. The direct effects of ecological interactions (e.g. competition, coevolution, escalation, symbiosis, exploitation of vacant ecospace) are well appreciated and have been a principal focus for explaining evolutionary radiations. Studies of modern marine food webs, however, suggest that as much as half of the adjustments a community makes to trophic perturbations derive from *indirect* effects such as keystone predation, trophic cascades, 'apparent competition', and 'habitat facilitation' (Menge 1995), not to mention the broader concepts of key innovations, key species, and 'ecosystem engineering' (Lawton and Jones 1995). Moreover, a recognition that shifts in trophic structure can cascade both down and up food chains multiplies the potential effects of trophic innovation, and raises the issue of whether marine ecology is controlled primarily from the 'bottom up' (i.e. by nutrients, primary productivity, and small organisms) or from the 'top down' (i.e. by predation and larger organisms). If a case can be made for some of these ecological effects—direct or indirect—scaling up to an evolutionary level (Jablonski and Sepkoski 1996), then there is a sound basis for explaining the Cambrian 'explosion' as an ecological phenomenon.

Food webs must have started off simply (i.e. as chains) and been built from the bottom up (e.g. the evolution of carnivores was obviously preceded by that of herbivores, etc.). Thus, for a time, every newly evolved tier served as 'top predator'. The effects of such addition to the top of an accreting trophic pyramid would, in the first instance, have cascaded down, triggering adaptive (presumably defensive) responses in underlying levels. It would also, however, have set the scene for the evolution of yet another tier above. Thus the simple evolution of heterotrophs—a key innovation—may have induced a mutual feedback system of diversification between trophic levels, rapidly escalating to give rise to a fully fledged Cambrian ecosystem (Stanley 1973). Recent advances in Proterozoic palaeontology preclude a blanket application of this 'cropping hypothesis', but it does appear to hold when applied to the Proterozoic–Cambrian plankton record (Butterfield 1997). Notably, the phytoplankton, which represents the vast majority of all marine primary productivity, underwent a major diversification in the Early Cambrian, in marked parallel with the Cambrian radiation of large animals. Since phytoplankton ornamentation (Fig. 1.2.3.1a,b) is invisible to most large animals, it would appear that its sudden diversification was a top-down response to the grazing activities of small animals newly introduced to the plankton. Indeed, alongside the direct evidence of

fossil meso-zooplankton (Fig. 1.2.3.1c), the phytoplankton record itself can be interpreted as a proxy for the evolution of Early Cambrian zooplankton. Zooplankton make up the bulk of animal biomass in modern oceans and, by repackaging unicellular phytoplankton as nutrient-rich particles some 10–100 times as large, link the microscopic world of marine primary productivity to the macroscopic world of large animals. The evolution of meso-zooplankton may thus have been the key innovation behind the Cambrian 'explosion' of large animals.

Although clearly a prerequisite for large animals in the pelagic realm, the effects of zooplankton evolution on benthic ecology are less immediately obvious. Rapid sedimentation of zooplankton faecal pellets has been invoked in the oxygenation of the late Proterozoic sea floor (Logan *et al.* 1995), and would also have enhanced the benthic delivery of labile, nutrient-rich organic compounds (see Section 1.1.4). At the same time, the simple effect of repackaging phytoplankton into much larger particles would have produced a more concentrated and exploitable resource for the contemporaneous benthos. Burrowing, in particular, is likely to have increased in response to the introduction of zooplankton faecal pellets, which in turn would have had profound consequences on the physical, chemical, and biological characteristics of sediments, fundamentally altering the benthic environment. Such far-reaching effects may account for much of the major biogeochemical perturbation that accompanied the Proterozoic–Phanerozoic transition (e.g. C isotope shifts, major phosphogenic events). This is often viewed as a cause of the Cambrian radiations through a bottom-up injection of nutrients, but is more likely—at least in the first instance—to be a top-down consequence of adding the new tier of zooplankton (Butterfield 1997). There are, of course, other behaviours that link the pelagic and benthic realms, although these may be of more limited or local importance. They include benthic suspension feeding, most notably in the widespread development of archaeocyathid reefs in the Early Cambrian, benthic grazing and predation by pelagic organisms (e.g. anomalocaridids), and the activities of planktotrophic metazoan larvae. All of this inevitably resulted in a more closely coupled and mutually dependent plankton and benthos, and an increasingly complex trophic structure. As links multiplied, and food webs increased in breadth and complexity, the strength and predictable consequences of particular links was necessarily reduced. By the same token, however, the stability of the system was surely enhanced as routes through the food web became increasingly varied (cf. McCann *et al.* 1998). Thus, paradoxically, the very simplicity of early metazoan ecosystems made them singularly susceptible to change.

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1.2.4 The Origin of Vertebrates

M.P. SMITH and I.J. SANSOM

Introduction

Although pre-Silurian vertebrates have been known since the late 1880s, they have generally been considered to be low in diversity and a relatively insignificant prelude to the principal radiation of the group in the Late Silurian and Devonian. Recent discoveries have demonstrated, however, that Ordovician vertebrate faunas are not only more abundant and widespread than hitherto suspected but also contain a far greater diversity of groups. Furthermore, there is now firm evidence that the fossil record of vertebrates extends farther back in time, into the Cambrian, and that their initial radiation was underway during this period.

Ordovician vertebrates were first discovered by the United States Geological Survey in the Harding Sandstone of south-eastern Colorado, USA. The specimens were drawn to the attention of Charles D. Walcott (also

notable for his later discovery of the Burgess Shale), who published a description of the vertebrate fauna in 1892. Reports of Ordovician vertebrate remains from outside North America remained extremely limited, and often erroneous, and it was not until the latter decades of the twentieth century that agnathan remains of this age were firmly identified elsewhere. The first reports were from the Amadeus Basin, Northern Territory, Australia, where complete, articulated specimens of the genus *Arandaspis* are present. A related genus, *Sacabambaspis*, occurs in the Llanvirn of Bolivia and Argentina. These two taxa are united within the Arandaspida (Fig. 1.2.4.1) (Forey and Janvier 1994), the key characters of which include dorsal and ventral headshields formed from single large plates, paired openings to the pineal and parapineal photosensory organs, extreme anterior positioning of the eyes, and multiple branchial ducts covered with protective rhombic plates and arranged in a slanting row. Specimens of *Sacabambaspis* also include details of the oral region, rarely preserved in agnathans, where the lower 'lip' bears a series of finger-like structures, covered in minute scales, that may have opened like a fan to assist in feeding. Disarticulated microvertebrate remains have also been recorded from the Ordovician of Australia, and include arandaspids together with some unassigned forms. Ordovician microvertebrate material is also known from the Timan-Pechora province of Russia and, more equivocally, from North China. However, with the exception of the Harding Sandstone faunas, diversity remains low at all of these localities on the basis of current evidence.

The Harding Sandstone of Colorado

The Harding Sandstone Formation is a thin unit of quartz arenite which was deposited during middle Caradoc (Ordovician) time along the south-eastern flank of the Transcontinental Arch, a ribbon of emergent basement which ran south-west to north-east from Arizona to Wisconsin during the Ordovician. The sediments are exclusively marine, were deposited in an inner shelf to shoreface transition, and contain a fauna which includes cephalopods, bivalves, and conodonts, in addition to the fish fauna. Walcott documented three vertebrate taxa:

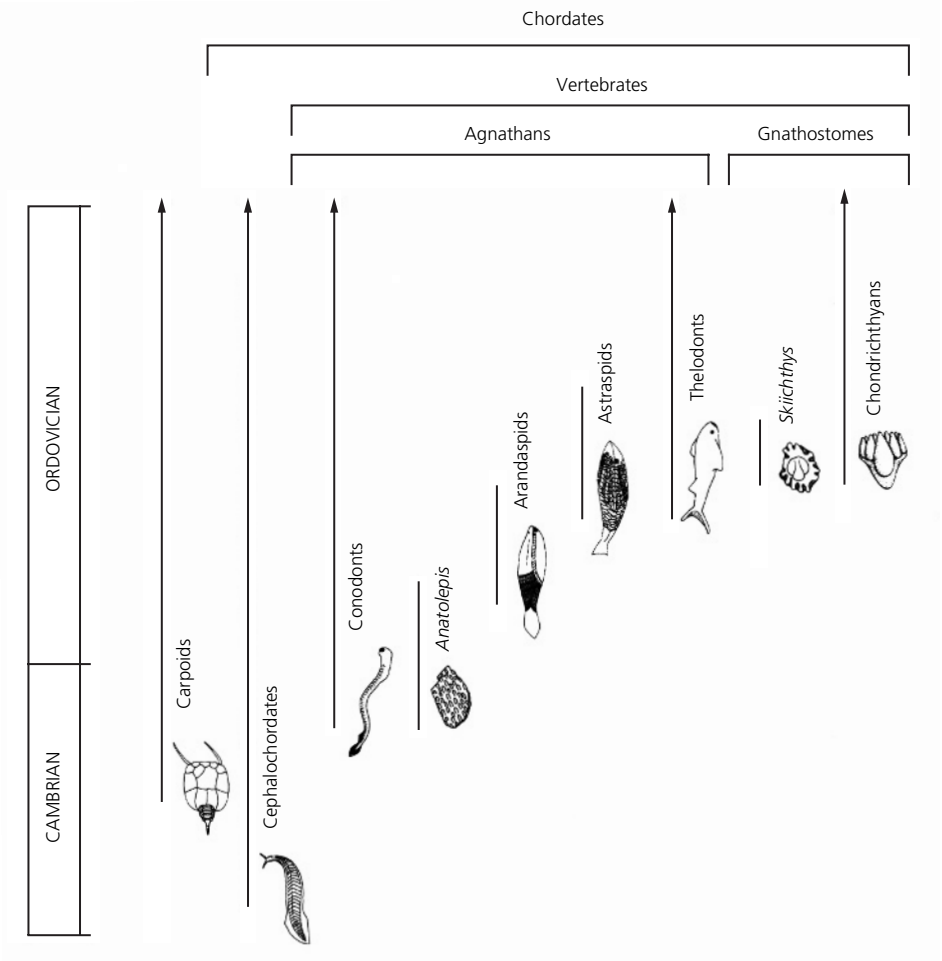


Fig. 1.2.4.1 Stratigraphic distribution of Cambrian and Ordovician vertebrates, together with carpoids and cephalochordates.

Astraspis desiderata, *Eriptychius americanus*, and *Dictyorhabdus priscus*. The last was described by Walcott as the notochordal sheath of a chimeroid chondrichthyan (the group to which extant rat fish and elephant fish are assigned) but subsequent histological investigations have shown that it is not a vertebrate; its zoological affinities remain enigmatic. *Eriptychius* is known from abundant disarticulated exoskeletal fragments, but *Astraspis* is the only genus which is sufficiently well preserved to permit detailed anatomical studies. The taxon differs markedly from the arandaspids of Australia and South America in the possession of a tesserated headshield, open branchial ducts, a covered pineal region, and the presence of dentine and enameloid which forms the raised tubercular ornament of the exoskeletal plates (Sansom *et al*. 1997). *Astraspis* and the arandaspids are not closely related, although both constitute sister groups to a more advanced group of agnathans, the heterostracans (see Fig. 1.2.4.3a) (Forey and Janvier 1994).

Recent micropalaeontological work has revealed that the vertebrate biodiversity of the Harding Sandstone has been considerably underestimated. These studies of individual isolated scales, plates, and fragments have revealed disarticulated remains of at least 10 other taxa, in addition to the heterostracomorph agnathans *Astraspis* and *Eriptychius*, which together comprise some 90% of the residues. Significantly, these not only contribute to an overall increase in species diversity, but also represent the first appearances of a number of major fish groups. One of these taxa, *Skiichthys halsteadi*, has scale morphologies and histology which suggest a relationship with either the acanthodians or placoderms, and indicates the possible presence of gnathostomes (jawed fish) in the Ordovician (Smith and Sansom 1997). Further evidence for the presence of mid-Ordovician gnathostomes comes from shark-like scales which also occur in the sandstone (Sansom *et al.* 1996). Together, these indicate that the origin of gnathostome fish does not form part of the Silurian radiation of fish groups, as traditionally believed, but lies in the early part of the Ordovician.

Cambrian vertebrates

Although the occurrence of a small number of species of Ordovician fish has been accepted since Walcott's original description, the same cannot be said of Cambrian vertebrates, the existence of which has remained hotly disputed. *Anatolepis* was first described from the Valhallfonna Formation (Arenig–Llanvirn, Ordovician) of north-eastern Spitsbergen as a heterostracan agnathan. Fragments of exoskeletal armour assigned to the genus (Fig. 1.2.4.2a) have subsequently been found from a large number of localities in Laurentia, the North American palaeocontinent, in sediments ranging from Late Cambrian to late Early Ordovician age. Although initially described as a vertebrate, *Anatolepis* was not widely accepted as such for many years, with alternative hypotheses of affinity centring on the similarity of the scales to the armour of some merostome arthropods. Histological work on Cambrian and Ordovician material has, however, demonstrated that the ornamented tubercles are formed of typical dentine (M.P. Smith *et al.* 1996), a tissue found only within vertebrates (Fig. 1.2.4.2b). Each tubercle is underlain by a pulp cavity from which dentine tubules radiate before further subdividing to produce a terminal dentine network close to the surface of the scale. The individual tubercles are connected by a lamellar tissue which grew centrifugally and contains

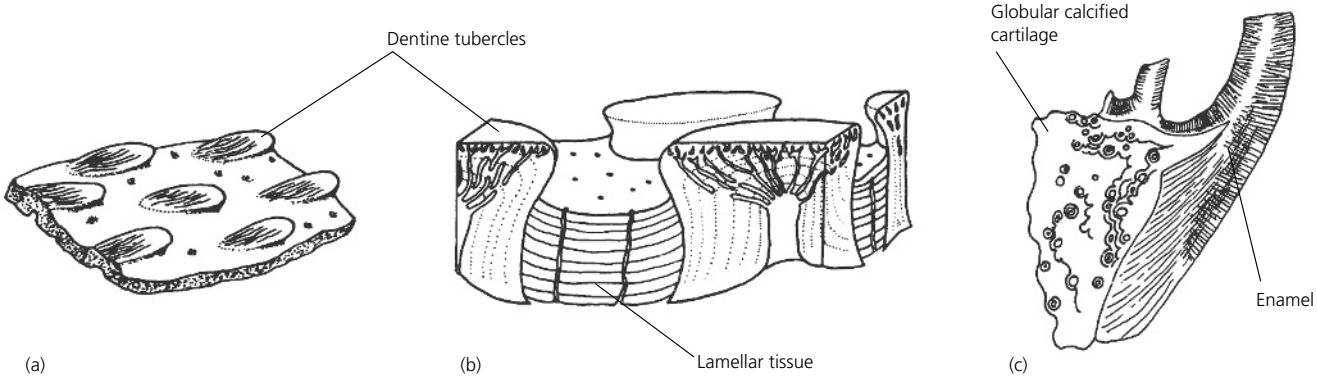


Fig. 1.2.4.2 Cambrian vertebrates. (a) Fragment of exoskeletal armour of the Late Cambrian–Early Ordovician fish *Anatolepis*. (b) Block diagram of the distribution of hard tissues in *Anatolepis*. (c) Line drawing to illustrate tissue distribution in the Late Cambrian–earliest Ordovician conodont *Cordylodus*. (b, After M.P. Smith *et al.* 1996.)

pore canals. Cambrian scales have also been claimed from Australia, but in this case the histology is rather equivocal and confirmation awaits the description of further material. The presence of *Anatolepis*, together with conodonts (see below), in the Late Cambrian demonstrates not only that vertebrates had made their first appearance by the end of the Cambrian, but also that their initial diversification was underway by this time.

Evidence for vertebrates deeper into Cambrian time is scanty and more equivocal, but for more primitive chordate sister groups it is more secure. *Pikaia* from the Burgess Shale is perhaps the most widely known prevertebrate chordate fossil taxon (Fig. 1.2.4.1) and is of probable cephalochordate affinity. Its anatomy is broadly comparable with that of extant cephalochordates (amphioxus) although it does differ in having short protrusions in the pharyngeal area and a pair of anterior tentacles. A recently described, and older, specimen from the Chengjiang Lagerstätte of China (see Section 3.4.3) is closer in size and morphology to extant representatives of cephalochordates, including the presence of multiple narrow pharyngeal openings, through which efferent water passed (Shu *et al.* 1996). *Metaspriggina*, another Burgess Shale taxon, is a third unequivocal Cambrian chordate with preserved soft parts (Simonetta and Insom 1993), but is known only from a single tail and, consequently, is of limited utility in analysing cephalochordate–vertebrate relationships. Most tantalizingly, a single specimen from the Burgess Shale, which has an undoubtedly chordate trunk, also preserves details of the head morphology (Simonetta and Insom 1993). The head resembles, at least superficially, the cartilaginous cranial skeleton of modern lampreys, one of the two groups of living agnathans (Fig. 1.2.4.3). If confirmed, this unnamed specimen demonstrates the presence of unarmoured agnathan vertebrates within the Middle Cambrian and goes some way towards rooting the origin of vertebrates within the Early Cambrian radiation of animal groups.

A confusion of conodonts

For 130 years after their first description in 1856, the affinity of conodonts developed into one of the classical debates in palaeobiology. Conodonts are known almost exclusively from their apatitic tooth-shaped elements and range from the uppermost part of the Cambrian to the end of the Triassic. It is clear that each species possessed a variety of differing morphologies of element, together referred to as an apparatus, and from rare instances of the preservation of intact apparatuses (but without associated soft tissue) it can be inferred that the elements were arranged in a bilaterally symmetrical array which was differentiated from anterior to posterior. With only the morphology of the elements and apparatus as guidance, the group was, inevitably, compared and assigned to a wide variety of organisms, ranging from cnidarians to vertebrates, and even to plants and algae. A majority of the animal groups to which conodonts were assigned possessed biting or grasping structures, and the comparisons were largely ones of functional analogy rather than homology (see Section 4.1.9).

The discovery of the first bona fide soft parts in 1983 rapidly shifted the focus of the debate. A total of 12 specimens of conodonts with preserved soft parts are now known, 10 of which come from the Granton Shrimp Bed of Edinburgh, Scotland (Aldridge *et al.* 1993). Single specimens are also known from the Early Silurian of Wisconsin, USA, and the Late Ordovician of South Africa (see Section 3.4.4), but these add relatively little information regarding the anatomy of conodonts. The Granton conodonts are elongate, 21–55 mm in preserved length, and possessed a laterally compressed trunk with V-shaped myomeres, a notochord, and a ray-supported asymmetrical caudal fin. The apparatus lies along the line of bilateral symmetry with the S and M elements of the ramiform basket at the anterior and two pairs of P elements to the posterior. Two lobate structures at the anterior termination have been interpreted as the supporting cartilages for large eye capsules and other, more equivocally preserved structures have been interpreted as a dorsal nerve cord, otic capsules, and possible branchial structures. On the basis of the soft tissue evidence, conodonts lie crownward of myxinoids (hagfishes) as the sister group of all other vertebrates with biomineralized tissues (Aldridge *et al.* 1993; Donoghue *et al.* 1998).

Histological investigation of conodont elements has revealed a range of hard tissues which are consistent with this phylogenetic relationship. In the majority of conodont taxa, the crowns of elements are composed of apatite crystallites arranged normal to incremental growth lines (Fig. 1.2.4.2c); alternatively, the crystallites may lie obliquely to the growth lines (Sansom *et al.* 1992). The former is identical to vertebrate enamel and the latter is considered to be a homologous tissue (Sansom *et al.* 1992; M.M. Smith *et al.* 1996).

White matter, an additional tissue found within the crown of conodont elements, is currently of enigmatic origin. Cell lacunae and canaliculi have been identified within white matter and it has been postulated that this tissue represents a form of cellular dermal bone (Sansom *et al.* 1992). The lacunae and canaliculi have now been documented from a variety of conodont taxa, and fall within the size range of these structures for vertebrates, but developmental considerations render it unlikely that the tissue is dermal bone.

The cavity within the base of the element is filled, in

different taxa, by a surprising variety of tissues, collectively termed basal bodies. These tissues include both globular calcified cartilage, which directly underlies enamel (Fig. 1.2.4.2c), and dentine; the latter is variably developed across a range of conodont taxa (Sansom *et al.* 1992; M.M. Smith *et al.* 1996). At present, the reason for this histological disparity is not clear. However, the full range of tissues is present in the earliest conodonts (Fig. 1.2.4.2) of Late Cambrian and Early Ordovician age.

The carpoid heterodoxy

An alternative, heterodox, view of early vertebrate evolution and relationships has been propounded by R.P.S. Jefferies in a series of papers over the course of four decades (see Jefferies 1986). On the basis of detailed anatomical studies on carpoids, an extinct group of asymmetrical echinoderm-like animals (Fig. 1.2.4.1), Jefferies has advanced a hypothesis which differs from generally accepted relationships in a number of fundamental ways. Firstly, and most significantly, Jefferies considers tunicates and vertebrates to be more closely related to each other than either is to cephalochordates (Fig. 1.2.4.3c), in contrast to the more conventional view that the cephalochordates are the sister group of vertebrates (Fig. 1.2.4.3b). Secondly, Jefferies claims to be able to identify stem and crown group representatives of all of these terminal taxa within the carpoids. These claims

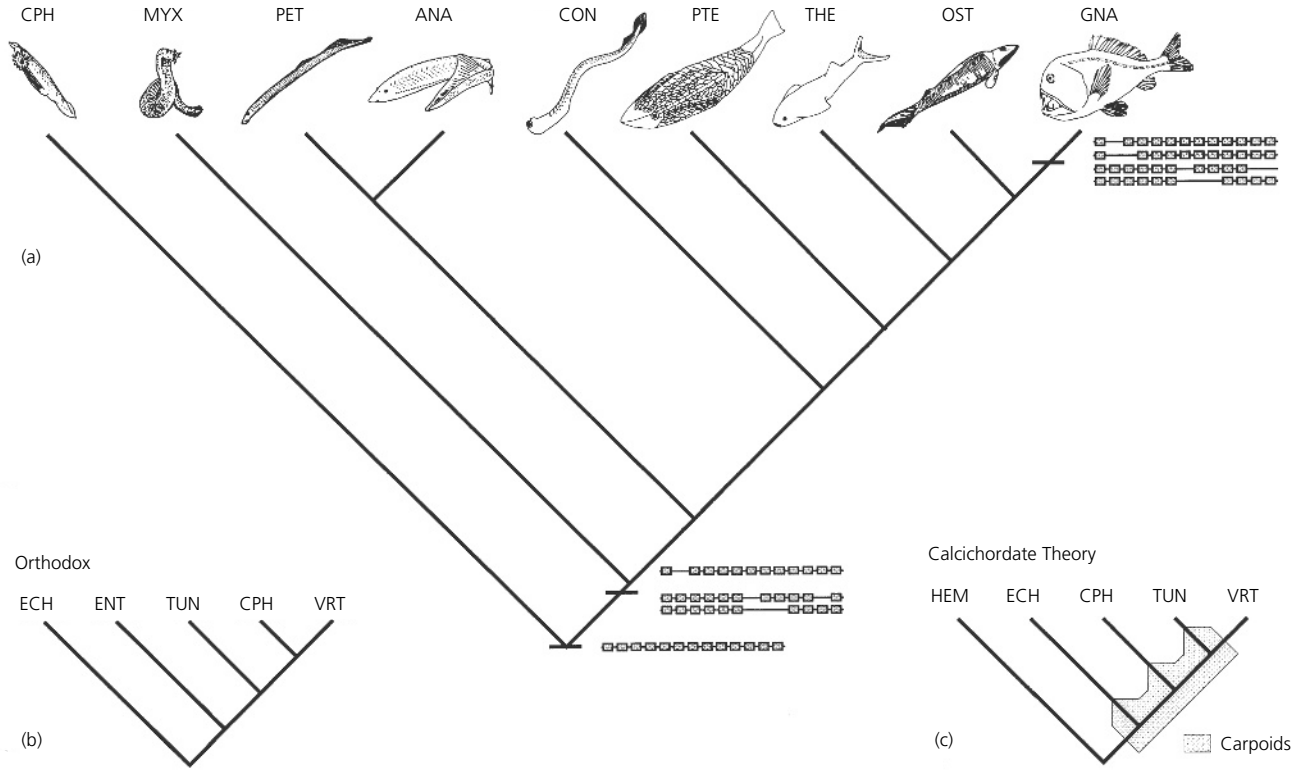


Fig. 1.2.4.3 Proposed phylogenetic relationships of jawless vertebrates and deuterostome sister groups. (a) Phylogenetic relationships of primitive vertebrates with the numbers of homeobox gene clusters indicated. Cephalochordates have a single *Hox* cluster, the primitive condition seen in other phyla. The situation in lampreys is unclear, but they probably have two or three clusters whereas gnathostome vertebrates (jawed fish and crownwards) have four *Hox* clusters. (b) Relationships of higher deuterostome groups obtained in most phylogenetic analyses. The 'hemichordates', comprising enteropneusts and pterobranchs, are generally considered to be polyphyletic and only the enteropneusts are incorporated on this diagram. (c) Relationships of higher deuterostome groups in Jefferies' Calcichordate Theory; the hemichordates are treated as a monophyletic group. Tunicates (represented by extant sea squirts and salps) are considered to be more closely related to vertebrates than either is to cephalochordates. The area of the cladogram occupied by the carpoids in Jefferies' theory is shaded. ANA, anaspids; CON, conodonts; CPH, cephalochordates; ECH, echinoderms; ENT, enteropneust 'hemichordates'; GNA, gnathostomes (jawed vertebrates); HEM, hemichordates; MYX, myxinoids (hagfishes); OST, osteostracans; PET, petromyzontids (lampreys); PTE, pteraspidomorphs (which include *Astraspis*, arandaspids and heterostracans); THE, thelodonts; TUN, tunicates; VRT, vertebrates. (a, After Forey and Janvier 1994 and Meyer 1998.)

have been firmly refuted by echinoderm palaeontologists who tend to view the carpoids as an 'aberrant' group of early echinoderms, but Jefferies' Calcichordate Theory has proved difficult to overturn when details of the morphological data are taken into account. The debate is currently unresolved, but cannot be ignored. A number of lines of argument may be taken in further testing the Jefferies model. Firstly, new discoveries of vertebrates and their relatives in the Cambrian allow a more constrained appraisal of the alternative cladograms and stratigraphic distributions. Chordates, in the form of cephalochordates, first appear in the Lower Cambrian Chengjiang Lagerstätte and vertebrate diversification was certainly underway by the Late Cambrian, as indicated by the presence of both conodonts and *Anatolepis*. In contrast, the most primitive of Jefferies' 'stem vertebrates', *Chinianocarpus*, first appears in the mid-Early Ordovician and *Placocystites*, the most derived, is restricted to the Wenlock. The preservation potential of carpoid calcite skeletons is significantly greater than that of soft-bodied chordates yet, if Jefferies' model is correct, it is the carpoid stratigraphic ranges that are significantly attenuated by non-preservation. Quantitative parsimony tests of the alternative cladograms using stratigraphic data would be a useful contribution to the debate. Secondly, additional, computer-based, cladistic studies of both extant and fossil faunas may go some way toward breaking the current impasse over interpretations of phylogenetic relationships between extant crown groups. At present, a majority produce topologies which have cephalochordates as the sister group of vertebrates, in opposition to the Calcichordate Theory.

Early vertebrate relationships

The application of phylogenetic (cladistic) analysis has greatly facilitated the appraisal of evolutionary relationships amongst early vertebrates (Fig. 1.2.4.3a). Despite this, published cladograms remain relatively unstable in comparison with those derived for higher vertebrate groups and it is probable that this will continue to be the case for some time. Nevertheless, the recent recovery of microvertebrates from Cambrian and Ordovician strata, together with the increasing quantity of soft bodied data available, provide important information regarding the timing and tempo of the initial radiation of vertebrate groups. Similarly, advances in the understanding of homeobox regulatory mechanisms have provided insights into possible underlying developmental controls. *Hox* genes have a fundamental role in the regulation of gene expression relating to the formation of body plans and structural elements, and are probably present in all metazoans. Cephalochordates and most other metazoans possess a single cluster of *Hox* genes, whereas tetrapods possess four, and two investigated groups of teleost fishes have six (Meyer 1998). The situation in agnathan fishes is unclear but it seems that lampreys possess two or three clusters. The duplication events which increase the numbers of *Hox* clusters coincide with major periods of innovation and diversification in the evolutionary record—it is unlikely that they are unrelated but further work is needed to elucidate the interrelationship. In recent years, data from palaeobiology, genetics, and evolutionary developmental biology have contributed to a dramatic change in the understanding of the origin and earliest evolution of vertebrates. It is likely that the continued trend towards integrative work will engender rapid progress towards a fuller understanding of the origin of vertebrates.

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1.3 Palaeozoic Events

1.3.1 Ordovician Radiation

A.I. MILLER

Introduction

It has long been known that the first major burst of global diversification among marine animals took place early in the Palaeozoic Era, but the complexity of this interval has become apparent only more recently. The diversification is divisible roughly into two major components: the Cambrian explosion and the Ordovician radiation. Whereas the Cambrian explosion and its Vendian antecedent were characterized by the origin and initial diversification of basic body plans at the phylum and class levels, the Ordovician radiation was manifested mainly by an unprecedented burst of diversification at lower taxonomic levels. During the Ordovician Period, there was a three- to four-fold increase in the global richness of marine animal families and genera relative to Cambrian levels. Moreover, there was a fundamental transition in the overall composition of the marine biota: as the period progressed, the relative contributions of trilobites and other organisms characteristic of the Cambrian fauna declined in the face of a substantial diversification of articulate brachiopods, stenolaemate bryozoans, stalked crinoids, and other groups that dominated Palaeozoic assemblages thereafter. Gastropods, bivalves, and other taxa that would come to dominate sea floors in the post-Palaeozoic also experienced appreciable Ordovician diversification.

Despite the pattern of continuous diversity increase and transition in taxonomic composition that is apparent at the global scale through most of the Ordovician, there is growing evidence that this does not simply reflect the activity of global-scale processes operating at the rates implied by synoptic diversity compilations. Instead, the global signal may represent the sum of disparate transitions taking place around the world in response to local or regional causes (Miller 1997). To investigate this and other issues, researchers worldwide have sought to deconstruct the global Ordovician signal into its geographical, environmental, and morphological components. Data for these studies have been compiled both from the worldwide literature and from a new generation of field, laboratory, and systematic work tailored to address questions of biodiversity at local or regional scales in the light of the global signal. In addition, the Ordovician has been a focal point for studies that have sought to evaluate diversification through quantitative assessment of morphological diversity (disparity: see Section 5.1.3), rather than through the more traditional metric of taxonomic richness. Because of this activity, the Ordovician radiation is becoming something of a proving ground for understanding how a major, long-term diversity transition transpires.

Dissection of the global pattern

When Ordovician diversity patterns among higher taxa at the global scale are more finely subdivided temporally or taxonomically, they exhibit attributes not appreciated fully in coarser treatments. Trilobite families and genera, for example, exhibited a pronounced global transition through the Ordovician (Adrain *et al*. 1998): families and genera belonging to a group that collectively dominated trilobite biotas during the earliest Ordovician (dubbed the 'Ibex' fauna after the earliest of the four North American epochs) declined steadily in taxonomic diversity through most of the Ordovician, giving way to another group of families and constituent genera that diversified appreciably in the Middle and Late Ordovician (dubbed the 'Whiterock' fauna, after the second of the four North American Ordovician epochs). The Whiterock fauna alone contributed to trilobite diversity after the Late Ordovician mass extinction. The reasons for these different evolutionary patterns are not yet understood entirely, but the two faunas apparently flourished in different geographical and environmental regimes, and exhibited different rates of evolution. On these bases, the traditional global paradigm of evolutionary faunas, which places trilobites in the Cambrian evolutionary fauna and tends to view the class as broadly in decline after the Cambrian, should be amended to accommodate the recognition that the Whiterock fauna was diversifying, rather than declining, during the Ordovician.

Geographical and palaeoenvironmental variations

The foregoing discussion not only illustrates the need to continue evaluating the details of diversification at the global level, but also points to the importance of understanding the extent to which these patterns varied geographically or environmentally. The radiation of the Whiterock trilobite fauna, for example, was more appreciable at low latitude than at high latitude (Adrain *et al*.

1998). In a similar vein, substantial latitudinal and environmental differences in Ordovician diversification have now been recognized among a broad range of biotas. For example, there were significant Lower to Middle Ordovician faunal differences among two western Argentinean basins that are currently in close proximity, but which were isolated from one another during the Early and Middle Ordovician (Waisfeld and Sánchez 1996). In the carbonate-dominated Precordillera Basin, which likely comprised a microcontinent located at low latitude, articulate brachiopods and sponges were the predominant faunal elements. By contrast, the siliciclastic-rich Northwestern Basin, which was part of the Gondwanan supercontinent at high latitude, contained a fauna rich in trilobites and molluscs. Clearly, these faunal differences were consequences of differences in climate and depositional regimes among the two regions. With respect to the dynamics of the Ordovician radiation, they illustrate the extent to which the timing and nature of major biotic transitions varied from region to region.

More broadly, diversification throughout the Ordovician differed significantly among Ordovician palaeocontinents (Miller 1997). This may have been attributable, in part, to differences among palaeocontinents in their geological attributes, including the extent of siliciclastic influx. For example, by the late Middle and Late Ordovician, Laurentia (much of present-day North America) contained an abundant and diverse bivalve fauna, whereas South China did not (Fig. 1.3.1.1). Bivalves first diversified in siliciclastic settings at high latitudes, but did not begin to flourish in Laurentia until later, as part of the 'globalization' of the class (Babin 1993). The lack of a similar diversification in South China may have reflected its geology. The level of siliciclastic influx in eastern Laurentia increased significantly during the Middle and Late Ordovician because of the onset of the Taconic orogeny, whereas South China did not experience nearly as extensive an increase in siliciclastics in the absence of similar orogenic activity.

Abrupt local and regional transitions

It is not surprising that various Ordovician biotas exhibited a propensity to occur in particular palaeoenvironments or climatic regimes. However, investigations of the Ordovician radiation have served to illustrate the extent to which the presence, as well as the waxing or waning, of different physical milieus can affect biodiversity. That the patterns observed in global diversity compilations may owe their generation to such transitions is perhaps best illustrated by considering biotic transitions at the local or regional levels. For example, an abrupt

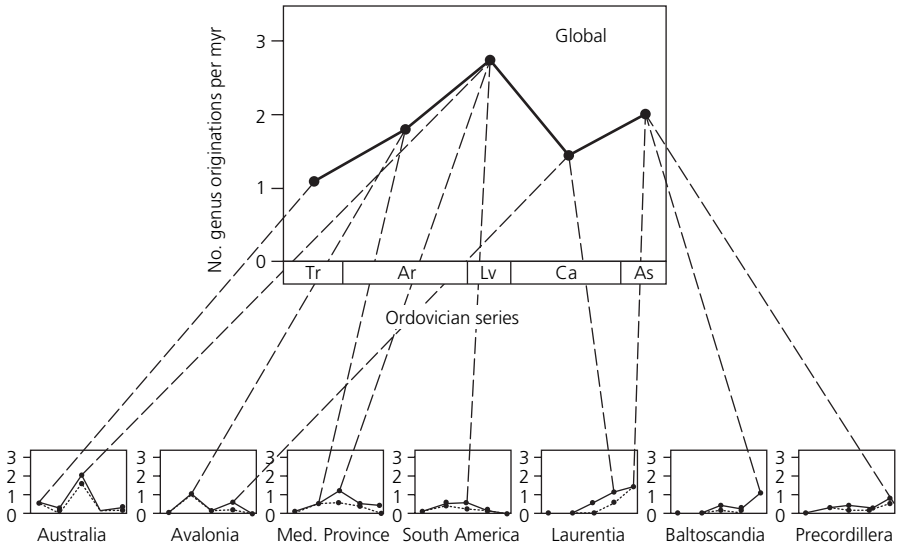


Fig. 1.3.1.1 Patterns of bivalve genus origination among palaeocontinents during the Ordovician radiation, in comparison with the global pattern. Dashed lines illustrate instances in which bivalve diversity for a particular palaeocontinent contributed appreciably to the global time series. Two time series can be distinguished in the palaeocontinental graphs. In each case, the upper curve depicts rates of bivalve first appearance regardless of whether the genera first appeared earlier on another palaeocontinent (i.e. immigration plus origination); the lower curve depicts rates of first appearance only for genera that originated on the palaeocontinent. Data for determining origination rates per million years are from a database of Ordovician genus occurrences, updated from a version described by Miller (1997) and other papers. Abbreviated series designations are for the five series of the updated British standard: Tr, Tremadocian; Ar, Arenigian; Lv, Llanvirnian; Ca, Caradocian; As, Ashgillian.

Middle Ordovician transition among biotas of eastern North America was associated with the onset of the Taconic orogeny: a biota that flourished in warm tropical settings was replaced by one adapted to the cooler, more turbid conditions brought about by the local effects of the orogeny (Patzkowsky and Holland 1993). In this instance, elements of the older biota survived elsewhere in warmer waters, and repopulated part of the study area when suitable conditions returned.

A similarly abrupt biotic transition is recognized at the base of the Middle Ordovician in the Great Basin of western North America (Droser *et al.* 1996). There, articulate brachiopods and other faunal elements increased greatly in abundance, relative to trilobites. Moreover, the contributors to trilobite diversity changed significantly in the interval, at least partly in concert with broader, global transitions (Adrain *et al.* 1998). Combined with the case described earlier for the Middle Ordovician of eastern North America, the pattern in the Great Basin points to the need to further investigate regional patterns around the world, in order to determine the extent to which such transitions permeate Ordovician strata. It may be that the gradual biotic transitions apparent in global compilations of taxonomic diversity were actually built of abrupt, physically induced transitions, the timing of which varied from region to region around the world, thereby imparting the gradual global appearance (see Miller 1998). For understanding the causes of the Ordovician radiation, this distinction is crucial. If the global pattern is also recognizable from region to region around the world, it would suggest that the causes of the radiation were global in scope. Alternatively, if the global signal is the aggregate record of varying regional patterns with unique explanations, a different view emerges. The ongoing investigations of Ordovician strata worldwide should reveal the extent to which the radiation was controlled by local or regional vs. global processes. In this context, the radiation should provide an excellent object lesson concerning the relationships among diversification patterns at different scales.

Morphological diversity

Although the majority of research on the Ordovician radiation has focused on the assessment of taxonomic diversity, a significant new avenue of enquiry is emerging: the analysis of morphological diversity (disparity: see Section 5.1.3), based on direct morphological measurement and statistical analysis of large numbers of the constituents comprising a higher taxon. When compared to and contrasted with taxonomic diversity, temporal patterns of morphological diversity for a higher taxon may provide a different perception of its evolutionary dynamics. For example, analyses of trilobite cranidia have revealed that the morphological diversity of trilobites increased from the Early Ordovician into the Middle and Late Ordovician, whereas the overall taxonomic richness of trilobites declined through the same interval (Foote 1993). Thereafter, trilobite taxonomic diversity continued to fall, but morphological diversity did not decline substantially until after the Devonian. The Ordovician patterns contrast strongly with those exhibited during the Cambrian: the Cambrian increase in taxonomic diversity actually took place in conjunction with declining morphological diversity from the Early Cambrian into the Middle and Late Cambrian (Foote 1993). This further enhances the view that the Ordovician radiation was rather different from the Cambrian explosion.

By categorizing morphological attributes based on whether they were external or internal features of the skeleton, it becomes possible to gain additional insight into the constraints on diversity (Wagner 1995). During the early radiation of gastropods, including the Early Ordovician, diversification was accompanied by a more substantial degree of morphological change than it was thereafter. Beyond that, it has been suggested that external features more likely reflect ecological attributes of the organism than internal features, which would be expected to more directly reflect phylogeny. Over seven time intervals from the Late Cambrian to the Silurian, there was a continuous decline in the magnitude of morphological change among internal features, but, following a precipitous Early Ordovician drop, there was no such decline among external features. On this basis, it appears that the constraints on morphology were primarily phylogenetic rather than ecological (Wagner 1995).

Implications for other Phanerozoic intervals

The research highlighted herein springs directly from a wealth of questions posed by the earlier, more synthetic studies of the 1970s and 1980s. Against the backdrop of these efforts to synthesize and quantify at the global scale, it might seem odd that the focus in the 1990s shifted back to local and regional levels. And yet, there is a fundamental difference between local research in the 1990s and that from an earlier research era. Local research today is almost always conducted with a desire to understand how some regional biota relates to issues of global significance. It is research conducted with a broader objective, instead of being an end in itself.

In this respect, the cumulative record of research on the Ordovician radiation provides an excellent model for efforts focused on other Phanerozoic intervals. Although other intervals were characterized by different species than those that dominated the Ordovician, large-scale biotic transitions have occurred repeatedly throughout the Phanerozoic and may have been governed, broadly,

by the same mechanisms that caused the Ordovician transitions. For example, on a global scale, the Devonian Period was characterized by the initial decline of the Palaeozoic evolutionary fauna, which was dominated by immobile, suspension-feeding faunal elements. It has been suggested that the decline of taxa with this lifestyle was caused by interactions with diversifying, deep-burrowing deposit-feeding organisms; among other things, the deposit-feeders are thought to have undermined the substrates upon which the suspension-feeders lived. However, as an alternative, the transition might not have been caused by these sorts of direct interactions, but rather by local and regional changes to physical habitats that were detrimental to suspension-feeders and favourable to deposit-feeders. From an environmental perspective, orogenic activity increased in several regions during the Devonian to an extent that, in some instances, dwarfed Ordovician tectonic events. The erosion of uplifted source areas produced substantial influxes of siliciclastic sediments that would have favoured the infiltration and diversification of deposit-feeders. If this was the case, the transition should be manifested regionally in Devonian strata as relatively abrupt stratigraphic transitions from carbonate to siliciclastic sedimentation, with concomitant changes in faunal composition to a deposit-feeding biota.

Thus, a common theme for the Ordovician, Devonian, and the rest of the Phanerozoic is that a better understanding of the causes of global biotic transitions may require their dissection into local and regional components.

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1.3.2 Rise of Fishes

J.A. LONG

Introduction

Fishes are generally defined as free-swimming aquatic vertebrates which have fins and respire through gills. The earliest fossil fishes, however, are not easily recognized by their body and fin shapes, but by the possession of bone, an organically mineralized tissue which supports and protects the soft tissues and allows for more efficient attachment of muscles (Fig. 1.3.2.1). The advent of bone heralded the onset of great diversity of the first jawless fishes, the agnathans (Long 1995).

The oldest fishes

The oldest definite fossil vertebrates are the remains of scales composed of bone-like tissues from the Late Cambrian Georgina Basin of central Queensland, Australia (Young *et al.* 1996). Early Ordovician fish remains from central Australia include several forms known from scales, such as *Areyongia* and *Apedolepis* (Young 1997). The first well-preserved impressions of complete jawless fish armours occur in the Middle Ordovician of Australia. *Arandaspis* had well-developed dorsal and ventral bony shields, with distinct rows of squarish branchial plates over the gills. It was a precursor to the more successful heterostracan fishes, like *Pteraspis*, which had a single branchial plate covering the gills. Such fishes were prevalent in Silurian and Early Devonian seas, and to a lesser extent, freshwater habitats, largely occupying the niches of benthic detrital and filter feeders. The bone of heterostracans lacked bone cells, and has been termed 'aspidin'. (See Section 1.2.4 for more details on the origins of vertebrates.)

Agnathan diversity

Many kinds of jawless fishes evolved throughout the Silurian and Devonian (Fig. 1.3.2.2). These include armoured forms with a scoop-shaped solid bony shield like the osteostracans (e.g. *Cephalaspis*), the naked lamprey-like anaspids (e.g. *Jaymoytius*), and the heavily scaled thelodonts (e.g. *Thelodus*). Finds from Canada indicate that some thelodonts, the Furcacaudiformes, had laterally compressed bodies with well-developed stomachs (Wilson and Caldwell 1998). Thelodonts in general had an internal soft anatomy (evidenced by impressions in *Thelodus*) suggesting close affinity to jawed fishes (gnathostomes). All early agnathans had

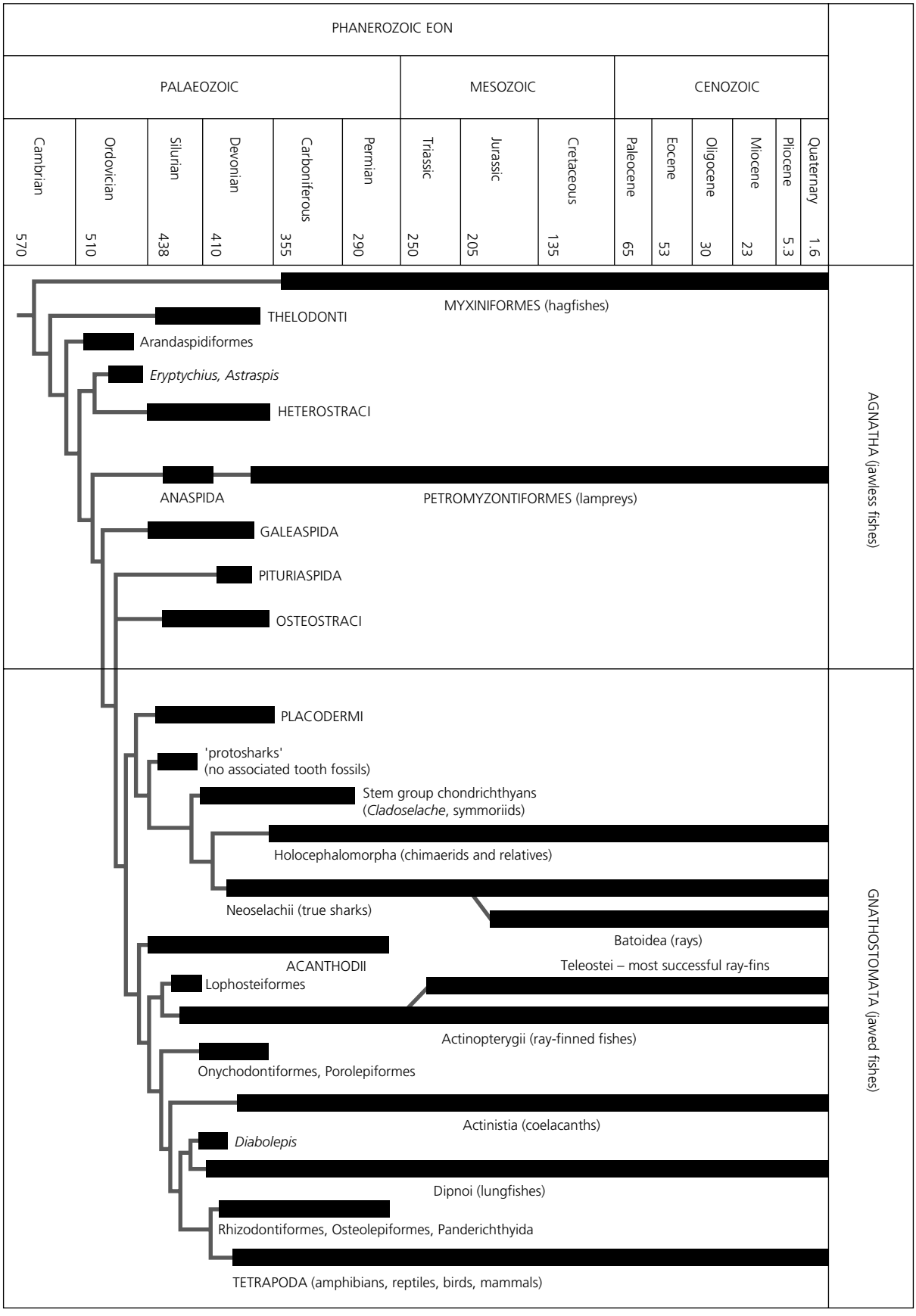


Fig. 1.3.2.1 Major radiations of fish groups through time.

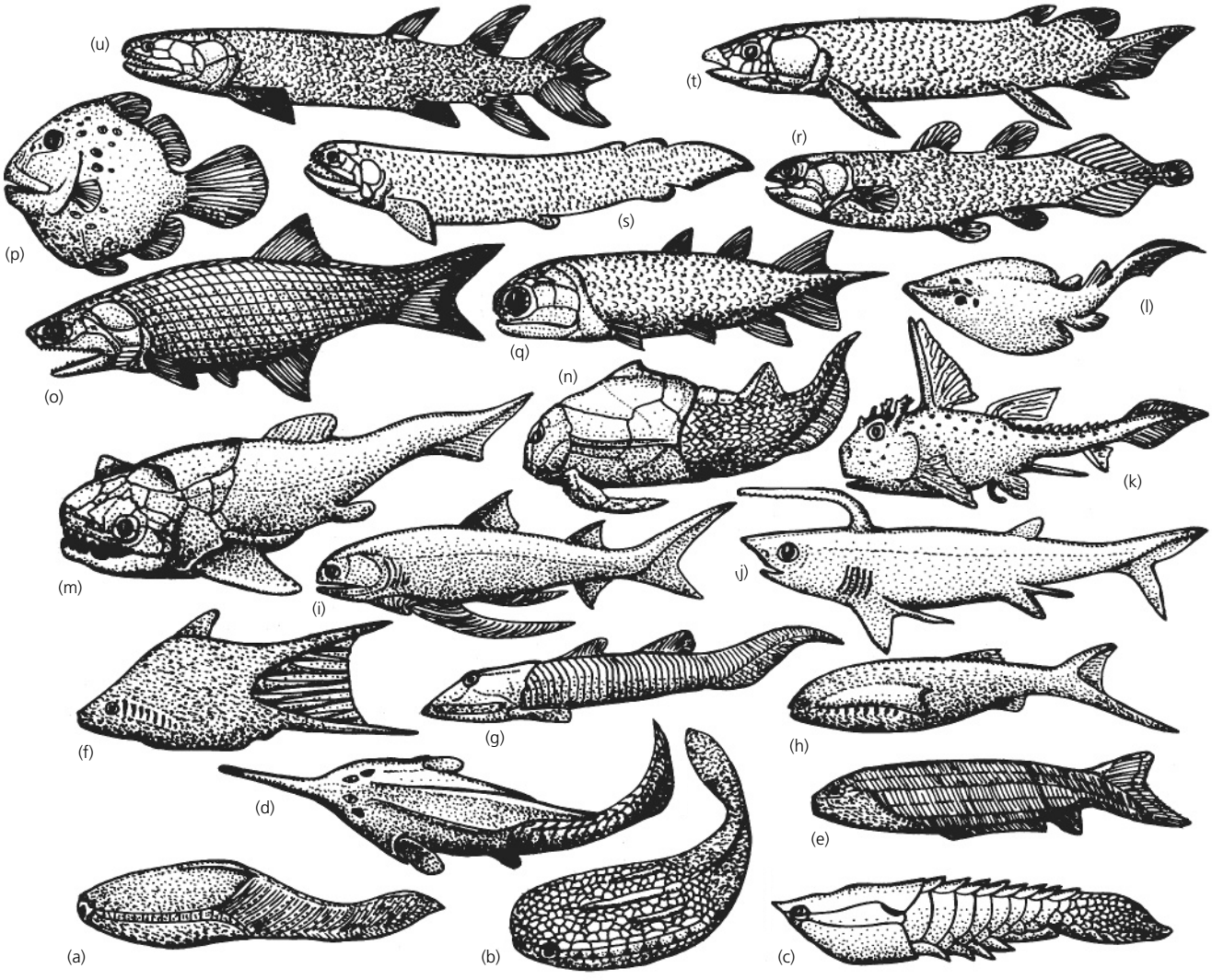


Fig. 1.3.2.2 Diversity of major fish groups through time (a–h, agnathans; i–u, gnathostomes). (a) *Arandaspis* (Arandaspidiformes; Ordovician). (b) *Eriptychius* (Astraspidiformes; Ordovician). (c) *Anglaspis* (Heterostraci; Silurian). (d) *Pituriaspis* (representing Pituriaspida and Galeaspida; Devonian). (e) *Birkenia* (Anaspida; Silurian). (f) *Furcacauda* (Furcacaudiformes; Devonian). (g) *Ateleaspis* (Osteostraci; Silurian). (h) *Thelodus* (Thelodontida; Silurian). (i) *Gyracanthides* (Acanthodii, Climatiiformes; Devonian–Carboniferous). (j) *Falcatus* (Chondrichthyes, Selachii; Carboniferous). (k) *Echinochimaera* (Chondrichthyes, Holocephalomorphi; Carboniferous). (l) *Rhinobatis* (Chondrichthyes, Selachii, Batoidea; Jurassic–Recent). (m) *Mcnamaraspis* (Placodermi, Arthrodira; Devonian). (n) *Sherbonaspis* (Placodermi, Antiarchi; Devonian). (o) *Mimia* (Osteichthyes, basal Actinopterygii; Devonian). (p) *Eoplectus* (Osteichthyes, Actinopterygii, Teleostei; Eocene). (q) *Strunius* (Osteichthyes, Onychodontiformes; Devonian). (r) *Hadronector* (Osteichthyes, Coelacanthiformes; Carboniferous). (s) *Strepsodus* (Osteichthyes, Rhizodontiformes; Carboniferous). (t) *Dipterus* (Osteichthyes, Dipnoi; Devonian). (u) *Eusthenopteron* (Osteichthyes, Osteolepiformes; Devonian).

well-developed sensory-line systems. Osteostracans possessed fields of sensory organs along the sides and top of their shields.

The osteostracan fishes appear to be the closest group to the gnathostomes because they share perichondral bone enveloping the braincase, a large median head vein, and true bone with cell sites (Forey and Janvier 1993). The headshields of osteostracan fishes indicate that the first gill arches were well forward of the eyes, immediately above the mouth. Osteostracans presumably had cartilaginous gill arch supports, as shown by impressions of gill structures on the visceral surface of their shield. Primitive agnathans, like heterostracans, lacked pectoral and pelvic fins. These are found in anaspids as extensions of the fin-folds, but only osteostracans had muscular pectoral fins which were internally attached to a cartilaginous ossification, the scapulocoracoid.

The origins of jaws

Jaws may have first originated in fishes by modification of the front gill arch support bones. The first primitive set of jaws and teeth would have formed when dermal scales, with a tooth-like structure and shape, invaded the mouth and pharynx. Primitive jawless fishes had many more paired gill arches than the jawed fishes; some anaspids possessed 20 or more paired gill pouches. Some agnathans had tooth-like scales lining the buccal cavity (e.g. thelodonts) which could have acted as 'prototeeth' in the reduction of food. Furthermore, the dermal scales of most jawless fishes are constructed of dentinous tissues underlying the enameloid crown, with a bony base. Thelodonts even have a pulp cavity in the base of the scales, making these scales practically 'teeth' in terms of their histology.

The appearance of jaws should naturally herald the abundant appearance of teeth in the fossil record at the same time. Gnathostomes (jawed vertebrates) include the first fishes with jaws and teeth: chondrichthyans, acanthodians, placoderms and osteichthyans, and their evolutionary descendants, the tetrapods (amphibians, reptiles, birds, mammals). Sharks, for example, have hundreds of teeth in their mouths which they grow and shed continuously through life. The average modern shark may shed up to 20000 teeth into the sediment, although Palaeozoic sharks may not necessarily have shed as many teeth as modern forms. Shark skin contains thousands of tiny placoid scales which are also shed into the sediment after death, and readily identified as fossils.

Early sharks and their relatives

The oldest shark-like scales come from the Late Ordovician Harding Sandstone of North America (see Section 1.2.4) and the Early Silurian of Mongolia, yet the oldest shark teeth are of lowest Devonian age, some 30 million years later. As the numbers of teeth and scales are both high per individual shark, the absence of shark teeth in Silurian strata would seem to be a real observation, suggesting that the first sharks had scales of recognizable morphology, akin to those of modern sharks, yet they probably lacked teeth. The appearance of the first teeth most likely correlates with the evolution of jaws in sharks.

Sharks possibly first arose by the Early Devonian in Gondwana, where their teeth are commonly found in some deposits (e.g. Spain, Australia, Antarctica, South America). The Middle Devonian Aztec Siltstone of Antarctica has an unusually high diversity of sharks in both species' numbers and size of teeth, suggesting that Gondwana may well have been the place where toothed sharks underwent their first major radiation. By the Middle Devonian sharks teeth are commonly found throughout the world, and by the Late Devonian more than 50 species are known. The first of the modern sharks, or neoselachians, may date back as far as the Middle Devonian, represented by teeth of *Mcmurdodus* which have multilayered enameloid. *Hamiltonichthys*, from the Lower Carboniferous, was the oldest of the hybodontid shark lineage, a group prevalent in the Mesozoic Era. In the Lower Carboniferous some very large sharks had evolved, like *Edestus giganteus*, from North America, which possessed serrated teeth up to 7–8 cm high on a continuous whorl. Such megapredators would have reached 6 m or more in length. Another major chondrichthyan group, the holocephalomorphs, represented today by the chimaerids and rabbitfishes, appeared in the early Carboniferous. Some sharks of this time, like the petalodonts, had unusual crushing or nipping teeth, possessing few sets in the jaws.

Sharks radiated and diversified throughout the late Palaeozoic and Mesozoic. The largest Palaeozoic predatory sharks may have been the edestids, like *Helicoprion*, whose coiled tooth whorls occur in the middle Permian. If these large whorls sat on the tip of the lower jaws, estimated sizes of 10 m would not be unlikely for these sharks. Huge lamnid sharks evolved in the mid Tertiary, like *Carcharocles megalodon* with teeth 18 cm high, suggesting a total body length of about 15 m.

Acanthodians

The oldest fishes with jaws and teeth preserved intact are the acanthodians, which date back to the Early Silurian. They are often represented in microscopic residues from dissolved limestone as isolated teeth, scales, and fin spines. Acanthodians have been likened to 'spiny sharks' in past literature, although their

affinities appear to lie closer to the higher jawed fishes, such as osteichthyans (true bony fishes), because of scale structure and the gross morphology of their braincase. The oldest acanthodians include forms with distinct gnathal bones on to which strong teeth are ankylosed. This group, the ischnacanthids, were moderately large predators in the Early Devonian seas; some, like *Xylacanthus grandis* from Spitsbergen, reached sizes of 2–3 m. The climatiforms (e.g. *Climatius*) had elaborate dermal shoulder girdle armour and some had many additional spines along the ventrolateral ridge of the body. Acanthodiforms, such as *Acanthodes*, were filter-feeding forms which lacked shoulder girdle armour and had extensive gill rakers for sifting food; they also possessed otoliths (ear stones) for improving 'balance' during swimming manoeuvres. The group survived until the end of the Permian Period.

Placoderms

The most successful of all the early jawed fishes were undoubtedly the placoderms, which appeared in the Early Silurian and reached a peak of diversity during the Middle–Late Devonian. Their name means 'plated skin', referring to a mosaic of bony armour plates that enveloped their heads and trunks. They possessed shark-like tails and in their overall anatomy were much akin to chondrichthyans. Placoderms have alternatively been placed as possible relatives of the bony fishes (osteichthyans) because of their dermal bones and internally ossified braincases. However, the teeth which developed on placoderm jaw bones were not real teeth with roots set into a discrete jaw bone, like those of the osteichthyan fishes, but well-developed pointed cusps that protruded from the jaw bone itself. Placoderms exhibit a multitude of dentition types, revolving around rows of pointed cusps on gnathal bones, or clusters of small denticles or pointed cusps on sheets of bone.

The largest group of placoderms were the arthrodires, which includes the biggest forms, the dinichthyids (e.g. *Gorgonosteus*) reaching 6 m or more. The small antiarchs had external bone-covered props for pectoral fins. One of these, *Bothriolepis*, was ubiquitous in the Middle–Late Devonian, and is represented by over 100 species worldwide. Other groups include the flattened ray-like rhenanids and their heavily armoured relatives the acanthothoracids, the petalichthyids, and the flattened phyllolepids. Placoderms can often be identified from isolated remains because of their unusual plate shapes and dermal ornamentation, making them useful in Devonian biostratigraphic and biogeographical studies. The placoderms became extinct at the end of the Devonian Period, possibly being displaced by the increasing diversity of chondrichthyans.

Osteichthyans

The osteichthyans (true bony fishes) appeared by the Late Silurian, represented by isolated scales, teeth, and rare isolated bones of small ray-finned and lobe-finned fishes. The Osteichthyes comprise: the ray-fins (Actinopterygii), which today form more than 99% of all living fishes and are represented by over 23 000 species (e.g. trout, salmon); and the Sarcopterygii, which have muscular, fleshy lobed fins and include the lungfishes (Dipnoi), and the 'crossopterygians' (a paraphyletic mixture of groups). Although there is only one surviving species, the coelacanth *Latimeria chalumnae*, the 'crossopterygians' include many extinct groups that diversified during the middle Palaeozoic (e.g. Onychodontiformes, Porolepiformes, Osteolepiformes).

The ray-finned fishes were represented in the Devonian by primitive palaeoniscoids like *Cheirolepis* and *Mimia*. The group radiated rapidly by the beginning of the Carboniferous, and over 50 families are known during the late Palaeozoic. Most of the heavily scaled primitive forms gave way to those having thinner round scales, with less rigid cheek and jaw bone arrangements; this enabled more efficient feeding and respiratory mechanisms, such as the buccal-pump system, to evolve. This line of evolution saw the rise of holostean and subholostean fishes in the late Palaeozoic (today represented by gars and bowfins, e.g. *Amia*, *Lepisosteus*) and the first of the modern ray-fins, the teleosteans, by the Late Triassic. Teleosteans have advanced tail fin skeletons with many supporting bones, plus mobile cheeks and detached jaw bones. Their first gill arch (hyoid), which supports the jaws, is often vertically or forwardly inclined. Many of the modern families of fishes had appeared by the close of the Cretaceous Period, and the first teleosteans adapted specifically to life on reefs had appeared by the Eocene Period.

In the Devonian Period the most diverse group of bony fishes were the sarcopterygians (over 100 species); the ray-fins were only a minor component of fish faunas (about 10 species). The earliest sarcopterygians had a shiny tissue, cosmine, that covered the dermal bones and scales and was lost in more advanced lineages. Cosmine may have functioned as an electrosensory tissue.

The ability to gulp air and transgress environmental boundaries evolved only within lungfishes during the Middle Devonian (e.g. *Dipterus*), becoming prominent in the Late Devonian. This gave them an edge on other groups, with later forms developing a further enhanced survival strategy—the ability to aestivate (e.g. *Gnathorhiza*). Lungfishes diversified into forms with crushing tooth plates (e.g. *Chirodipterus*) and others with denticulated palates (e.g. *Griphognathus*, Campbell and Barwick 1987). Post-Devonian lungfishes were largely freshwater forms. Today there are three living lungfish

genera, the most primitive of which is *Neoceratodus forsteri* from Australia which dates back to the Cretaceous Period.

Some of the advanced osteolepiform fishes appear to have developed the ability to breathe air independently, as they had evolved a palatal nostril (a choana) by the Middle Devonian (Long *et al*. 1997). Osteolepidids were a common component of most Devonian fish faunas, in many cases taking the role of top predator. More advanced osteolepiforms, like *Eusthenopteron*, from the Late Devonian of Canada, lost the cosmine layer and had rounded scales (Jarvik 1980). The largest of these predatory lobe-fins were the rhizodontiforms, which dominated the lakes and rivers of the Carboniferous Period. Forms like *Rhizodus* may have reached 6–7 m in length.

The panderichthyid fishes are morphologically closest to the elpistostegalid amphibians, known from Scotland and Russia, in having identical skull-roof patterns, pectoral and pelvic girdles, and endoskeletons which approach the morphology of the basic tetrapod limbs more closely than any other fish. A primitive rhizodontid pectoral skeleton (*Sauripterus*) with eight fin radials supporting the pectoral fin has been described from North America. This matches the eight digits occurring in the limbs of the Devonian amphibian *Acanthostega*. The first tetrapods evolved by the end of the Frasnian stage of the Late Devonian, and at least eight genera had appeared by the close of the Devonian Period.

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1.3.3 Evolution of Reefs

R.A. WOOD

Introduction

In principle, any sessile marine organism can form a reef; indeed, the geological record shows that many different microbial, algal, and metazoan communities have formed reefs over the last 3.5 billion years (Fig. 1.3.3.1) (Fagerstrom 1987). Most of these communities, particularly those from the Palaeozoic, grew under ecological and environmental controls profoundly different from those that govern the functioning of modern coral reefs. Not only has the global distribution of reefs varied considerably through geological time—determined largely by fluctuating global sea level, and latitudinal gradients of temperature and calcium carbonate saturation—but more importantly the trophic demands of reef building organisms have changed, as has the degree of biological disturbance faced by immobile biota occupying shallow marine environments.

Reefs are discrete carbonate structures constructed by organic components that develop topographic relief upon the sea floor. Many direct and indirect biological processes promote the necessary high rates of *in situ* carbonate production to form a reef, including the activities of microbial communities, the aggregation of skeletal organisms, and the precipitation of inorganic cements within cavernous reef frameworks. An understanding of how reef-building organisms have responded to the changing demands of a sessile lifestyle, the mechanisms responsible for their aggregating behaviour, and how extrinsic physicochemical factors control carbonate production, are therefore all fundamental to the study of reef evolution.

The distinctive character of Palaeozoic reefs

Although some Palaeozoic reefs achieved rates of accretion similar to that shown by modern coral reefs (e.g. 3–4 mm/year for the Permian Capitan Reef of Texas and New Mexico), both the community structure and relative contributions of inorganic and organic carbonate were often profoundly different. Palaeozoic reefs appear to have grown in the absence of photosymbiosis and, in some examples, much of the preservable biodiversity was housed within cryptic communities. Moreover, reef construction by relatively fragile organisms was made possible by the absence of widespread bioerosion, and by rapid rates of early lithification that resulted from both microbial activity and inorganic cementation processes.

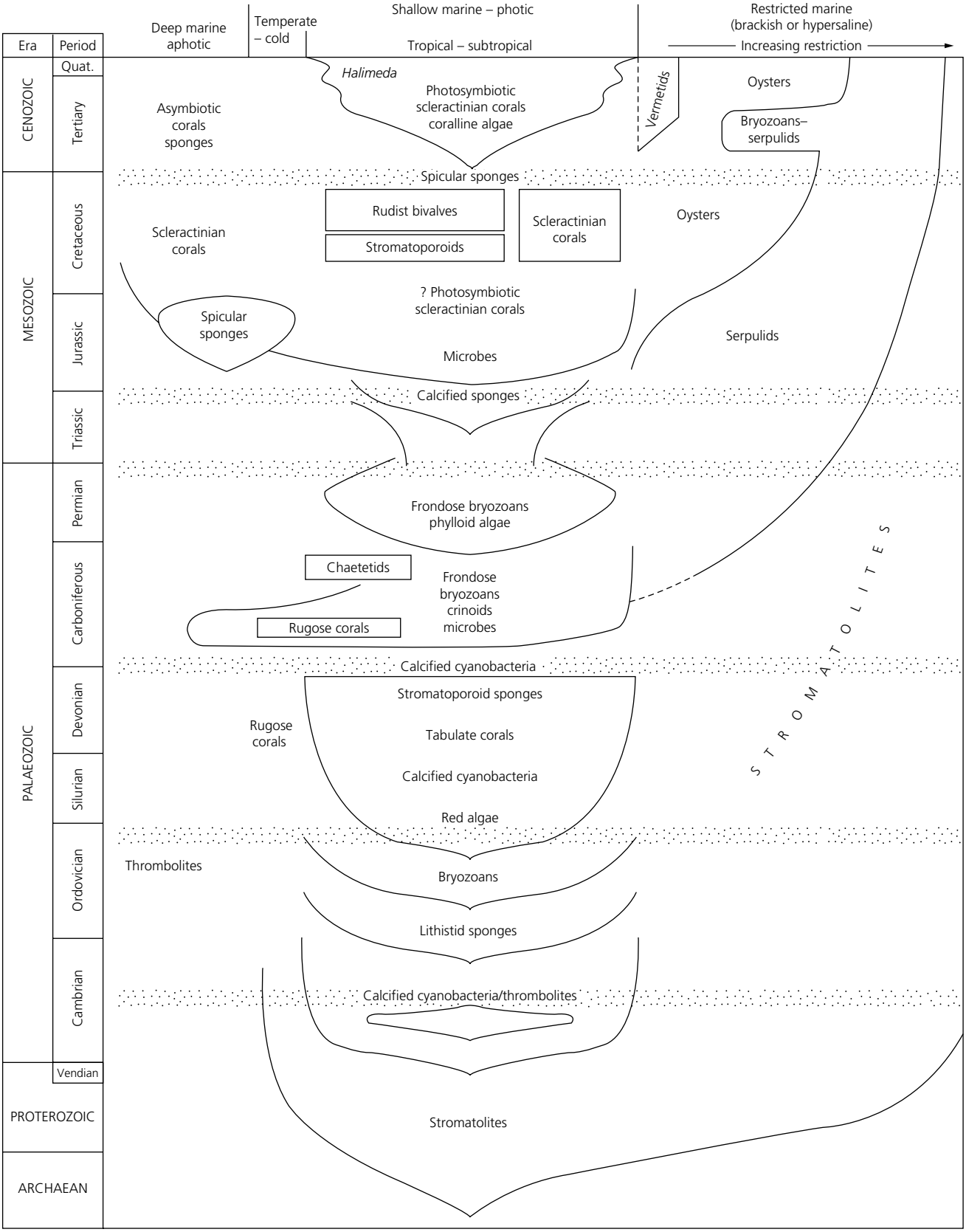


Fig. 1.3.3.1 A succession of many different organisms have built reefs through geological history, with the incumbency of many terminating during mass extinction events (stippled areas). (From Wood 1999.)

Stromatactis is a common but enigmatic structure found within many Palaeozoic reefs, consisting of cement-filled laminar voids within fine-grained carbonate, with either flat or undulose lower surfaces and irregular or digitate upper surfaces. Even though stromatactis may have more than one origin, it is strangely unknown from reefs younger than the Permian. However, the absence of stromatactis in non-reef, micritic Palaeozoic carbonates does not support an entirely non-biological origin, and the common presence of geopetal sediments and fibrous cement infill mitigates against formation entirely by processes involving replacement or dissolution. It is likely that many stromatactis structures will prove to have a reef framework origin, forming as a result of the growth of inconspicuous reef-building organisms or microbially induced structures.

The complexity of communities

Suitable substrates for colonization by benthic organisms have always been a limited resource, and it is now clear that habitat selection for small refuges was in operation as soon as open frameworks developed, some 1.9 billion years ago. From this time onwards, reef biotas have been differentiated into distinctive open surface and cryptic communities (Wood 1999).

Some of the earliest weakly calcified metazoans known from the terminal Neoproterozoic (e.g. *Cloudina*) (see Section 1.2.2) were sessile, gregarious, and probably heterotrophic organisms that were capable of forming limited topographic relief. Borings have also been recorded from this time (although probable sponge borings and silt-sized microspar grains resembling 'chips' from clionid-type sponges are first known from the Lower Cambrian), and a deposit-feeding fauna associated with reef cavities had developed by the earliest Cambrian (Zhuravlev and Wood 1995).

The earliest skeletal metazoan reefs appear at the base of the Tommotian, where it is exposed on the Aldan River, Siberia. These were already ecologically complex, with a framework of branching archaeocyath sponges, a cryptic biota of small archaeocyaths and calcified cyanobacteria, and an associated fauna of diverse small shelly fossils. With the widespread appearance of new groups of sessile, calcified organisms inferred to have been suspension- or filter-feeders, metazoan reef communities became established globally by the mid-Early Cambrian. This biota produced one of the most diverse and ecologically complex reef ecosystems known from the Palaeozoic (Fig. 1.3.3.2).

The importance of microbial communities

Microbialites are calcareous organosedimentary deposits that form by the interaction of benthic microbial communities with detrital or chemical sediments. Although the recognition of microbialites in the geological record is problematic and controversial, presumed microbialites are now recognized to be both common primary framebuilders and secondary encrusters within many Palaeozoic reefs: indeed, it is probable that they are more important than currently recognized (Pratt 1995; Webb 1996). Ancient reefs that consist of significant amounts of cement and putative microbialite, such as the celebrated Late Devonian Canning Basin reefs, Western Australia, and the Permian Capitan Reef, nonetheless formed substantial topographic barriers that separated deep basins from shallow lagoons behind. These two sources of carbonate can alone account for up to 75% of the reef rock volume (see Fig. 1.3.3.3).

Lower Carboniferous Waulsortian mounds—distinctive steep-sided reefs characterized by a core facies containing many generations of micrite, complex micrite-supported cavity systems infilled by marine cements including stromatactis, and fenestrate bryozoans—are also recognized to have formed under a stabilizing biological control. Most authors now agree that diverse and complex microbial processes were important in Waulsortian reef formation, whilst the contribution of skeletal organisms was variable and probably relates to differences in local depositional setting and opportunistic colonization. Encrusting, often cryptic stromatolites and thrombolites, and occasional putative cyanobacterial colonies, offer direct evidence of microbial activity, and the encrustation and boring of microbialite by invertebrates confirms both the primary origin and early lithification of this carbonate (Webb 1996).

Many modern microbialites appear to form only in environments where the growth of potential competitors for substrate space is excluded, and where oceanographic conditions create a water chemistry favourable for carbonate precipitation. The temporal distribution of microbialites over geological time scales may therefore be controlled by physicochemical factors, including the saturation state of sea water driven by changes in pCO_2 or Ca/Mg ratios, or global temperature distribution (Webb 1996). It has been suggested that the decline in abundance of reefal microbialite after the Jurassic resulted from the relatively reduced saturation state of sea water. This may have lowered supersaturation levels below a threshold for abundant microbialite formation, thereby restricting microbialite formation to cryptic reef habitats where abnormal chemistries can develop. Such a scenario might also be related to the disappearance of stromatactis at the end of the Palaeozoic.

The rapidity of early lithification

Many Palaeozoic reefs are characterized by large

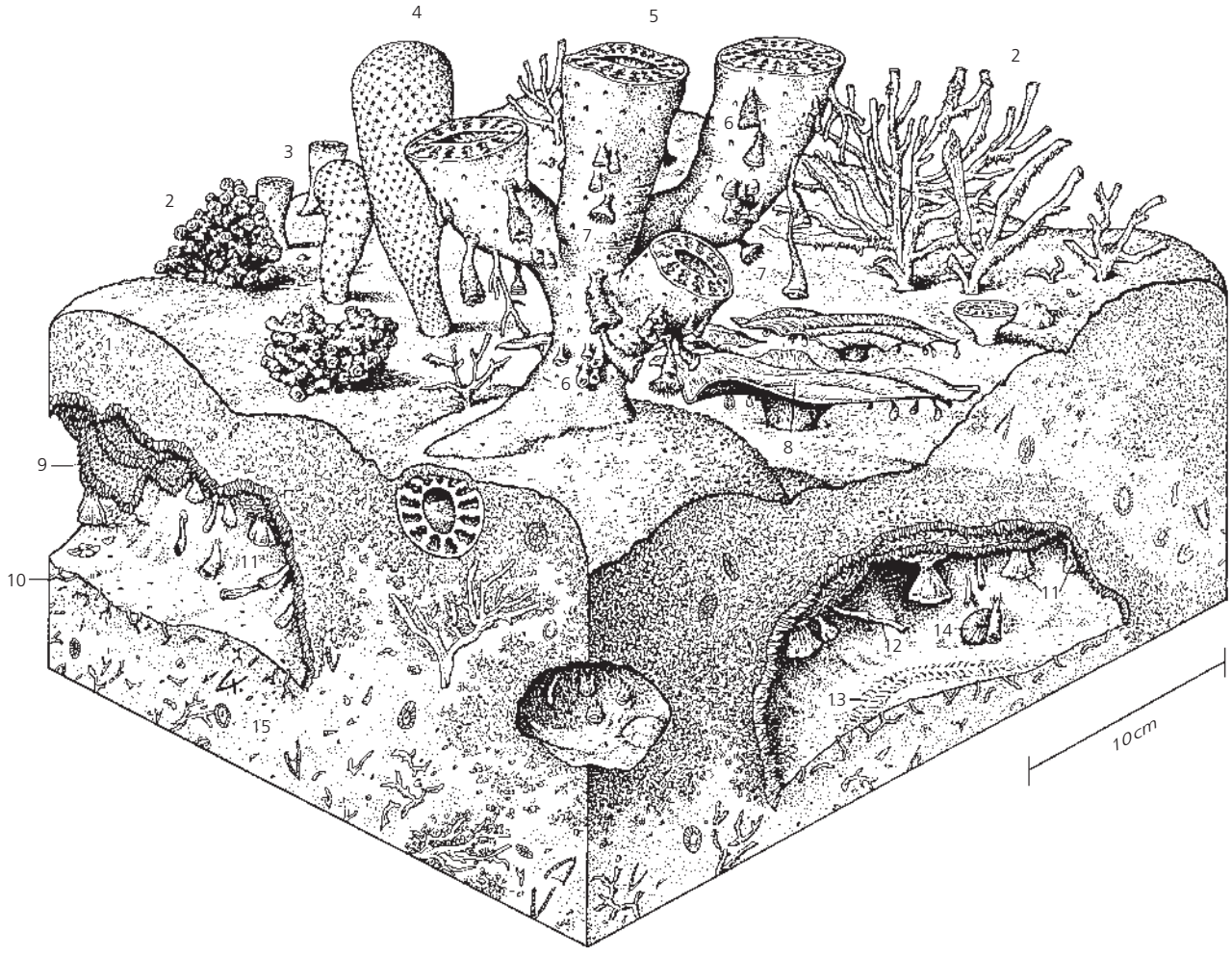


Fig. 1.3.3.2 Reconstruction of a Lower Cambrian reef community. 1, *Renalcis* (calcified cyanobacterium); 2, branching archaeocyath sponges; 3, solitary cup-shaped archaeocyath sponges; 4, chancelloriid; 5, radiocyath (?sponge); 6, small, solitary archaeocyath sponges; 7, cryptic 'coralomorphs'; 8, *Okulitchicyathus* (archaeocyath sponge); 9, early fibrous cement forming within crypts; 10, microburrows (traces of a deposit-feeder) within geopetal sediment; 11, cryptic archaeocyaths and coralomorphs; 12, cryptic cribricyaths (problematic, attached skeletal tubes); 13, trilobite trackway; 14, cement botryoid; 15, sediment with skeletal debris. (From Wood 1999.)

amounts of early marine cement. The importance of early cementation in reef formation on Palaeozoic rimmed shelves is manifest by the numerous, huge reef talus blocks commonly incorporated into fore-reef strata and basin debris flows, and the extensive development of neptunian dykes (vertical fissures often filled with marine sediment and cement) and other fractures subparallel to reef fronts. The abundance of early cements in Palaeozoic reefs compared to modern coral reefs reflects the substantial size and persistence of framework cavities in the absence of bioerosion, and is also suggestive of a poorly understood post-Palaeozoic change in the carbonate chemistry of sea water.

There is also limited evidence for very rapid rates of cement growth within many Palaeozoic reefs, shown by the fact that some cryptic organisms abut against, and become distorted by, cavity cements (Zhuravlev and Wood 1995). This would suggest the operation of important feedback mechanisms for reef formation in the Palaeozoic which have yet to be explored.

Major events in the evolution of Palaeozoic reef communities

The development of modularity

Notwithstanding the great diversity of invertebrates that have contributed to reef-building over the course of the Phanerozoic, there appears to be a limited number of functional organizations that have evolved repeatedly and independently, suggesting that variations in life history as expressed by growth form have always been

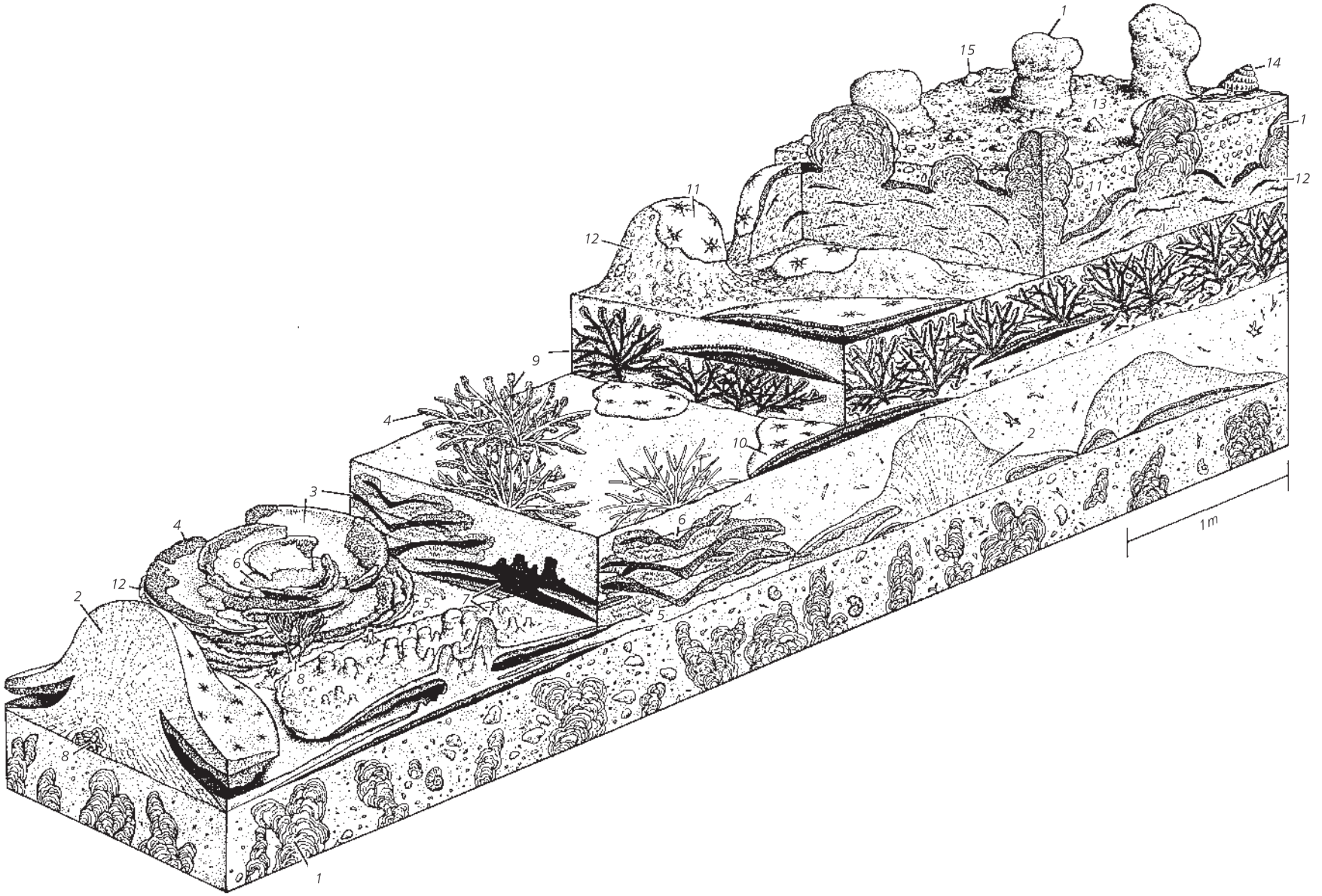


Fig. 1.3.3.3 Reconstruction of an Upper Devonian back-reef community, Canning Basin, Western Australia. Back-reef sediments show distinctive shallowing-upwards cycles from left to right, which are interpreted as the lateral zonation of four communities. 1, stromatolites; 2, domal stromatoporoid (*Actinostroma*); 3, inferred whorl-forming foliaceous stromatoporoids (?*Actinostroma* sp.); 4, calcified cyanobacterium (*Shuguria*); 5, fibrous cement; 6, geopetal sediment infill; 7, platy stromatoporoid; 8, crinoids; 9, branching stromatoporoid (*Stachyodes* sp.); 10, laminar stromatoporoid; 11, encrusting stromatoporoid (?*Clathrocoilona spissa*); 12, microbialite; 13, coarse clastic sediment; 14, gastropods; 15, oncolites. (From Wood 1999.)

important. Indeed, the processes controlling the distribution of ancient reef organisms appear to have been remarkably similar to those observed today (Jackson and McKinney 1991), as organisms with either densely aggregating growth or modular organizations have always been the most successful at acquiring necessary substrate.

Acquisition of a modular habit imparts many advantages to a reef-building organism, including the potential for unlimited growth and attainment of large body size, impressive powers of regeneration from partial mortality, and high fecundity. Not surprisingly, statistically significant increases in the proportion of forms with a modular organization is a widespread phenomenon in the history of many groups of reef-builders, including archaeocyath sponges, bryozoans, and corals. All these trends are polyphyletic, suggesting that there is a general premium on improving physiological interaction between modules regardless of taxonomic affinity (Jackson and McKinney 1991). While solitary and weakly integrated organizations were dominant within reef communities during the Cambrian and Lower Ordovician, encrusting skeletal invertebrates had become common by the mid-Ordovician, and by the mid-Devonian metazoan reef-builders had achieved a tremendous variety of modular morphologies, with individuals/colonies that could reach up to 5 m in diameter (Fig. 1.3.3.3) and with demonstrably impressive powers of regeneration. This resulted in the development of highly cavernous and tiered reef structures.

The reef landscape changed greatly during the course of the Phanerozoic. The majority of Palaeozoic reef metazoans lacked the means to gain secure and permanent attachment to a hard substrate, such that it is difficult to envisage such organisms living in the highly turbulent, surf-zone that reef corals and coralline algae occupy today. During the Palaeozoic, tropical shallow level bottoms often supported enormous populations of small erect bryozoans and stromatoporoid sponges: habitats which in the Recent show no apparent open surface community, only a diverse burrowing one. This disappearance might be explained by the Mesozoic marine revolution (see Section 1.4.1), which involved the dramatic rise of organisms with the ability to burrow deeply and to bore, gouge, or scrape: the armament which had provided ample protection against predators in the Palaeozoic had proved inadequate by the Cretaceous.

The role of mass extinctions

Although a succession of different ecosystems has formed reefs during Earth's history, the 'incumbency' of many of these long-lived ecosystems has been terminated by mass extinctions. Palaeozoic reef biotas suffered four major mass extinctions: at the end of the Early Cambrian, the end-Ordovician (see Section 2.4.2), the Late Devonian (see Section 2.4.3), and the end-Permian (see Section 2.4.4). Although not all mass extinction events preferentially affected tropical areas, there are data to suggest that all carbonate platform biotas are more susceptible to environmental perturbation than those occupying other habitats at low latitudes. Notwithstanding the dramatic reduction in the diversity of reef-associated metazoans, calcified cyanobacterial and microbial communities still persisted to build reefs where carbonate platforms continued to form, perhaps due to their reduced sensitivity to the sustained reductions in primary productivity often associated with mass extinction events. Indeed many reef ecosystems appear to be remarkably resilient to mass extinction events, which seem to have had little effect on the appearance of new reef biotas. While many mass extinctions are associated with a change to a new biota, the extinction event appears to have only accelerated changes that were often already apparent and advanced.

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1.3.4 Early Land Plants

D. EDWARDS

Introduction

Land plants encounter problems relating to water stress, uptake, and transport, and to aerial dispersal. Survival is associated with three major strategies: (1) drought avoidance via opportunism and ephemeral life cycles completed under favourable conditions; (2) desiccation tolerance in the vegetative state involving the capacity of cytoplasm to rehydrate and then function normally (poikilohydry); and (3) maintenance of an internally hydrated environment by biochemical and anatomical modifications (homoiohydry).

Extant land vegetation includes representatives of cyanobacteria, algae, bryophytes, and tracheophytes. The last are usually considered most successful in exploitation of terrestrial environments and are homoiohydric—possessing xylem (with lignin) for water transport, a waxy cuticle (cutin) for reducing evaporation, and stomata and an intercellular space system for gaseous transport. The poikilohydric lifestyle of many cyanobacteria, algae, and bryophytes is of particular significance in the colonization of unstable, ephemeral and highly stressed environments, and hence would have been important in pioneering land plants.

The *preservation potential* of land plants is linked to these strategies in that cutin and lignin are durable and may persist, albeit modified, in fossils, but in poikilohydric forms the only parts which might be expected to be fossilized are resting stages and diaspores. The latter, impregnated with sporopollenin, a complex fatty polymer, also characterize tracheophytes. Thus although there is no direct record of terrestrial cyanobacteria and algae in the early Palaeozoic, it seems likely that they were present. High ultraviolet (UV) radiation correlated with low atmospheric oxygen may have limited their distribution. Indeed it has been postulated that lignin evolved from precursors involved in UV absorbance, and that cutin and sporopollenin initially had a similar role.

Regarding higher plants, attempts to demonstrate tracheids of megafossils, thus providing unequivocal evidence for land vegetation, have traditionally dominated research. More recently the affinities of Ordovician and Silurian microfossils have been rigorously appraised in the search for alternative pioneering colonizers.

Terrestrialization

The first records and ranges of all fossils thought relevant to terrestrialization are documented in Fig. 1.3.4.1.

1 *Obligate permanent tetrads* are so named because they do not split into four spores (monads) on dispersal. They possess durable, smooth, unornamented walls, thought to be impregnated with sporopollenin (although this has not been chemically proven). Some are enclosed within a smooth or ornamented resilient envelope ('membrane'). Both forms are common in Llanvirn to late Llandovery assemblages when the first true triradiate monads appear. Thereafter tetrads become less common and occur only rarely in the Lower Devonian. Older monads with irregular triangular tears probably represent torn apart tetrads. Tetrads are thought to derive from land plants because of their resilient walls and production in fours (a meiotic configuration). As comparable tetrahedral tetrads occur in certain liverworts (e.g. *Riccia*, *Sphaerocarpos*), they are believed to derive from poikilohydric plants with bryophyte physiology and life histories (Gray 1985). The earliest *in situ* examples occur in terminal sporangia on smooth bifurcating axes (not a characteristic of extant bryophyte sporophytes). The axes lack the anatomical data enabling placement within either bryophytes or tracheophytes. Envelope-enclosed *obligate dyads* (**2**) have similar ranges to tetrads and were probably of similar derivation.

2 *Dyads*. Naked and enveloped permanent dyads, assumed to represent a departure from normal meiosis in that separation occurred after the first division, occur abundantly from Llanvirn to lower Llandovery when enveloped permanent dyads decrease dramatically.

3 *Hilate monads* (i.e. lacking a trilete mark in a normal circular contact face) appear in the Llandovery and then proliferate in numbers and diversity into the lower Devonian. The upper ranges of the three morphotypes are unclear.

Sculpturing of the exospore wall is first recorded in the Homerian. Hilate monads and permanent dyads occur in *Salopella*-shaped sporangia in the Lower Devonian, some terminating branching axes. Anatomical evidence for affinity is lacking, but transmission electron micrographs of dispersed naked dyads *Dyadospora murusattenusata* show lamellae in the wall that are characteristic of liverwort spores, although not exclusively so (Taylor 1997). *In situ* examples of dyads and hilate monads have homogeneous walls. Dispersed examples show greater ultrastructural diversity.

4, 5 *Monads with triradiate marks*. The earliest monads are smooth-walled, usually with equatorial thickening, e.g. *Ambitisporites* (which is later recorded in Přídolí *Cooksonia pertoni* sporangia). Sculptured monads occur

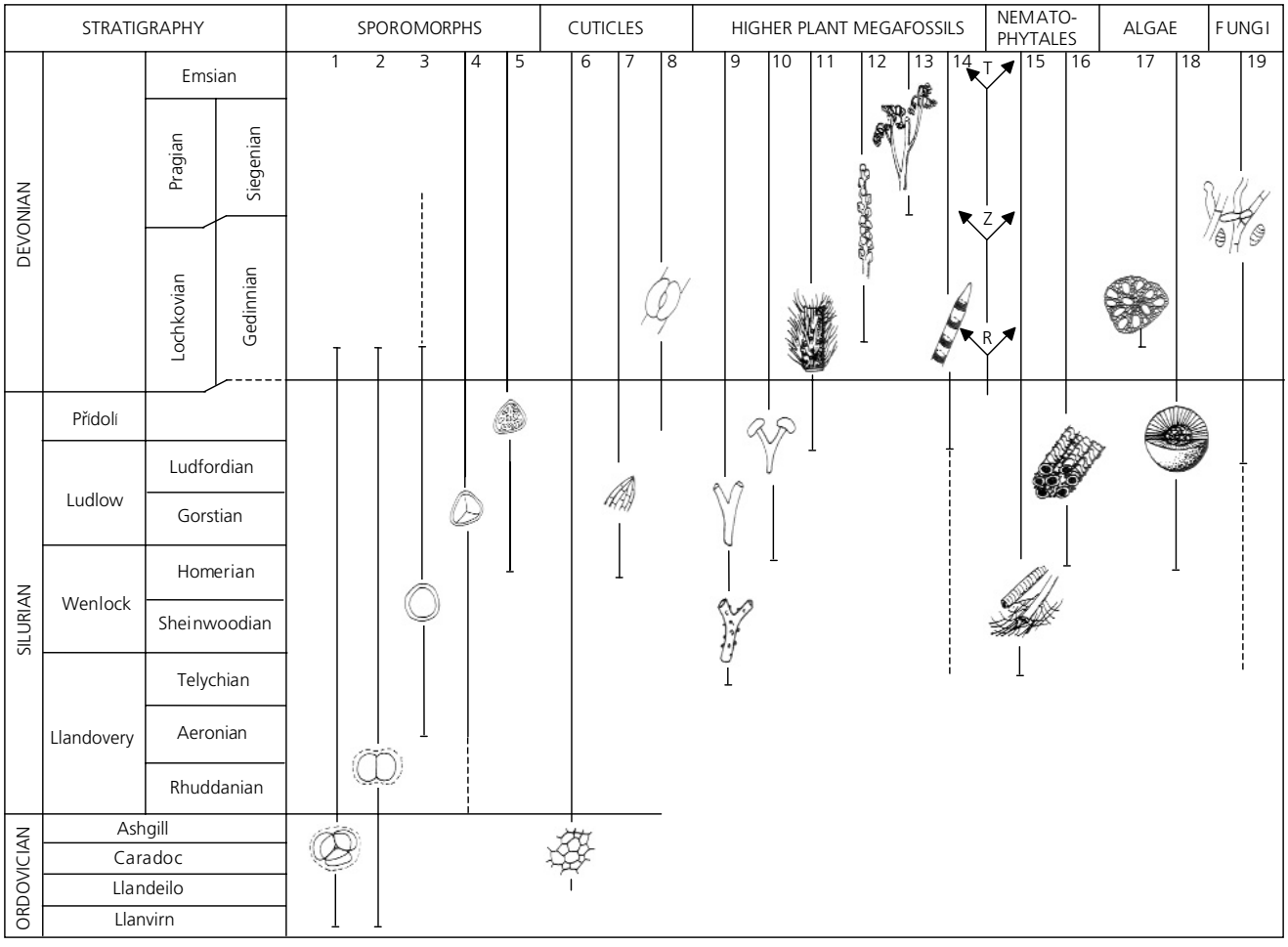


Fig. 1.3.4.1 First appearances and stratigraphic ranges of microfossils and megafossils relating to the colonization of land by plants. R, Z, and T refer to initial major radiations of the vascular plant subdivisions Rhyniophytina, Zosterophyllophytina, and Trimerophytina, respectively. For more complete explanation of 1–19, see text.

continuously from the Homerian, showing rapid diversification and proliferation in the Ludlow and Přídolí. The *in situ* examples, recorded from the Přídolí onwards (Edwards and Richardson 1996), demonstrate that spore characteristics can be diagnostic, e.g. those with well-defined contact faces (retusoid) characterize the zosterophylls, and with equatorial thickening (crassitate), *Cooksonia pertoni*. Greatest diversity is noted in small axial plants with terminal sporangia, termed rhyniophytoid because they reveal no anatomical detail for more precise assignment.

6 '*Nematothallus*'. Associated with the earliest sporomorphs are small cuticular fragments with one smooth surface, and the other a raised isodiametric reticulate pattern representing the outer cells of the tissue below. Unlike tracheophyte cuticle, they lack stomata and are usually imperforate. Recent analysis using pyrolysis-gas chromatography/mass spectrometry (Py-GC/MS) indicates a different chemical composition from that of coeval tracheophyte cuticles. In some instances they cover *Nematothallus*, a thalloid plant composed of tubes placed in the Nematophytales (**15**, **16**), a taxon for plants neither algal nor higher plant (Lang 1937).

Whether all durable spores derived from land plants remains in doubt, but this is not so for cuticles. Because they are imperforate, they may have been more permeable to gases and water than in tracheophytes, and hence their function in *Nematothallus* might have been different, e.g. primarily as UV screens, facilitating runoff, or in defence. It is unlikely that they belonged to the tetrad producers (**10**) because, although their first records are coincident, cuticles persist into the Emsian and are sometimes quite common constituents of Lower Devonian assemblages.

7, 8 *Higher plant cuticles*. Homerian fragments with larger, more strongly demarcated and aligned cells are interpreted as sporangial from comparison with dispersed and *in situ* Lochkovian examples from rhynio-

phytoid and dyad producers. Astomatous cuticles deriving from sterile axes occur in the northern hemisphere Ludlow. The earliest *direct* evidence for stomata (with two guard cells) comes from sterile and fertile axes in the Přídolí, with examples on *Cooksonia* and *Zosterophyllum* in the Early Devonian. However, since stomata are evident on Canadian Emsian *Baragwanathia abitibiense* they were probably also present on the earlier Australian Ludlow *B. longifolia*, where cells are not preserved.

9 *Sterile axes*. Those with dichotomous branching and peripheral support tissues (stereome), the earliest being Llandovery *Eohostimella*, are thought to derive from erect land plants. Late Silurian and Early Devonian examples (e.g. *Hostinella*) possess a central strand of tracheids (**14**), but whether or not pre-Ludlow representatives were vascular is unknown. Some may derive from plants of small stature in which tracheids had not yet evolved; others may possess conducting tissues of bryophytic nature (e.g. the Lower Devonian *Aglaophyton major* exhibits many homoiohydric characters and would be assigned to the Tracheophyta but for the moss-like conducting tissues). Particularly puzzling are some extensive pinnately branching axial systems named *Pinnatiramosus* with unequivocal xylem elements showing bordered pits, recorded from the marine Llandovery, Guilin, China. In size, morphology, and sophistication of anatomy, the fossils are closest to the roots of younger Palaeozoic spermatophytes. They are certainly more complex than those in the earliest lycophytes, of which *Baragwanathia* is first recorded in the Australian Ludlow. Its sterile leafy shoots are morphologically similar to Lower Devonian examples that from morphology, anatomy, and sporangia are herbaceous lycophytes.

10–13 *Fertile tracheophytes*. Wenlock *Cooksonia* (**10**) is generally accepted as the earliest erect pteridophyte-like plant. Reservations as to its affinity stem from absence of anatomy. Spores occur in the Přídolí, and stomata, stereome, and tracheids in Lochkovian examples. Other taxa (e.g. *Salopella*, *Steganotheca*) are usually assigned to the Rhyniophytina on general morphological similarity to later examples (e.g. *Rhynia gwynne-vaughanii*) but are better called 'rhyniophytoid' to emphasize our ignorance. A major radiation is recorded in the early Lochkovian: they then became insignificant constituents of land vegetation (Edwards and Davies 1990).

Zosterophyllum myretonianum (**12**) is the earliest fertile member of the Zosterophyllophytina: records of its characteristic branching (K- and H-shaped) occur in sterile Přídolí axes. The first major zosterophyll radiation is recorded in the late Lochkovian of South Wales. *Dawsonites* sp. (**13**), a fragment of a fertile truss of *Psilophyton* in the South Wales Pragian, marks the beginnings of the Trimerophytina, the Ludlow Australian record being less convincing. The trimerophytes diversified rapidly in the Emsian and are considered ancestral to ferns *sensu lato*, progymnosperms, and sphenopsids.

15 *Microfossils of tubular organization* are recorded as isolated tubes or wefts, from the Telychian into the Lower Devonian (Gensel *et al.* 1990). The most conspicuous tubes are internally sporadically thickened ('banded'), thus broadly resembling tracheids, but there is no evidence that they were lignified. The source plants are problematic: the banded tubes occur with smaller tubes in *Nematothallus* (Lang 1937) and have been found in plants with organization otherwise typical of *Prototaxites* (**16**). While possibly the remnants of cells in the sporangial wall of bryophytes, recent records of banded tubes attached to sporangial surfaces and axes, and their penetration between tissues, suggest a pathogenic or saprotrophic lifestyle. The habitats of such organisms, be they freshwater or terrestrial, remain as conjectural as their affinities. In that some smooth tubes have been recorded attached, rather than just adpressed to cuticles of *Nematothallus* (**6**) type, they may well derive from land plants. Further isolated examples include tubes with smooth, thick or thin walls, or filaments (occasionally branched) composed of elongate, narrow cells. The latter frequently occur in monotypic wefts or may be associated with wider smooth or banded tubes or even spores.

16 *Prototaxites* (Wenlock–Upper Devonian) is usually cited as a land plant because it occurs with tracheophyte assemblages in freshwater sediments. Its organization, in which narrow filaments surround wider, smooth tubes, is unique and hence, in the absence of reproductive organs, its affinities, possibly algal or fungal, remain unknown.

17 *Parka*, best known from the Scottish Lochkovian, a possible epiphyte in lacustrine habitats, may have some relevance to the ancestry of higher plants in that it has been compared with the charophycean *Coleochaete*, although the latter lacks the cavities with numerous alete spores found in *Parka*. Among the green algae, *Coleochaete*, with its parenchymatous organization, and protection, nutrition, and prolonged retention of the zygote, possesses the greatest number of advanced features in the Charophyceae; comparative biochemical and ultrastructural studies suggest that the Charophyceae show closest similarities with bryophytes and tracheophytes (Kenrick and Crane 1997).

18 *Pachytheca* is exceedingly common in certain marginal fluviatile and lacustrine Lower Devonian facies. Its frequent association with *Prototaxites* has led to the suggestion that it was involved in its vegetative reproduction. However, the fossils suggest that the organism comprised a sphere of a mucilage-like substance in which filaments of cyanobacterial dimensions were embedded. Its habitat is interpreted as freshwater, possibly littoral lacustrine.

19 *Fungi*. Although not considered plants, fungi are

included here because it has been suggested that initial terrestrialization was possible only after the development of a symbiotic association between a semiaquatic green alga and an aquatic oomycete fungus, and that in the colonization of nutrient-poor environments, the fungus would have exploited large volumes of substrate for minerals (cf. mycorrhiza today). Mycorrhiza occur in Pragian Rhynie chert *Aglaophyton* axes as hyphae within tissues and as resting spores, although the latter may be connected with saprotrophism (i.e. decomposition of dead organisms). Parasitic chytrids (simple, aquatic fungi) and the earliest lichen are also recorded in the Rhynie chert. Further evidence for terrestrial fungi are the ascomycetes (hyphae, probable conidia, and ascospores) from the Ludlow of Gotland, and similar, but more poorly preserved, material from the late Llandovery.

Terrestrial vegetation

It is postulated that moist land surfaces in the early Palaeozoic would have been coated with a green scum, perhaps initially of cyanobacteria and eubacteria, later joined by filamentous and unicellular algae (Gray 1993). Such an encrusting layer would have both physically stabilized and chemically broken down the substrate, releasing nutrients and, in stable environments, resulted in limited build-up of humus. From the Llanvirn onwards microfossils morphologically convergent with those from extant embryophytes suggest a novel vegetation comprising a 'turf' of small plants with bryophyte life-style that produced spores at the tips of unbranched or bifurcating leafless axes; aerial dispersal indicates the attainment of some stature. The appearance of *Ambitisporites* in the Llandovery heralded a new phase—that of pteridophyte-like plants with axial organization, again forming a 'turf' a few centimetres high. The larger size permitted by homoiohydry, the concomitant maintenance of turgor and hence a hydrostatic skeleton conferred potential superiority over poikilohydric forms in terms of wind dispersal of propagules and in shading, thus limiting the productivity of smaller forms. Throughout the Late Silurian there was an increase in diameter and length of fragments suggestive of larger axial plants; sprawling *Baragwanathia* probably formed thickets. Lower Devonian assemblages suggest that many of the tracheophytes grew in monotypic stands, extensive cover resulting from prolonged rhizomatous activity. Such plants would have provided mutual support—some Emsian trimerophytes were over 1 m tall. Truly arborescent plants with secondary wood appeared later in the Middle Devonian (see Section 3.4.5). As to habitats, the best direct evidence comes from the Rhynie chert (see Section 3.4.5), but as all these early embryophytes were homosporous (i.e. with spores of one size), the free-living gametophyte would have required moist conditions for reproduction. With regard to the route of terrestrialization for higher plants, physiological considerations support transmigration from fresh water on to land.

Much broader issues relating to these phases of terrestrialization include their impact on Palaeozoic atmospheres and climates. Thus in Berner's (1997) model of the concentration of carbon dioxide in the atmosphere during the Phanerozoic, the proliferation and eventual decomposition of tracheophytes throughout the Devonian is postulated as having contributed to a major drawdown of atmospheric CO_2 via chemical weathering of rocks, when Ca/Mg silicate minerals would have been weathered and subsequently precipitated in oceans as carbonates. The quantitative role of pretracheophytes in such weathering processes during the early Palaeozoic remains uncertain.

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1.3.5 Afforestation—the First Forests

S.E. SCHECKLER

Introduction

Although terrestrial ecosystems had begun by the Middle Ordovician (Retallack 1990; Beerbower *et al.* 1992), the typical growth plan of plants—axis construction via apical meristems (growing tips)—was uncommon before the Middle Silurian. The first plants were less than 0.5 m tall and simply constructed of progressively diminishing forked axes. Robust plant architectures are uncommon until near the end of the Early Devonian (Pragian–Emsian) (Fig. 1.3.5.1a) and result from more complex branching patterns of apical meristems. Main axis/overtopped-lateral-branch designs, and tissue patterns capable of meeting increased support and conductance requirements, became common in several plant groups, such as trimerophytes, cladoxylopsid ferns, and cormose lycopsids (whose members reached 2–3 m high) (Fig. 1.3.5.1a,b).

Plant size increased sufficiently by the early Middle Devonian (Eifelian) (Fig. 1.3.5.1b) so that 'trees' can be recognized, although they are small by modern standards (Chaloner and Sheerin 1979). More importantly, these trees became common and widespread as a result of root innovations that penetrated soils more deeply and stabilized floodplain habitats (Retallack 1990; Beerbower *et al.* 1992; Algeo and Scheckler 1998). The extent of terrestrial colonization, indicated by frequency, areal extent, and depth of palaeosols, and the abundance of macrofossil debris, dramatically surged as forest ecosystems became permanent additions to the landscape (Algeo and Scheckler 1998).

Trees radiated more or less simultaneously from three distinct lineages: woody aneurophyte progymnosperms and cladoxylopsid ferns, which are both trimerophyte allies, and cormose lycopsids (Fig. 1.3.5.1b). Each group persisted, expanded, and/or gave rise to new groups of tree-sized descendants throughout the Late Devonian and Early Carboniferous, but each used different 'styles' of growth, branching, and tissue design.

New Late Devonian groups include archaeopterid progymnosperms (the first truly large woody trees to form extensive forests), 'seed-fern' gymnosperm shrubs, giant reed-like calamite sphenopsid trees, additional but taller cormose lycopsid trees, a variety of woody vines (sphenophyll sphenopsids and cladoxylopsids), and sprawling rhizomatous zygopterid ferns (Fig. 1.3.5.1c). Further additions in the Early Carboniferous include forest and swamp trees, and shrubs of progymnosperm, gymnosperm, and stigmarian lycopsids. These components produced patchy vegetation characterized by monotypic-stand growth where many local habitats were filled by plants with clade-specific biological adaptations of rooting, growth architecture, or reproduction.

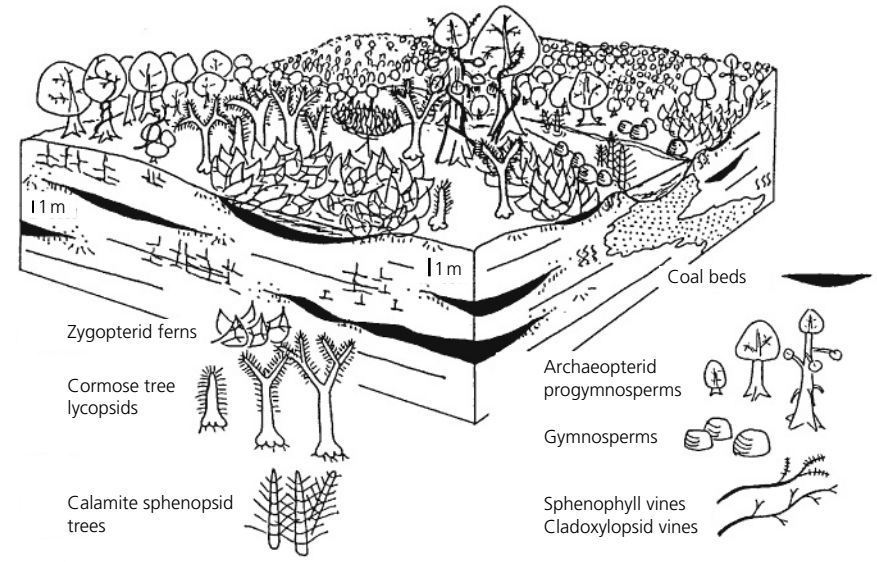
Mechanical/physiological properties of early trees

Progymnosperms and gymnosperms (lignophytes) used the innovations of bifacial (from both sides) vascular cambium (the growing layer producing wood cells inward and bark cells outward) and cork cambium (the growing layer repairing splits and wounds within bark) to produce thick woody trunks and branches (Beck 1988; Stewart and Rothwell 1993; Taylor and Taylor 1993). Wood and bark simultaneously accommodated the load bearing, fluid transport, and starch storage needs of perennially elongating and thickening trunks and limbs, and cork cambium formed a renewable outer protective surface.

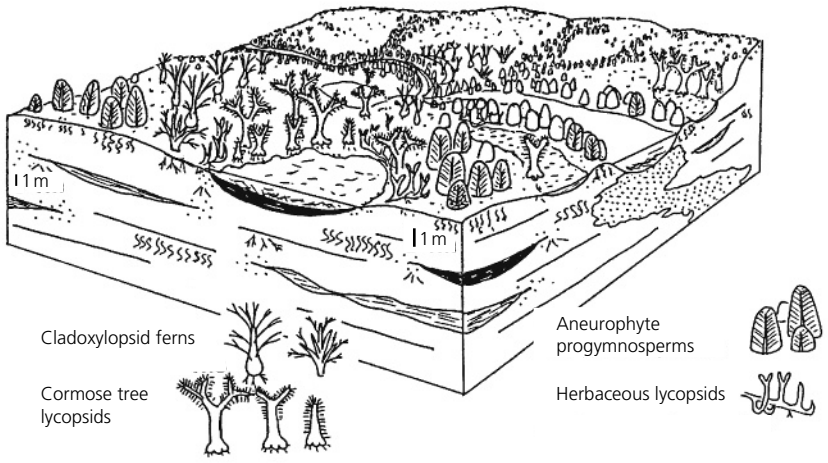
Aneurophyte progymnosperms and 'seed-fern' gymnosperms (Fig. 1.3.5.1b,c) were smaller shrub-like plants with less cambial growth, but they had pronounced outer cortex networks of interconnected fibre bundles, which made them flexible, yet stiff and wiry. Unequal apical branching produced highly branched trunks with successions of decreasing lateral branches (aneurophytes) or unbranched trunks with crowded megaphyllous leaves (seed-ferns). Such growth 'styles' produced short-lived trees with predictable final shapes and only limited abilities to regrow following injury. They occurred typically in dense stands, where branch/leaf contact with adjacent shrubs helped to support the grove.

Late Devonian *Archaeopteris* trees (10–30 m tall progymnosperms with vigorous woody growth) (Fig. 1.3.5.1c) produced many large lateral branches from later-formed buds (similar to modern gymnosperms) that enabled them to produce new branches following injury or crown senescence. Anchorage by vigorous, perennial, and highly branched root systems made these lignophytes sturdy forest components. Some *Archaeopteris* had buttressed trunk bases where the main roots joined. Extensive, deeply rooted palaeosols show that these woody trees formed streamside gallery forests and dense forest patches on coastal plains (Fig. 1.3.5.1c) (Retallack 1990; Beerbower *et al.* 1992; Algeo and Scheckler 1998).

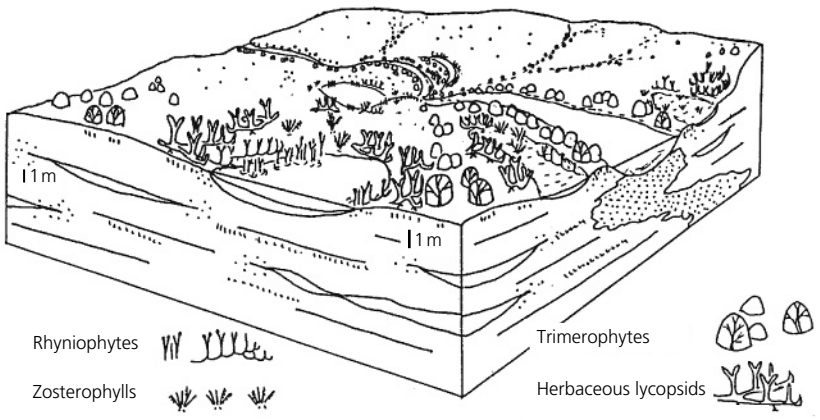
Cormose and stigmarian lycopsids (Fig. 1.3.5.1b,c) also had vascular cambium, but it was unifacial (growing layer produced wood only inward) and limited in both extent and duration. Little wood was produced, so that only a small xylem core supplied their fluid transport needs. Tree lycopsids had thick primary



(c) **Late Devonian (Famennian)**



(b) **Middle Devonian (Eifelian–Givetian)**



(a) **Early Devonian (Pragian–Emsian)**

Fig. 1.3.5.1 (a–c) Reconstructed Devonian landscapes. (Modified from Algeo and Scheckler 1998.)

cortex with vigorous periderm that produced thick 'secondary cortex' which provided both mechanical support and storage capacity. They are found in wetland deposits and had swollen trunk bases from which thick, hollow, unbranched (or once forked), and short (less than 1 m) 'stigmarian rootlets' emerged to penetrate wet muds or sands (Retallack 1990; Stewart and Rothwell 1993; Taylor and Taylor 1993). Unbranched young trunks were clothed by long thin leaves (Fig. 1.3.5.1b,c). Upon reaching certain heights or states of maturity, trunk apices forked equally (in Middle–Late Devonian taxa) or unequally (some Early Carboniferous taxa) to form small crowns of successively smaller lateral branches that interpenetrated in close stands (Fig. 1.3.5.1b,c). Crown branching is associated with the onset of reproduction. Although hardly woody by lignophyte standards, these lightweight, swollen-based, unbranched (or branched with small crowns) trunks, 5–20 m in height, were easily supported and anchored in wetland habitats. *In situ* stumps show that they were often closely spaced.

Cladoxylopsid trees (Fig. 1.3.5.1b) had thick much-branched trunks (2–3 m tall) with swollen bases from which tufts of branched roots emerged. Long (1–2 m) branches covered the trunk or formed a crown of digitate/forked branches that bore smaller forked, leaf-like branchlets. Internally, trunks and branches had many separate but vertically interconnected xylem strands that form the anatomical signature of this clade (Stewart and Rothwell 1993; Taylor and Taylor 1993). Pith is of loose, soft tissues, while cortex is mostly parenchymatous but may have an outer rind with clusters of tough sclereid cells; fibres are mostly absent. Cork cambium was absent, suggesting that axes of different widths were achieved by apical meristem growth (i.e. large axes had large growing tips). These were lightweight axes with high strength to weight ratios. The disposition of many separate xylem bundles resulted in some strands being under tension while those on the other side of an axis were load-bearing and under compression. Branches with this multistranded design were also rotationally flexible. Trunks were stiffer as a result of xylem augmentation (resembling cambium activity) of some bundles. Cladoxylopsid trees were ubiquitous but uncommon components of drier floodplain habitats. Other cladoxylopsids were flexible vines and climbers.

Reproduction of early trees

Although clonal vegetative propagation was common among Devonian herbaceous lycopsids, trimerophytes, and zygopterid ferns, most trees freely shed spores as their sole means of reproduction. Distance of spore dispersal relates to spore size (buoyancy), wind speed, and height of release. Two syndromes characterize the first trees: free-sporing homospory (where dispersed small spores germinate into free-living, potentially bisexual gametophytes) and free-sporing heterospory (where dispersed large or small spores germinate into female or male gametophytes, respectively, that are mostly confined to and dependent upon food reserves stored within each spore). The latter syndrome is temporally linked to emergence of tree-sized plants.

Heterospory may have been selected for as increased plant height made spore dispersal more effective (Chaloner and Sheerin 1979). This perhaps had a positive feedback in that taller plants had increased reproductive success (by farther dispersal or by regulating population biology via unisexual gametophytes). Competition for light is cited as the primary selection factor for increased plant height and crown spread; larger plants were better competitors for scarce light in increasingly crowded landscapes. Another possible feedback is greater leaf surface area for photosynthetic CO_2 capture, made necessary by rapid global atmospheric CO_2 drawdown in the Middle–Late Devonian (Berner 1997, 1998; Algeo and Scheckler 1998) that resulted from increased photosynthesis and production of thick chemically weathered soils. Regardless of which factors selected for tree size, nearly all Middle–Late Devonian large trees were heterosporous.

Early gymnosperms (mid-Famennian) exploited another type of heterospory where one functional megaspore (female) was retained inside its sporangium (ovule) while the microspores (pollen) were freely dispersed for potential capture by the tubular tips of female sporangia (pollination biology). Unique to seed plant heterospory is the parasitic nutrition of both female and male gametophytes that makes their growth independent of environmental water, sunlight, or fungal mutualism. The emergence of seed biology is linked to adaptations of early gymnosperms for pioneering dry habitats (Beerbower *et al.* 1992).

Devonian landscapes

Early Devonian

The expansion and diversification of plants in the Early Devonian (Fig. 1.3.5.1a) protected floodplains and soils from erosion, so that secondary succession (regrowth/replacement of taxa after disturbance) became dominant over primary succession (colonization of bare substrates and replacement of pioneer taxa as sites/soils matured). Bank-dwelling plants stabilized stream channels and promoted meandering rather than braided stream courses. These and floodplain dwellers served to delay and lessen the effects of devastating flash floods so that soil formation on interfluves was less frequently and less critically interrupted by sedimentation

or scour (Retallack 1990). As forests appeared in Middle–Late Devonian (Fig. 1.3.5.1b,c) they had an even greater impact (Algeo and Scheckler 1998).

Late Silurian and Early Devonian rhyniopsids and zosterophylls were small, rhizomatous plants that formed local monotypic patches by clonal growth. Bottoms of shallowly buried rhizomes or corms bore only tufts of rhizoids or short roots for anchorage and absorption. They utilized mainly surface water and were probably limited to habitats with nearly continuous moisture.

By mid–late Early Devonian (Pragian–Emsian), however, new plant architectures emerged. Tall main axes of trimerophytes bore overtopped lateral branches. Lycopsids had robust forked aerial axes covered by small leaves (Fig. 1.3.5.1a). Rhizomes of both groups produced sparse, small forked roots that penetrated shallow soils. Root penetration of floodplain deposits is absent or scarce before the Pragian, but is common thereafter. Subsurface water and dissolved soil nutrients were utilized so that slightly drier habitats could be colonized.

Middle Devonian

Trailing, herbaceous lycopsids often dominated local beds, with rhizomatous clones producing large monotypic patches. By the Givetian, however, tree-sized lycopsids with solitary, non-clonal growth were common (Fig. 1.3.5.1b).

Trimerophyte relatives also produced solitary trees, such as those of cladoxylopsid construction, and aneurophyte and archaeopterid progymnosperms. All had non-laminated leaves or branchlets that allowed light penetration for understorey vegetation. Tiered ecosystems, that vertically stratified light and humidity, are linked to heterospory and they also promoted niche diversification of understorey plants. Stabilized floodplains developed local microclimates and distinctive soils that produced horizontally complex, patchy vegetation (Fig. 1.3.5.1b).

Late Devonian

Archaeopteris appeared in the early Late Devonian (Frasnian) and rapidly spread worldwide (Fig. 1.3.5.1c). All species except one had laminated leaves that made deeply shaded forests. *Archaeopteris* grew in well-drained to waterlogged soils and formed dense, streamside galleries, whereas drier interfluves supported other herbaceous or shrubby plants, such as cladoxylopsid shrubs/vines and trailing lycopsids (Retallack 1990; Beerbower *et al.* 1992). *Archaeopteris* tolerated many soil conditions (wet to seasonally dry) and formed extensive floodplain forests of only a few species (Beerbower *et al.* 1992; Algeo and Scheckler 1998). Most wetland habitats, however, were occupied by tree lycopsids or zygopterid ferns. Late Devonian riparian landscapes were thus marked by abrupt, small-scale, spatial heterogeneity (Fig. 1.3.5.1c).

Archaeopteris shed its leafy branches after one season of growth, possibly during a dry season. Deep litter accumulated in these forests and provided the innumerable branches preserved, during floods, in fluvial sediments. If the branches were shed throughout the year, then forest floors would have remained shady. However, if most leafy branches were shed during a dry season, then understorey vegetation had wide seasonal variation in light and humidity. Large amounts of fuel accumulated in *Archaeopteris* forests. Coupled with rising pO_2 as pCO_2 fell, fire became important for succession by Famennian times (Beerbower *et al.* 1992; Berner 1997, 1998; Algeo and Scheckler 1998).

Global impacts of forests

Forest expansion stabilized stream banks and floodplains and dramatically increased sediment retention time, so that more clay was produced on floodplains (Retallack 1990; Algeo and Scheckler 1998). Increased depth and areal extent of rooting changed soil chemistry. Carbon sequestration (by increased soil silicate formation and primary production, more recalcitrant plant biomolecules (e.g. lignin), and burial of trunks, roots, and branches in marine and terrestrial sediments) transformed global atmospheric chemistry (less CO_2, more O_2). Global cooling, pronounced extinctions of marine invertebrates, and the initiation of wildfire conflagrations are among the effects that can be attributed to afforestation (Beerbower *et al.* 1992; Berner 1997, 1998; Algeo and Scheckler 1998).

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1.3.6 Terrestrialization of Animals

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Introduction

The diversity of animals on land greatly exceeds that in the sea; this is almost entirely accounted for by the insects, which make up 70% of all animal species alive today. However, of over 30 animal phyla, only the arthropods, molluscs, annelids, and vertebrates have significant numbers of macroscopic terrestrial representatives. A larger set of phyla includes those with very few terrestrial species, cryptobiotic representatives, and internal parasites on terrestrial organisms. The body plans of some highly successful marine groups seem to have precluded their terrestrialization; these include the sipunculid, echiuroid, and priapulid worms, cnidarians, lophophorates, chaetognaths, pogonophores, hemichordates, and echinoderms. No phylum originated on land, and no major terrestrial clade has become extinct, as far as is known. Outstanding questions on terrestrialization are: (1) what physiological mechanisms enabled animals to emerge on to land, and did each taxonomic group use similar mechanisms; (2) what routes on to land did animals use and did they terrestrialize simultaneously, suddenly, or gradually; and (3) how were the earliest terrestrial ecosystems organized? Some evidence comes from comparative physiology, but palaeontology can test hypotheses based on neontology, give evidence for plant–animal interactions, and uniquely can provide the dimension of time.

Animals moving on to land from the sea experience profound changes in all aspects of life (Little 1983). On land, water supply is variable, and commonly seasonal. Oxygen is more available in air than in water because the diffusion coefficient (partial pressure per unit length) of oxygen in air is 11.0, but in water is 0.000 034, so supply of oxygen to tissues by diffusion is an option in terrestrial animals with small cross-sections. Support is more of a concern in the less viscous aerial medium than in water, but once this problem is overcome, locomotion becomes easier and faster. The difference in refractive index between air and water poses a problem for visual sense organs in transition, but high-frequency vibrations can be perceived more easily in air, resulting in a greater use of sound by terrestrial animals. On land, internal fertilization is the norm, and greater protection (e.g. from drought) is necessary for the developing embryos. Changes in nutrition, ion balance regulation, and excretion are also necessary for terrestrialization.

Four groups of land animals can be defined on their management of water availability. (1) Aquatic animals avoid the problem by living in interstitial water in soils; these include microscopic protozoans, ostracods, and nematodes. (2) Cryptic forms differ from those in group 1 by being macroscopic, but similarly inhabit environments of constantly high humidity, such as soil and tropical forest litter; included in this group are earthworms, leeches, flatworms, isopods, slugs, insect larvae, and some amphibians and myriapods. (3) Poikilohydric (desiccation-tolerant) organisms require high humidity to function but can tolerate desiccation by rehydrating when conditions become favourable again; cryptobiotic rotifers and mites belong to this group, as do some animals with desiccation-tolerant dormant stages, such as the eggs of fairy shrimps and tardigrade tuns (cysts). (4) Homoiohydric organisms have achieved the true conquest of the land by the use of waterproof cuticles, transport systems, and osmoregulation; in this group are tetrapods, insects, arachnids, and some isopods and molluscs.

Many terrestrial animals took the littoral route on to land; living in the highly variable environment of the seashore gave them preadaptations for life on land. Others took different routes, via fresh water for example, and there is evidence that some Late Silurian terrestrial biotas occupied a saltmarsh habitat.

Fossil evidence of terrestrialization

There are two main types of fossil evidence for terrestrial life: body fossils and trace fossils—direct and indirect evidence, respectively. Trace fossils include burrows and trackways in subaerial sediments, coprolites, and plant damage; other evidence for terrestrial life, such as chemical fossils, could be included here. Trace fossils can provide evidence that animals were present on land, possibly what they were doing, but not necessarily what kind of animal left the traces. Body fossils give direct indications of the type of animal present, but it may be unclear whether or not it lived in a terrestrial environment. Commonly, the nature of the sediment provides the clue to terrestriality. However, there are some good morphological indicators: gills and lungs have different

morphologies, with the latter normally being enclosed in the body and connected to the outside by stigmata; trichobothria are fine hairs sensitive to airborne vibrations which could not function in water; a hanging stance, plantigrade foot, and leg-rocking joints occur in land arthropods; and copulatory systems are generally necessary in terrestrial animals but not aquatic ones.

Body fossils

A study of the fossil record (Fig. 1.3.6.1) reveals that modern land animal groups did not terrestrialize simultaneously. There is no fossil record of free-living terrestrial flatworms, nemerteans, or nematodes, although fossil examples of parasitic and aquatic nematodes are known, mostly from ambers. Oligochaete annelids are known from the Carboniferous, though they may not have been terrestrial at that time. Two groups of land snails, helicinid prosobranchs and stylommatophoran pulmonates, are recorded from the Upper Carboniferous. The earliest basommatophoran pulmonate is Late Jurassic in age, although basommatophorans are thought, on comparative morphological grounds, to be ancestral to other pulmonates. The development of ground shade and deciduous leaf litter (probably in the Early Carboniferous) may have been necessary before land snails could be assured of the damp conditions required for colonization. The record of Onychophora begins with marine lobopodians from the Cambrian, but no fossil terrestrial forms are known. A possible marine tardigrade larva has been described from Cambrian Orsten of Siberia. Tardigrades withstand periods of desiccation by forming cysts known as tuns. Aerial dispersal of tuns may have enabled these tiny creatures to have inhabited moist environments alongside the earliest terrestrial plants.

'Myriapods', once thought to be a monophyletic clade allied to insects, have been shown to be paraphyletic. There is insufficient evidence to confirm that supposed myriapods in Cambrian marine sediments are, in fact, arthropods, but good milliped and centiped fossils occur in Late Silurian and Devonian strata, including scutigeromorph centipeds among the earliest land animals (Jeram *et al.* 1990). By Devonian times, myriapods had reached greater ordinal diversity than today, and some reached giant proportions (2 m) in the Carboniferous forests. All extant hexapods are terrestrial or secondarily aquatic. Evidence for a closer hexapod–crustacean than hexapod–myriapod relationship is emerging, though precisely at what point(s) in the phylogeny of hexapod ancestors terrestrialization occurred is unclear. There seems to have been independent evolution of respiratory organs numerous times amongst tracheates, possibly corresponding to separate terrestrialization events. The earliest apterygotes are found in Devonian rocks, but the first pterygotes are Carboniferous in age.

Amongst chelicerates, eurypterids ranged from Ordovician to Permian and were predominantly aquatic animals, but from the Silurian onwards some were amphibious, as evidenced by their accessory lungs and subaerial trackways. They illustrate a failed attempt at terrestrialization. Scorpions, close relatives of eurypterids, succeeded in terrestrialization by converting gills into lungs. Whilst all Silurian scorpions appear to have been aquatic, book lungs appear first in Lower Devonian scorpions, and aquatic, terrestrial, and amphibious forms probably coexisted through the Devonian. All other arachnids are primarily terrestrial today. The oldest are the trigonotarbids, extinct relatives of spiders, with unequivocal terrestrial features such as book lungs. Trigonotarbids are among the oldest land animals, from the Silurian of Shropshire (Jeram *et al.* 1990), and are common in all early terrestrial ecosystems. Mites, pseudoscorpions, and spiders are also found in Devonian strata, and by Carboniferous times there were more arachnid orders than today; the spiders radiated more dramatically in later periods.

The fossil records of many crustacean groups are generally good because of their mineralized exoskeletons. However, the terrestrial groups show very short fossil ranges. The first amphipods are Upper Eocene, although it has been suggested, on biogeographical grounds, that their origins lie in the mid-to-late Mesozoic, or earlier. The terrestrial talitrids, with no fossil record, are considered by some to have emerged on to land when the first angiosperm forests became established in coastal regions. The isopods have a long fossil record, from the Upper Carboniferous, with their supposed origins in the Devonian, but the terrestrial Oniscidea are known only from the Eocene onwards. Similarly, whilst crabs and crayfish first appeared in the Jurassic, the important crab radiations did not occur until the Cretaceous and Palaeogene, with true terrestrial forms appearing in Neogene times.

No fewer than 10 genera of tetrapods are known from Late Devonian deltaic and lacustrine palaeoenvironments worldwide. Morphological and sedimentological evidence suggests that these animals were aquatic carnivores at that time. A 20 myr gap in the tetrapod record during the Early Carboniferous makes it difficult to relate these early examples to later, terrestrial forms. Tetrapod origins and evolution are discussed in Section 1.3.7.

Trace fossils

Although the first body fossils of terrestrial animals appear in the Late Silurian (Jeram *et al.* 1990), trace fossils attributed to their activities are known from the Ordovician. Trackways in subaerial deposits in the Caradocian Borrowdale Volcanic Group of north-west England may have been produced by animals making limited

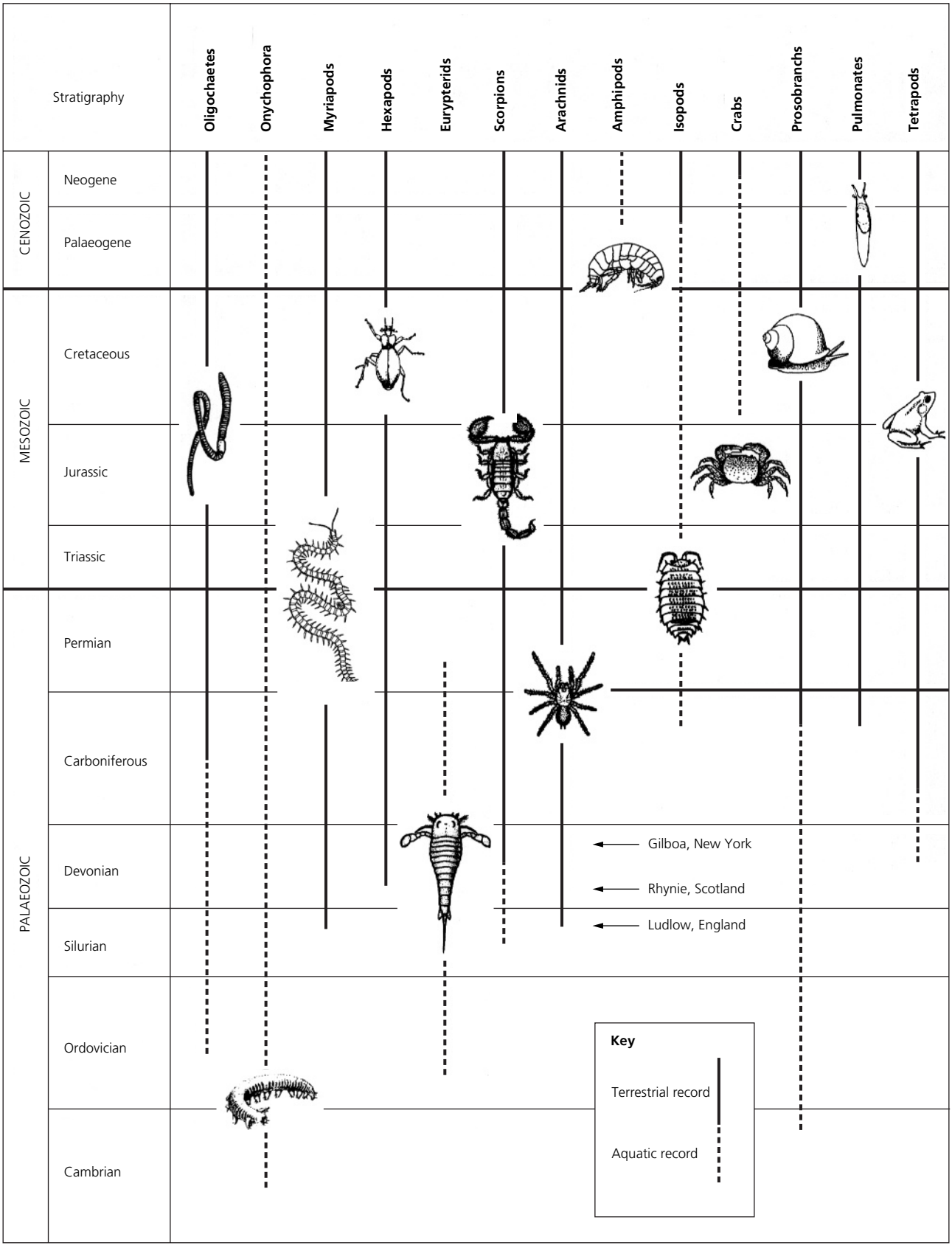


Fig. 1.3.6.1 Fossil record of terrestrial animals and their forebears, and stratigraphic positions of three major early terrestrial Lagerstätten.

excursions on to land or, indeed, they could have been terrestrial. Meandering, subvertical, back-filled burrows in an upper Ordovician palaeosol in Pennsylvania bear some resemblance to modern milliped burrows, but it is impossible to say what produced them. Late Silurian trackways, attributable to terrestrial or semiterrestrial arthropods, are relatively abundant. For example, a rich diversity of trackways and burrows in the Upper Silurian Tumblagooda Sandstone of Western Australia is considered the work of myriapods, eurypterids, scorpions, and euthycarcinoids. Whilst some were made under water, a large number represent animals walking on sediments exposed to the air, and possibly on dry, windblown sand. Annelid traces, including burrows and faecal pellets, occur in palaeosols from the Carboniferous onwards; they may have emerged on to land with the first humic soil. Evidence for terrestrial locomotion by Devonian tetrapods is ambiguous.

Another line of trace fossil evidence comes from coprolites. Coprolites bearing plant remains provide direct evidence of plant–animal interaction in early terrestrial ecosystems. Upper Silurian and Lower Devonian coprolites attributable to small arthropods have been described. For example, coprolites packed with different spore types are known from Silurian and Devonian sites in the Welsh Borderland (Edwards *et al*. 1995). The coprolites were initially thought to be sporangia, but their regular shape, lack of a sporangial wall, presence of up to nine spore types in some specimens, and other debris, ruled out this possibility. The coprolites were probably produced by terrestrial detritivores (litter-feeders) which were ingesting spores and spore masses but not digesting them, in a similar way to modern millipeds. Plant damage, probably caused by arthropods, is common in some early terrestrial ecosystems, such as the Rhynie chert (see Section 3.4.5). Damaged specimens of *Psilophyton* from the Lower Devonian of Gaspé, Québec, include several types of wounding and wound reaction, suggesting attack by animals with sucking mouthparts and subsequent response by the plants. Possible coprolites were also found both within and outside these plant stems. It is likely that the main interactions between plants and animals in the earliest terrestrial ecosystems were directly through sap-feeders and indirectly through litter decomposers.

Ecosystems

The best-known early terrestrial Lagerstätte is still the Rhynie chert (396 Ma) of Scotland, first described in detail in the 1920s (see Section 3.4.5). Over the last 30 years, however, a number of other early terrestrial ecosystems have become almost as well studied (Fig. 1.3.6.1), including the Gilboa, New York, and Ludlow, England, Lagerstätten (see reviews: Shear 1991; Edwards and Selden 1993; Shear and Selden, in press). This work has revealed that the familiar plant–herbivore–carnivore food chain of today's world had not evolved by the Devonian period. The animals present in Siluro-Devonian Lagerstätten were either carnivores (e.g. arachnids, centipeds) or occupied the decomposer niche (e.g. Collembola, millipeds). Tetrapod herbivory is not known before the Late Carboniferous. In fact, many modern food chains, such as the soil ecosystem, are decomposer-based, and herbivores commonly rely on gut microorganisms to break down green plant matter before it can be ingested. The evolution of herbivory may have been a result of gradual short-circuiting of the decomposer food chain by animals harbouring decomposing microorganisms in their guts, thus enabling the aerial parts of green plants to be eaten. The development of the tree habit may have provided a stimulus in this direction.

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1.3.7 Origin of Tetrapods

M.I. COATES

Introduction

The origin of tetrapods, i.e. amniotes (mammals, birds, reptiles) and amphibians (frogs/toads, salamanders, apodans), has been linked traditionally to vertebrate terrestrialization. Scenarios of this key event usually include sparsely vegetated, seasonally arid Devonian

floodplains or coastal mud flats, thus favouring air-breathing fishes able to struggle from one drying pool to another (see Ahlberg and Milner 1994; Clack 1997). Lobe-fins (sarcopterygians) have long been recognized as including candidates most likely to survive such conditions. Of these, *Eusthenopteron* (Fig. 1.3.7.1a), the best-known member of the extinct osteolepiforms, has often been illustrated as an actual tetrapod forebear, half emerged, on the banks of some Palaeozoic swamp or shoreline. The anticipated ancestor–descendant sequence was apparently confirmed in the 1930s and 1950s by discoveries in East Greenland of Devonian (Famennian) tetrapods: near-complete skeletal remains of *Ichthyostega* (Fig. 1.3.7.1d) and incomplete skulls of *Acanthostega* and *Ichthyostegopsis* (see Coates 1996). *Ichthyostega* fulfilled expectations by incorporating a fish-like notochordal braincase, subopercular bone, and a ray-supported tail-fin within an otherwise tetrapod-like skeleton. Such primitive features have remained conspicuously absent from published accounts of Carboniferous coal-measure, and earlier, tetrapods (Ahlberg and Milner 1994).

Prior to the late 1980s, research on tetrapod origins developed in two principal directions. First, descriptions of further Carboniferous and Permian taxa broadened knowledge about Palaeozoic tetrapod diversity and led to the recognition of (and conflicting hypotheses about) major taxonomic groups (Ahlberg and Milner 1994). These include baphetids (loxommatids), colosteids, aïstopods, nectrideans, and microsaurs, together with possible amphibian relatives (temnospondyls, e.g. *Balanerpeton*, Fig. 1.3.7.1e) and possible amniote relatives (anthracosaurs and captorhinids). These discoveries occurred within a small number of well-documented fossil ecosystems, extending knowledge of early tetrapod habitats from the Famennian floodplains and mud flats of East Greenland to sites such as the Viséan shallow lake of East Kirkton and the Westphalian deltas and coal-

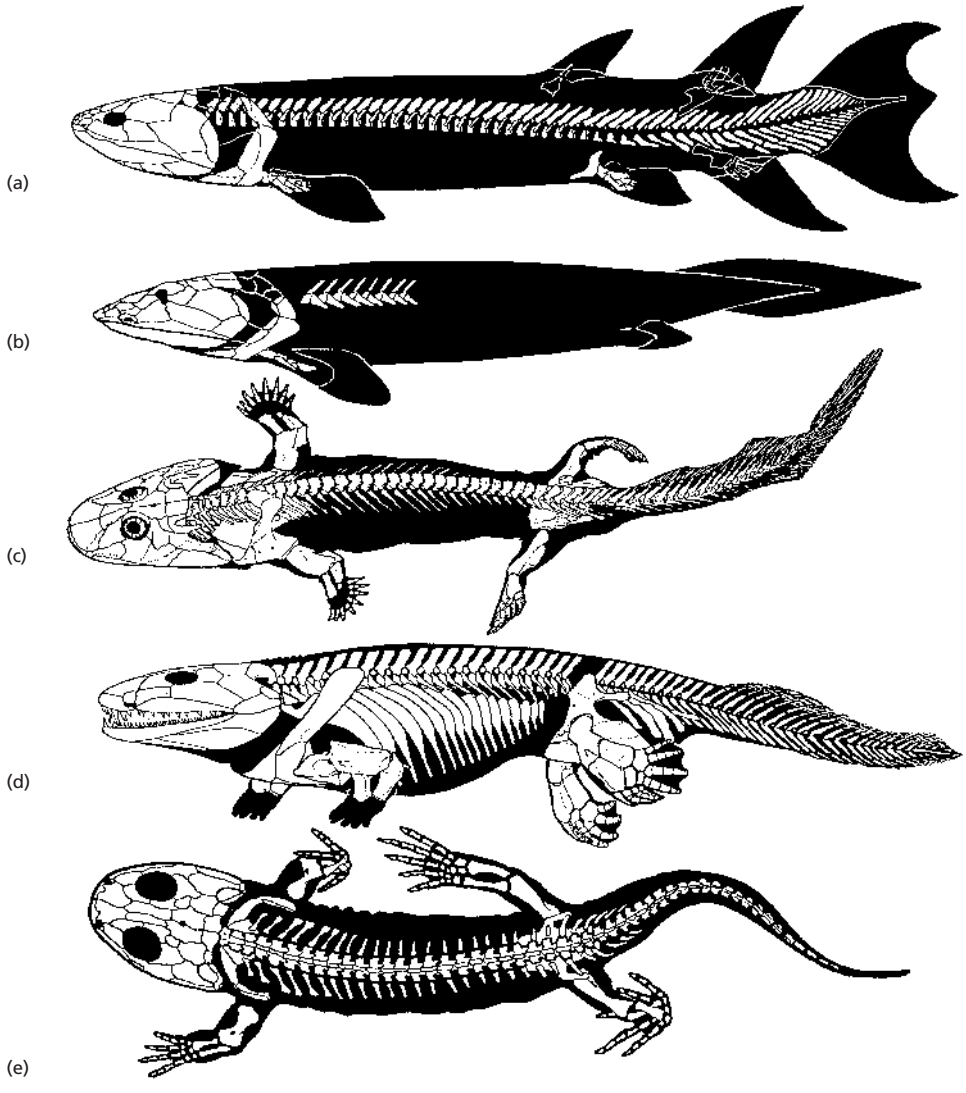


Fig. 1.3.7.1 Silhouette diagrams of tetrapod total-group members. (a) *Eusthenopteron* (Osteolepiformes; Mid–Upper Devonian). (b) *Panderichthys* (Panderichthyidae; Mid–Upper Devonian). (c) *Acanthostega* (plesion stem-tetrapod; Upper Devonian). (d) *Ichthyostega* (plesion stem-tetrapod; Upper Devonian; new reconstruction including caudal ribs). (e) *Balanerpeton* (Temnospondyli; Viséan). In (a) and (b) fin-rays and scales are omitted, while dermal bones of opercular flap, upper shoulder girdle, and rear of the skull roof, plus endoskeletal fin supports are shown in outline only; in (c) gastralia, carpal and tarsal osteoderms are omitted. This convention is intended to clarify comparison of retained skeletal features throughout the genera illustrated.

swamps of Nyrany (Czech Republic), Mazon Creek (Illinois), and Joggins (Nova Scotia) (Ahlberg and Milner 1994; Clack 1998).

Second, the application of cladistic methodology to sarcopterygian and tetrapod interrelationships provided a more rigorous framework within which to examine theories of tetrapod origin (see Ahlberg and Milner 1994). One new phylogeny challenged assumptions about the ancestral relation of osteolepiforms to tetrapods, and proposed lungfish as the tetrapod sister-group. An alternative model retained lungfish as the extant sister-group (cf. Fig. 1.3.7.2), but also presented a series of osteolepiform–tetrapod synapomorphies. These included features of the pectoral fin and girdle, as well as resolving arguments about the choana (the internal nostril shared by all tetrapods and certain sarcopterygians). Significantly, this work foreshadowed subsequent studies which identified the importance of fossils for determining primitive conditions and character polarity.

Cladistic techniques also helped to clarify the anatomical gulf between osteolepiforms and *Ichthyostega* plus more advanced Carboniferous genera, by means of specifying, on a character by character basis, the mor-

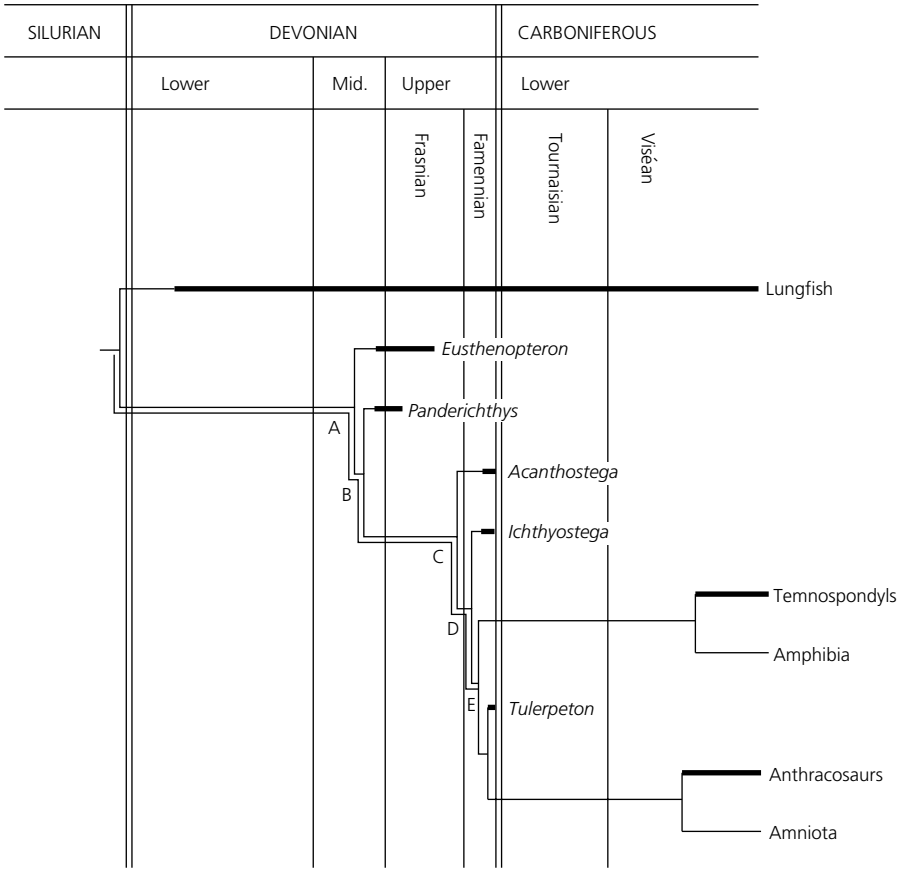


Fig. 1.3.7.2 Phylogenetic tree of the tetrapod stem-group and basal crown-group radiation, excluding less completely known taxa and many Carboniferous tetrapod clades. Node A is node uniting *Eusthenopteron* and higher tetrapods; not the base of the tetrapod stem, the defining characters of which are uncertain. Node E is base of tetrapod crown-group; extent of stem-group marked by double line. Node A: palatal nostril present; shoulder girdle with socket; humeral head convex. Node B: skull flattened dorsoventrally; snout length increased; orbits dorsal; frontal bones present; body flattened dorsoventrally; dorsal and anal fins absent; elongate leaf-shaped tail fin; ribs enlarged; shoulder girdle enlarged; humerus flattened dorsoventrally. Node C: nasal bones meet at midline; compact undivided braincase; opercular bone series absent; prepelvic vertebrae interarticulate; ribs two-headed; fish-like dermal bones reduced/lost from shoulder girdle; rudimentary scapular blade; loss of fin-rays from pectoral and pelvic appendages; digits present; simple ankle and wrist; pelvis enlarged; sacrum present. Node D: ulnar olecranon process (weight-supporting elbow joint); tail fin reduced; more tetrapod-like, robust shoulder girdle; pelvic girdle with greater buttressing. Node E: cranial sensory lines in grooves; occipital condyles present (consolidated neck joint); scapular blade well developed; complex wrist and ankle joints; tail fin-rays and internal skeletal supports absent. (Adapted primarily from Coates 1996; with taxon ranges from Clack 1997; selected characters supporting nodes A–E adapted from Ahlberg and Milner 1994 and Coates 1996.)

phological differences and similarities between fish-like and tetrapod-like anatomies. However, the fish–tetrapod transition can now be addressed in much greater detail following the discovery of new data on panderichthyids (Fig. 1.3.7.1b), a sarcopterygian group yielding increasingly tetrapod-like characteristics; new specimens of *Acanthostega* and *Ichthyostega*; the discovery of a Russian Famennian tetrapod, *Tulerpeton*; and the identification of Late Devonian tetrapod fragments from Pennsylvania, Scotland, Latvia, and Australia.

New data: *Panderichthys*, *Acanthostega*, *Ichthyostega*, and others

Panderichthyids include *Panderichthys* (Fig. 1.3.7.1b) and *Elpistostege* (Clack 1997) from the Frasnian of Latvia and Canada, respectively. They possess tetrapod-like dorsally placed orbits, flattened skulls, enlarged ribs, fin distribution, and details of humeral morphology (Coates 1996). However, these apparently advanced characters are associated with primitive features such as a jointed braincase resembling the generalized sarcopterygian condition (Carroll 1996), and many key skeletal features (such as the pelvic girdle and fin supports) remain undescribed. Given their likely phylogenetic proximity to tetrapods it is probably significant that, unlike the pike-shaped *Eusthenopteron* (Fig. 1.3.7.1a), the tetrapod-like body form of panderichthyids indicates a shallow-water predatory niche (Ahlberg and Milner 1994).

Specimens of *Acanthostega* (Fig. 1.3.7.1c) collected in 1987 reveal the most completely known skeletal anatomy of any Devonian tetrapod (Coates 1996 and references therein). Superficially, *Acanthostega* resembles a generalized Carboniferous tetrapod, but numerous aspects are even more fish-like than those of *Ichthyostega*. These include a larger ray-supported tail fin; an axial skeleton with a barely regionalized neck; short ribs in which the two heads (characteristic of tetrapod ribs) are only weakly differentiated; a shoulder girdle retaining a flange (postbranchial lamina) usually associated with the rear of an internal gill chamber; sensory canals fully enclosed within skull bones; and a branchial skeleton including a massive ceratohyal plus at least three gill arches. Its eight-digit limbs include a radius and ulna resembling those of *Panderichthys* and *Eusthenopteron*, while the broad, flat tibia and fibula articulate with a simple ankle like that of *Ichthyostega* (Fig. 1.3.7.1d).

Polydactyly has emerged as an unanticipated feature of all known Devonian tetrapods (Coates 1996). *Acanthostega* limb patterns are matched by the six-digit limbs of *Tulerpeton* and what has turned out to be the seven-digit hindlimb of *Ichthyostega* (Coates 1996). Absence of complex wrists and ankles in *Acanthostega* and *Ichthyostega* is probably primitive relative to conditions in *Tulerpeton* and more advanced tetrapods. This is consistent with the more conventionally tetrapod-like tibia and fibula of *Tulerpeton* and the presence of ankle characteristics shared with Carboniferous tetrapods and especially anthracosaurs (Coates 1996).

Although several details of the anatomy of *Ichthyostega* are unknown (the neck, sacrum, wrist, and forelimb digits; Fig. 1.3.7.1d), it is increasingly clear that it differs considerably from *Acanthostega* and any other Palaeozoic tetrapod known in significant detail (Coates 1996). The large forelimb, flexed permanently at the elbow, combined with a hindlimb resembling a cetacean flipper, indicates a resting body-posture like that of a seal rather than more conventional primitive tetrapod analogues. Furthermore, the caudal ribs, just behind the pelvis, are unusually massive and bladed like the series enclosing the trunk (Fig. 1.3.7.1d), but the functional significance of these is obscure (beyond insertion for musculature).

Abundant detailed information about the East Greenland tetrapods has accelerated the identification and corroboration of fragmentary remains attributed to Devonian tetrapods, and at least five further genera have been recognized from sites in Australia, Latvia, Scotland, and North America (Carroll 1996; Coates 1996). Increased Devonian tetrapod skeletal data have likewise informed interpretations of possible trackway evidence. A recent survey identifies the most plausible examples as those known from the Devonian of Australia, Scotland, and Ireland (Clack 1997).

Like the Devonian tetrapod catalogue, the Carboniferous record has also been enriched by new taxa and localities. Nevertheless, a real problem persists with the dearth of specimens from the Tournaisian and lower Viséan (Fig. 1.3.7.2). The crucial contents of this gap of at least 25 million years are predicted by the range of tetrapods found in sites such as East Kirkton, from the Scottish Viséan (Clack 1998). East Kirkton is one of the earliest definitively terrestrial tetrapod localities. In addition to numerous plants, invertebrates, and somewhat fragmentary fish remains, this fauna also includes likely stem-amniotes, stem-amphibians, and representatives of groups whose affinities are much less well understood (Clack 1998). Such sudden diversity, relative to the Devonian record, emphasizes the point that numerous, fundamental, branching events in tetrapod phylogeny must have occurred in the Early Carboniferous. Other notable additions to the list of Carboniferous sites include the Viséan St Louis Formation of Delta, Iowa, including a primitive anthracosaur-like species (Coates 1996), and the discovery of a similarly aged tetrapod locality in Australia (Milner 1996).

New patterns and possible processes across the fish–tetrapod divide

These new data have contributed to several reanalyses of primitive tetrapod phylogeny. Representative cladograms such as those in Ahlberg and Milner (1994), Carroll (1996), Coates (1996; summarized in Fig. 1.3.7.2), and Clack (1998) share important features. Perhaps most significantly, *Panderichthys*, *Acanthostega*, and *Ichthyostega* emerge consistently as successive sister-groups to the basal radiation of the lineages leading to modern amphibians and amniotes (cf. Fig. 1.3.7.2). It seems likely that this sequence will be a robust feature of future phylogenies. Major differences between such trees increasingly concern the position of the node from which modern tetrapod diversity radiates. At one extreme, attachment of *Tulerpeton* to the amniote basal lineage implies that amphibian and amniote evolutionary histories diverged before the end of the Devonian (Fig. 1.3.7.2). At the other extreme, the amphibian–amniote divergence is placed much higher in the tree; temnospondyls are divorced from amphibians, and anthracosaurs are divorced from amniotes (cf. relationships discussed in Ahlberg and Milner 1994; Coates 1996). However, despite such major differences in tree topology, it is noteworthy that both versions of tetrapod evolution imply that amphibian and amniote ancestries diverged before the mid-Viséan.

With the possible exception of the temnospondyl *Balanerpeton* (Fig. 1.3.7.1e), all taxa shown in Fig. 1.3.7.1 can therefore be described as 'stem-tetrapods' and used to illustrate anatomical transformations spanning the traditionally accepted locus of the fish–tetrapod divide. Paradoxically, the origins of the tetrapod total-group (*all* taxa that are related more closely to the modern tetrapods than they are to lungfishes) and crown-group (the latest common ancestor of living tetrapods and all of its descendants) are thus distanced from the origin of limbs, important features of which (digits, carpus, and tarsus) appear between nodes B and C (Fig. 1.3.7.2) and continue to accrue, piecemeal fashion, throughout the crown-group. These and other transformation patterns are already contributing to debates addressing phylogenetic questions in other aspects of vertebrate evolution. Analyses of the fin–limb transition are central to many studies of the evolution of vertebrate limb development (Coates 1996; Johanson and Ahlberg 1998), while primitive stapedial and fenestra ovalis morphologies inform questions on middle ear evolutionary neurobiology (Clack 1998).

Palaeoecological settings for the earliest tetrapods remain poorly understood. Late Devonian terrestrial environments supported architecturally modern forests (Clack 1997) and probably supplied sufficiently shady, moist, and food-rich surroundings to sustain early forays of *Ichthyostega*-like species. The global distribution of Late Devonian tetrapods is known to have extended in an equatorial belt from Euramerica to East Gondwana. However, this pattern changes dramatically after the Lower Carboniferous, with the apparent loss of tetrapods from East Gondwana as it drifted southwards into the zone of the late Palaeozoic glaciation (Milner 1996). Compared with the classic scenarios of *Eusthenopteron* lurching between ephemeral pools, Devonian tetrapod habitats now appear more aquatic. Sedimentological data show that *Acanthostega* specimens are restricted to vegetation-choked active channels in a meandering river system, *Ichthyostega* originates from closely related deposits, and *Tulerpeton* comes from sediments indicative of a shallow, warm, epicontinental sea (Clack 1997). Anatomical data show that *Acanthostega* was fundamentally non-terrestrial, a gill-breather with paddle-like limbs and a large tail fin, while the extraordinary limb combination of *Ichthyostega* suggests that, at most, it was suited to only limited terrestrial excursions. These stem-tetrapods therefore appear to have continued the shallow-water habits of their *Panderichthys*-like forebears. Consequently, most features considered characteristic of tetrapods probably evolved *before* terrestrialization (see character-state changes listed from nodes B to D in Fig. 1.3.7.2).

Finally, one of the more intriguing questions arising from this revised picture of the fish–tetrapod transition concerns the rate and magnitude of evolutionary change. Combined morphological, ichnological, and phylogenetic evidence suggests that neither digited limbs nor crown-group tetrapods originated before the Frasnian (Clack 1997). The branching pattern in Fig. 1.3.7.2 may therefore illustrate a concentrated series of evolutionary events compressed into the Upper Devonian. Discussion about whether this reflects special developmental processes and/or qualifies as an episode of Simpsonian 'quantum evolution' (the idea that evolution occurs more rapidly at the origin of large-scale groups) has already begun (Carroll 1996). However, it seems equally likely that this reflects relative ignorance of neighbouring areas on the tree: the gap in the fossil record of critical forms during the Tournaisian, and the need for more information about the evolutionary diversification of primitive osteolepiform-like fishes (cf. Johanson and Ahlberg 1998).

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1.3.8 Carboniferous Coal-swamp Forests

W.A. DIMICHELE

Introduction

The 'coal swamp' is one of the most powerful images in palaeontology. Dense, dark, and damp—populated by strange trees, giant dragonflies, and sluggish tetrapods resting on rotting logs—a diorama can be found in almost every museum and is short-hand for the Carboniferous tropics. However appealing, this visual representation of the coal-swamp forest, based on analogy with modern tropical rainforests, is largely inaccurate. Carboniferous tropical plants were drawn from at least four classes and more than 10 orders, differing widely from each other in body plan and reproductive biology. The modern tropics, by comparison, are dominated mainly by flowering plants, an admittedly diverse yet phylogenetically restricted group. Coal-swamp plants have no modern analogues, thus requiring care when using today's forests as dynamic models for the ancient past.

What is a 'coal swamp'?

In broadest terms, coal swamps are mires—wet environments in which organic matter accumulates. Mires can be classified broadly along a physical gradient that simultaneously describes their three-dimensional geometry, nutrient, and hydrological status. In planar mires the surface is below or at water table for much of the year and ground water includes mineral nutrients; hence these mires are termed minerotrophic or rheotrophic. The Florida Everglades are a modern example. In domed, or ombrotrophic, mires peat forms above the regional water table with water input mainly from rainfall, creating nutrient starvation in more interior areas. Modern Sumatra is covered by ombrotrophic mires. Both types of mire likely existed during the Carboniferous, in proportions reflecting both local conditions and regional to global climate dynamics (Cecil 1990).

The coal-swamp environment was ecologically complex and included physical phenomena similar to those found in modern wetlands. Charcoal, for example, is a common component of Carboniferous coals. Charcoal layers several centimetres thick and hundreds of metres in lateral extent occur in coal beds and record conflagrations similar to those described in modern mires during droughts. Conversely, flooding brought many coal swamps to an end; tree stumps and logs are common in roof shales, raising the image of dead snags bordering the margins of man-made lakes. Tree falls and blowdowns also have been recorded from the coal–roof shale interface and from the patterns of macrofossil plant distribution within coal beds themselves (Wnuk and Pfefferkorn 1987).

The Late Carboniferous and Early Permian were global icehouse times (Gastaldo *et al.* 1996). Coal swamps reformed intermittently in the tropical lowlands in response to global climate and sea-level fluctuations. Mires are strong indicators of high rainfall, and perhaps relatively cooler temperatures in the tropics. The intercalation of coals and palaeosols indicative of seasonal moisture stress, and the cyclic alternation of marine and terrestrial sequences, indicate that the Carboniferous tropics were not climatically uniform through time.

Coals derived from tropical mires occur mainly in the upper parts of the Lower Carboniferous and throughout the Upper Carboniferous in Europe and North America. Euramerican climates became increasingly seasonally dry during the Early Permian and the locus of peat formation moved to the Chinese microcontinents, where typically Carboniferous coal-swamp floras survived into the Late Permian (Ziegler 1990).

The major plant groups

Coal swamps were forested ecosystems composed of five major tree groups. The growth architectures (Fig. 1.3.8.1), biologies, and ecologies of these groups were distinctively different and contributed to plant assemblages that were strongly differentiated by habitat (DiMichele and Phillips 1994).

The dominant plants of the wettest parts of Westphalian coal swamps were tree lycopsids, colloquially known as giant club mosses. Lycopsid trees reached 30 m in height and over 1 m in diameter at the base. They were supported by thick bark and had a small water conducting cylinder, separating the support and water conduction functions. Growth was determinate; many species produced crowns only in the final phases of life, coincident with cone production (a monocarpic reproductive strategy). Thus the analogy to modern dicot trees seen in reconstructions is incorrect. Lycopsid trees likely formed very open forests, spending most of their life cycle as unbranched poles. Height growth and crown formation

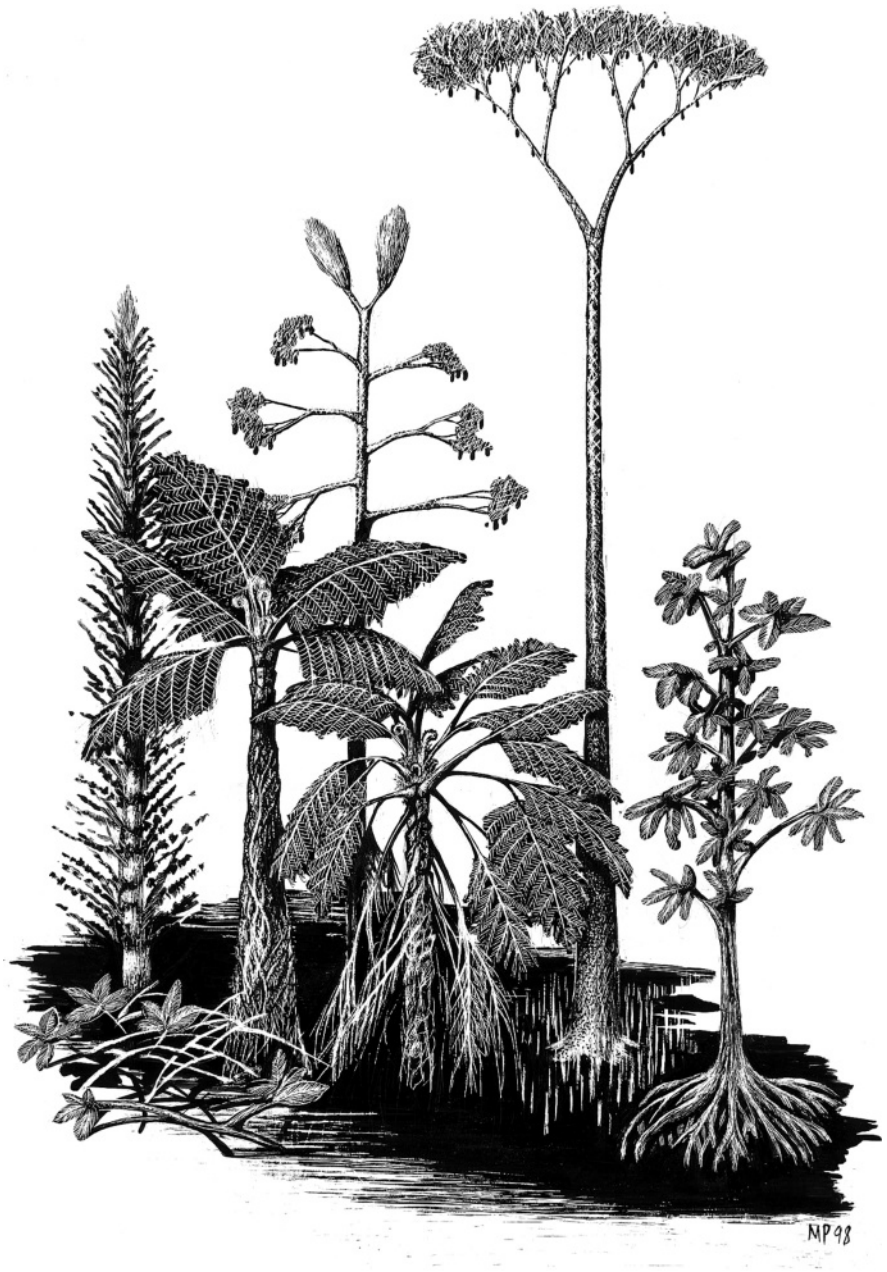


Fig. 1.3.8.1 Reconstructed growth habits of reproductively mature, selected Late Carboniferous coal-swamp plants. From left to right: a calamite tree; a scrambling cordaite; the tree fern *Psaronius*; the polycarpic lycopsid tree *Diaphorodendron scleroticum*; the seed fern *Medullosa*; the monocarpic lycopsid tree *Synchysidendron resinosum*; a mangrove cordaite tree. Maximum height is greater than 30 m. (Drawing by Mary Parrish.)

were intimately related to reproduction and dispersal rather than light capture. One group produced female reproductive organs that closely approached seeds in general morphology. Important stem genera are *Lepidodendron*, *Lepidophloios*, and *Sigillaria* among others. Roots are known as *Stigmaria*.

Cordaites were also dominant in some middle Westphalian mires. They were small, woody, seed-plant trees, similar in construction and reproductive biology to extant conifers, although with strap-like rather than needle-shaped leaves. Some cordaites have been interpreted as mangroves, based on prop roots and an association with marine indicators in coal beds. Cordaite-dominated fossil peats are often heavily rotted and cordaite wood is frequently bored by detritivorous arthropods, suggesting growth in periodically dry environments.

Stephanian (latest Late Carboniferous) coal swamps were dominated by marattialean tree ferns, a group still extant though not related to filicalean tree ferns of the modern tropics. The trunk of a marattialean was composed of a primary stem surrounded by a mantle of adventitious roots, which provided support for the tree habit. These roots were composed largely of air spaces, creating a 'cheap' means to attain large size. The crown was formed of fronds that could exceed 5 m in length,

packed with spore-producing reproductive organs. With massive reproduction, cheap construction, wide distribution, and low abundance, primitive Westphalian marattialeans appear to have been opportunists. They achieved large size in the Stephanian following major extinctions and vegetational reorganization. The common genus for stems is *Psaronius*; foliage is usually classified as *Pecopteris*.

Medullosan pteridosperms were small seed-plant trees that were locally important in mires throughout the Late Carboniferous. The group was dominant to subdominant in mineral-substrate floodplain habitats, and a subset of species occurred in mineral-rich, fire-prone parts of mires. Medullosans may have contributed to fires; their tissues were rich in resins, and large fronds, some over 7 m in length, may have remained attached to trunks after death. Seeds of many medullosans were over 5 cm in length. Pollen grains exceeded 300 µm in diameter, leading some to propose animal-mediated pollination. Common foliage types in mires include *Neuropteris*, *Alethopteris*, and *Linopteris*. Seeds are assigned to *Pachytesta*, stems to *Medullosa* and *Sutcliffia*.

The arborescent sphenopsids, or calamites, were closely related to modern horsetails and scouring rushes of the genus *Equisetum*. They were segmented, like modern horsetails, with all organs borne in whorls on supporting axes. Unlike their modern relatives, the calamites were woody, although the wood was notably parenchymatous. Common in disturbed, aggradational environments, such as stream and lake margins, sphenopsids were a persistent minor component of mires throughout the Late Carboniferous. They were the only arborescent group with a clonal habit, made possible by underground rhizomes. The common stem genus is *Calamites*. Foliage is assigned to *Annularia* and *Asterophyllites*.

Coal-swamp history

For over nine million years Westphalian coal swamps were dominated mainly by lycopsids and cordaites. The dominance of these groups reflects the commonness of the environments for which they were ecologically specialized: wet to flooded in the case of most lycopsids and periodically dry in the case of cordaites. Medullosans and specialized lycopsids occupied fire and flood prone habitats ecotonal between peat and clastic swamps. Tree ferns were interstitial opportunists in all but the wettest sites. A variety of fern and seed-plant ground cover and vines formed significant parts of this system.

Near the Westphalian–Stephanian boundary, major climatic changes, possibly associated with global warming, led to the extirpation of nearly two-thirds of coal-swamp species in the Euramerican parts of the tropics (Phillips *et al.* 1985). Most heavily affected by this

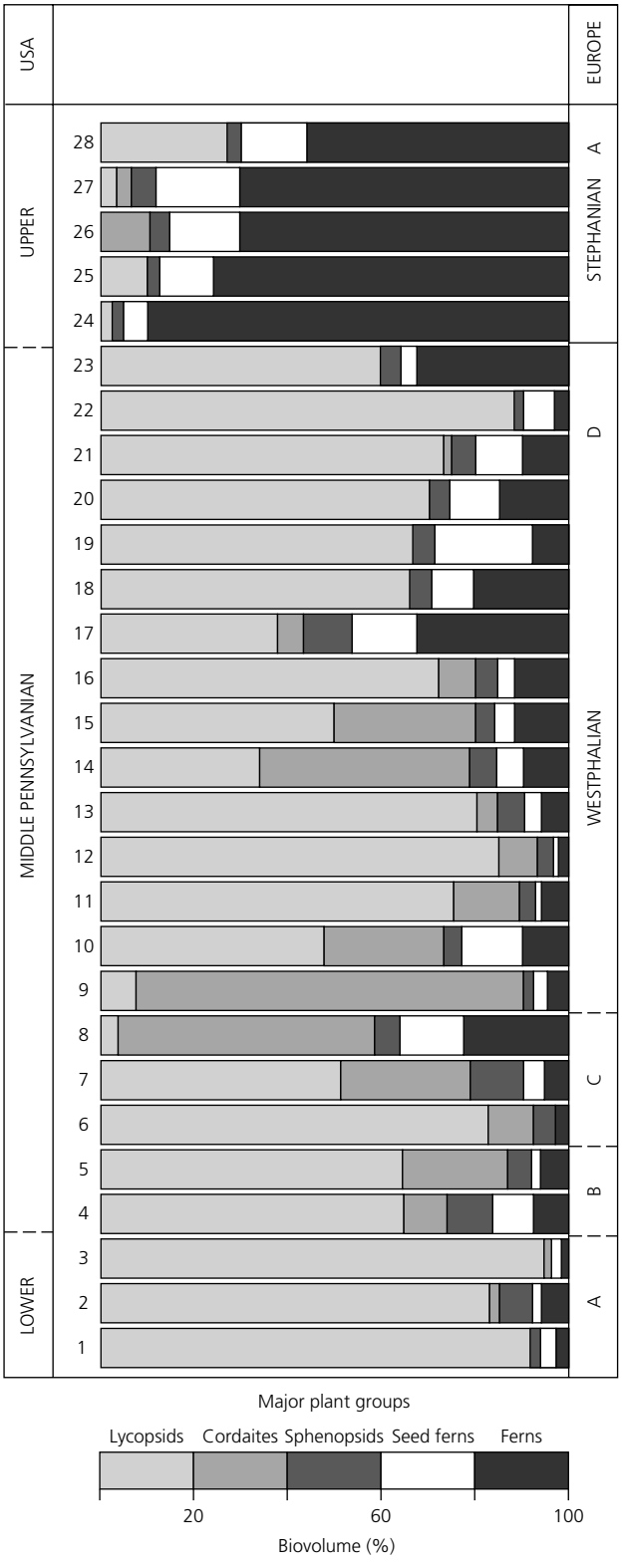


Fig. 1.3.8.2 Plant compositional changes on a seam-average basis of 28 selected Pennsylvanian (Upper Carboniferous) coals. Note major changes at the Westphalian–Stephanian boundary following extinctions of over two-thirds of the coal-swamp species. (From DiMichele and Phillips 1994; with permission from Elsevier Science.)

event were trees; over 90% of Westphalian tree species, of all taxonomic groups, failed to survive into the Stephanian. As a group, the lycopsids were devastated; all genera but *Sigillaria* disappeared from most parts of the tropics. Coal swamps with a flora very similar at the generic level to that of the Westphalian continued to survive in the Cathaysian parts of the eastern tropics into the Late Permian (Gastaldo *et al.* 1996). Climates in this part of the tropics remained aseasonally wet throughout most of the late Palaeozoic.

Stephanian mires in Euramerica were heavily dominated by marattialean tree ferns for more than six million years. Medullosan pteridosperms continued to be subdominant and, locally, the lycopsid tree *Sigillaria* was dominant in the wetter parts of mires. Furthermore, the significant floristic and vegetational differences between coal-swamp and mineral-substrate floodbasin floras that characterized the Westphalian, were much diminished during the Stephanian; tree ferns became dominant across the lowland, wetland landscape.

On either side of this major extinction and reorganization, mire vegetation was remarkably persistent, despite periodic changes in sea level and tropical climate (Fig. 1.3.8.2). Background species turnover was strongly channelled along ecomorphic lines, reflecting strong partitioning of ecological space by the major plant classes. Beginning in the Stephanian and continuing into the Permian, this ecological pattern broke down as the primitive lineages lost their position of dominance and were replaced first by ferns and then by seed plants, which remain dominant in most environments today.

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1.3.9 Rise and Diversification of Insects

C.C. LABANDEIRA

Introduction

Insects are the most speciose group of macroscopic organisms ever to inhabit the planet. They are the major player in generating associations with microorganisms, fungi, and especially vascular plants; collectively these interacting groups contribute overwhelmingly to the bulk of community structure in land and freshwater ecosystems. The ecological dominance of insects also extends to estimates of biomass, abundance of individuals, and complexity of trophic webs, a condition probably present since the late Palaeozoic when global diversity estimates, as well as site-specific tabulations, indicate that insects were taxonomically the dominant terrestrial group (Labandeira and Sepkoski 1993), at least in lowland vegetated environments.

Origin and earliest fossil records of hexapods

The sparse fossil record of mid-Palaeozoic hexapods, the pattern of colonization of land by Palaeozoic plant and arthropod groups, and temporal constraints on hexapod origins imposed by hypotheses of arthropod phylogeny on hexapod origins all suggest that the earliest hexapods probably appeared during the Late Silurian. Although often used as a synonym for 'Insecta', the term 'Hexapoda' designates the more inclusive clade that consists of the Collembola (springtails) and Protura (proturans), collectively termed the Parainsecta, as well as its sister-group, the Insecta, which encompasses all other hexapods.

Early hexapod phylogeny

Phylogenetic evidence for the derivation of hexapods from another arthropod clade is still in an exploratory phase. Currently there are five major hypotheses of the origin of the Hexapoda (Fig. 1.3.9.1), but each is sufficiently unstable that differences in methodological approach, changes in included taxa or characters, and consideration of the fossil record can result in significant topological shifts within cladograms. This field is rapidly changing, and evidence linking the genetics and developmental biology of major arthropod clades is being used to test major phylogenetic schemes.

One of the oldest views of arthropod phylogeny is diphyly, with two superclades: the Schizoramia, consist-

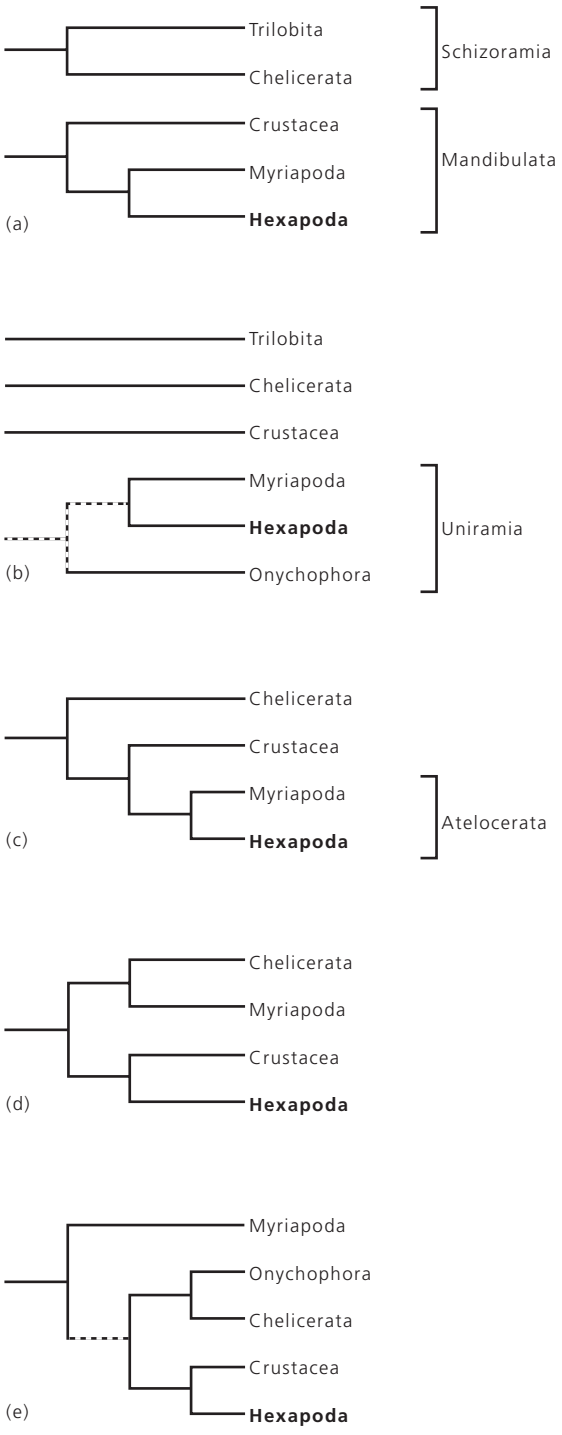


Fig. 1.3.9.1 Summaries of five hypotheses indicating the relationships of hexapods (in **bold**) to other major arthropod groups. (a) The hypothesis of arthropod diphyly, with Schizoramia and Mandibulata as distinct clades. (b) The hypothesis of extensive arthropod polyphyly, showing the traditional Uniramia as a distinct clade. (c) The hypothesis of arthropod monophyly, featuring the Mandibulata and its subgroup, the Atelocerata, as distinct clades. (d) One hypothesis of arthropod monophyly and a Crustacea + Hexapoda clade. (e) Another hypothesis of arthropod monophyly and a Crustacea + Hexapoda clade, with Onychophora included as arthropods. Branch lengths are arbitrary; dashed lines indicate nodes that are either theoretically inferred or not statistically valid. This is not an exhaustive list; see Fortey and Thomas (1997) for additional details.

ing of Chelicerata + Trilobita; and its sister-group, the Mandibulata, comprising the Crustacea and Hexapoda + Myriapoda (Fig. 1.3.9.1a). By contrast, Sydney Manton did not recognize these relationships, arguing instead for separate origins of the Trilobita, Crustacea, Chelicerata, and a Uniramia clade defined as Onychophora and Hexapoda + Myriapoda (Fig. 1.3.9.1b). Since her thesis was presented, arthropod polyphyly and the concept of the 'Uniramia' has largely been abandoned. Variations of two other major hypotheses receive most support from recent biomolecular and morphological studies. The first is the mandibulate/atelocerate hypothesis, consisting of a Crustacea and Hexapoda + Myriapoda clade that is a sister group to the Chelicerata, with or without inclusion of the Trilobita (Fig. 1.3.9.1c). The second, most recent, hypothesis posits a monophyletic Crustacea + Hexapoda clade that is a sister-group to other major arthropod clades, namely the Chelicerata + Myriapoda (Fig. 1.3.9.1d) or the Chelicerata + Onychophora with Myriapoda occurring as a basalmost clade (Fig. 1.3.9.1e). (See contributions in Fortey and Thomas (1997) for differing perspectives regarding the position of the Hexapoda within the Arthropoda.)

Within the Hexapoda, the position of the Parainsecta has always been controversial, particularly as the unique entognathous mouthparts and head sensory organs of the Collembola + Protura have frequently been cited as distinct from the Insecta. There is limited evidence that the Parainsecta may be separately derived from branchiopod crustaceans, a result that may explain why internal analyses of hexapods frequently result in an unresolved trichotomy involving the Parainsecta, the Diplura (which has variously been considered as parainsectan or insectan), and the Insecta. Nevertheless, the Insecta is generally regarded as monophyletic, and is united by several secure apomorphies. The most important evolutionary developments within the Insecta (Kukalová-Peck 1991; Fig. 1.3.9.2) were: (1) the transformation of the monocondylous mandible of the Archaeognatha into a robust mandible articulating with the head capsule by two condyles (Dicondylia); (2) the acquisition of wings (Pterygota); (3) the origin of holometabolous development (Holometabola), in which a larval stage became separated from its morpholo-

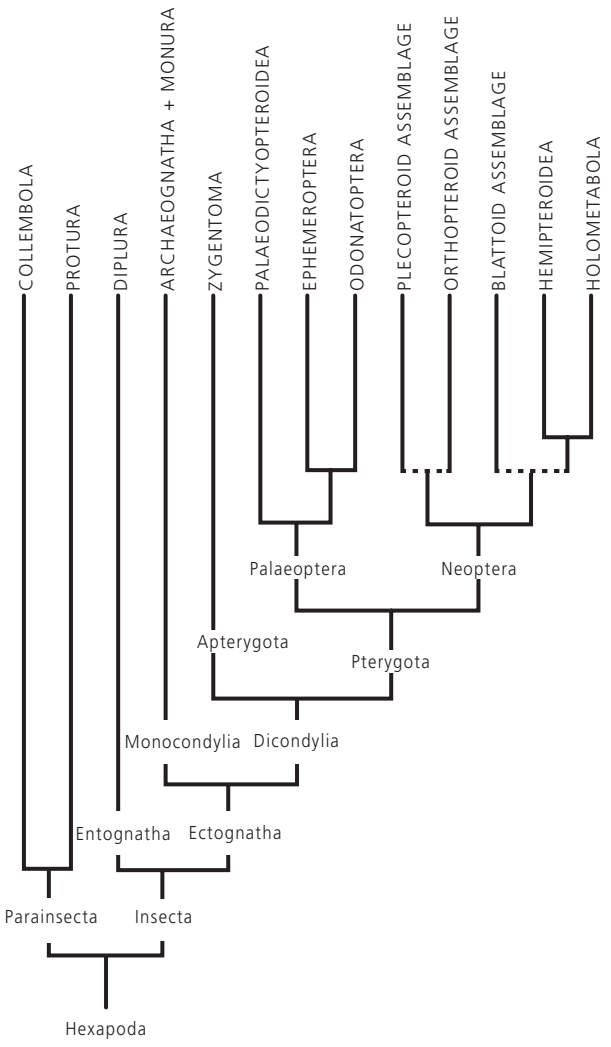


Fig. 1.3.9.2 Phylogeny of the major groups of hexapods, proposed by Kukalová-Peck (1991). Dashed lines indicate less secure relationships.

gically and ecologically distinct adult stage by a resting and non-feeding stage called the pupa; and (4) the invention of eusociality.

Devonian hexapods

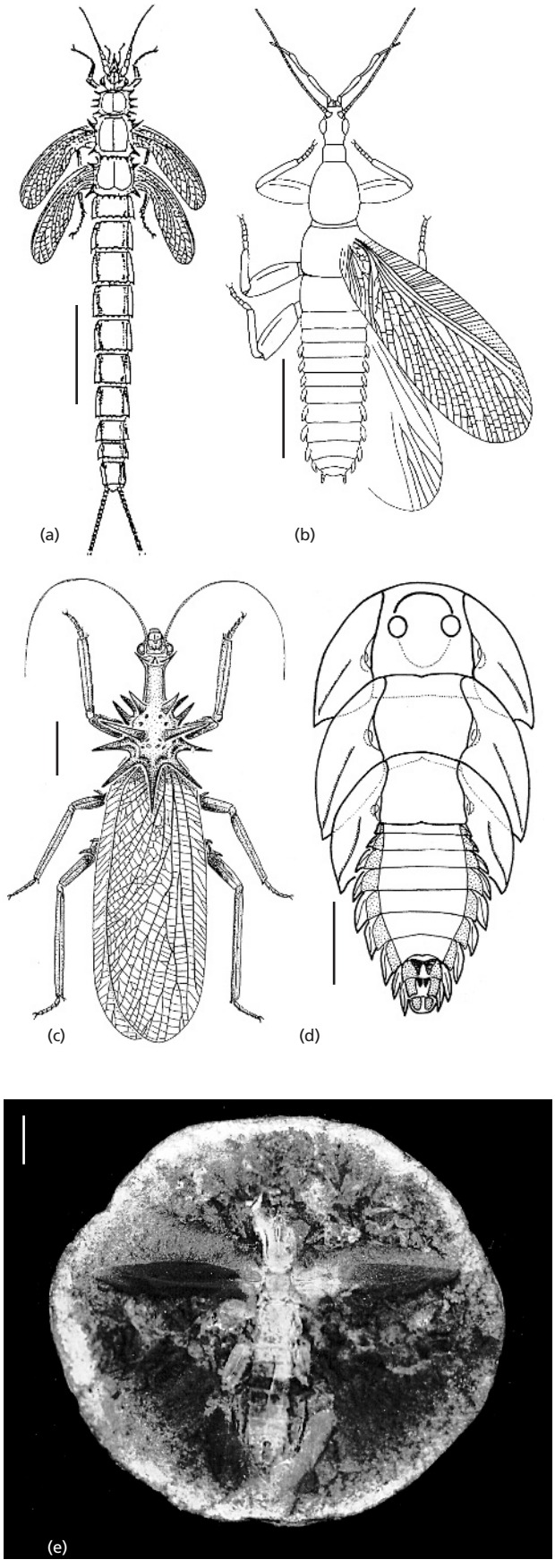
The earliest known hexapod is the springtail *Rhyniella* from the Rhynie chert of Scotland, of Early Devonian age, which occurs within a biota that includes primitive vascular plants and other arthropods, such as trigonotarbid spiders, mites, crustaceans, and myriapods (see Section 3.4.5). The earliest fossil insects are bristletails, known from a somewhat younger Early Devonian deposit from the Gaspé region of Quebec, Canada, and from the Middle Devonian of Gilboa, New York State. These earliest hexapod occurrences are unimpressive in diversity and abundance, presenting more questions than answers (Shear and Kukalová-Peck 1990). Hexapods are absent as fossils during a 55 million year interval from the Middle Devonian to the latest Early Carboniferous, during which time the major features of winged insects (Pterygota) must have evolved, based on the spectacular diversity of approximately 10 pterygote insect orders that appear suddenly at an interval straddling the Early to Late Carboniferous boundary (Brauckmann *et al.* 1995).

Insects in late Palaeozoic environments

During the early Late Carboniferous there was a dramatic appearance of diverse insect faunas at several major localities across equatorial Euramerica. A few middle Late Carboniferous to Early Permian localities yield faunas that are sufficiently diverse, abundant, and well preserved to have attracted considerable attention from palaeoentomologists. Two of the more notable insect fossil localities are in Illinois, USA. The first, Mazon Creek, is a celebrated body-fossil site in the north-central part of the state, of middle Late Carboniferous age. The second is the Calhoun Coal, a later Late Carboniferous trace-fossil deposit in the east-central region that provides a rare window into the associations of coal-swamp plants and their insects.

Late Carboniferous insects from an equatorial lowland

A relatively abundant assemblage of insects from Mazon Creek has been known for over 120 years (Carpenter 1997), consisting of approximately 175 known species, allocated to 38 families and 15 orders. This assemblage provides the earliest, well-documented glimpse of Palaeozoic insect life—inhabiting an emergent, equatorial landscape on a clastic delta that prograded southwesterly into a shallow epeiric sea. Insects from this deposit also originated from the 'uplands' surrounding this deltaic sedimentary wedge. Mazon Creek insects are preserved as moulds within flattened ovoidal concretions that are composed dominantly of siderite matrix, although the mineralized surfaces coating the entombed insects contain calcite, sphalerite, pyrite, kaolinite, and reduced iron oxides (Fig. 1.3.9.3e). These minerals were presumably formed in an anaerobic aquatic environment as insect carcasses were degraded by saprobic organisms that produced alkaline by-products resulting in early diagenetic mineralization. When carefully prepared, Mazon Creek insect fossils reveal considerable anatomical structure, such as minute venules and dark/light membrane patterns on wings. Other, typically preserved, features include sutures separating external body sclerites, cuticular ornamentation, spination, and the presence of delicate appendages such as



ovipositors, genitalia, abdominal exites, maxillary palpi, and antennae.

The major insect taxa recovered from Mazon Creek are typical of the Palaeozoic Insect Fauna, and are distinct at the highest taxonomic levels from the post-Permian Modern Insect Fauna, which consists overwhelmingly of familiar hemipteroid and holometabolous lineages that occur today. The fauna at Mazon Creek consists of the apterygote lineages Diplura (telsontails), Archaeognatha (bristletails), Monura, and Zygentoma (silverfish), as well as the pterygote lineages Protodonata (dragonflies), Palaeodictyoptera, Megasecoptera (Fig. 1.3.9.3a), Diaphanopterodea, Blattodea (cockroaches) (Fig. 1.3.9.3d), 'Protorthoptera' (Fig. 1.3.9.3b,c), Orthoptera (grasshopper-like insects), Caloneurodea, Hypoperlida (ancestral hemipteroids), Miomoptera, and probably Holometabola. Presumably the apterygote clades—those taxa primitively lacking wings—were generally detritivorous (Archaeognatha, Monura, Zygentoma) or probably predatory on other insects (Diplura). Clades of Pterygota that were primitively unable to flex their wings over their abdomen were large to gigantic in size, and were either top aerial predators (Protodonata) or had stylate mouthparts (Palaeodictyopteroidea) involved in piercing-and-sucking of plant tissues (Labandeira 1997). Mandibulate orthopteroid taxa, mostly the polyphyletic and varied 'Protorthoptera', but also oedischiid Orthoptera, may have been either detritivores or herbivorous consumers of plant foliage. By contrast, early members of the hemipteroid assemblage (Caloneurodea, Hypoperlida) bore mouthpart structures presaging those of Permian Hemiptera, including styliform mouthpart elements and a domed clypeal pump indicating imbibation of plant fluids or small particles such as spores. The enigmatic Miomoptera are considered holometabolous by some, although there is stronger evidence for the presence of early Holometabola with the recent discovery of a caterpillar-like larva (Kukalová-Peck 1991). If this assignment is true—and there is additional evidence for the presence of Holometabola from plant damage in a slightly

Fig. 1.3.9.3 A representative sample of Mazon Creek insects, from the middle Late Carboniferous of Illinois, USA. (a) Nymph of *Mischoptera douglassi* (Megasecoptera: Mischopteridae). (b) Adult of *Eucaenus ovalis* ('Protorthoptera': Eucaenidae). (c) Adult of *Gerarus danielsi* ('Protorthoptera': Geraridae). (d) Undetermined cockroach nymph, ventral view. (e) Siderite concretion of an unnamed eucaenid protorthopteran. Scale bars = 1 cm. (b, From Carpenter 1997, reproduced with permission of Northeastern Illinois University Press; a,c,d, from Kukalová -Peck 1991, reproduced with permission of Cornell University Press.)

younger Late Carboniferous deposit (Labandeira 1998)—then this diverse assemblage embodies three major evolutionary events that characterized the history of the Insecta (see above), with the exception of the origin of eusociality during the Early Cretaceous.

A Late Carboniferous community of insects on a tree fern

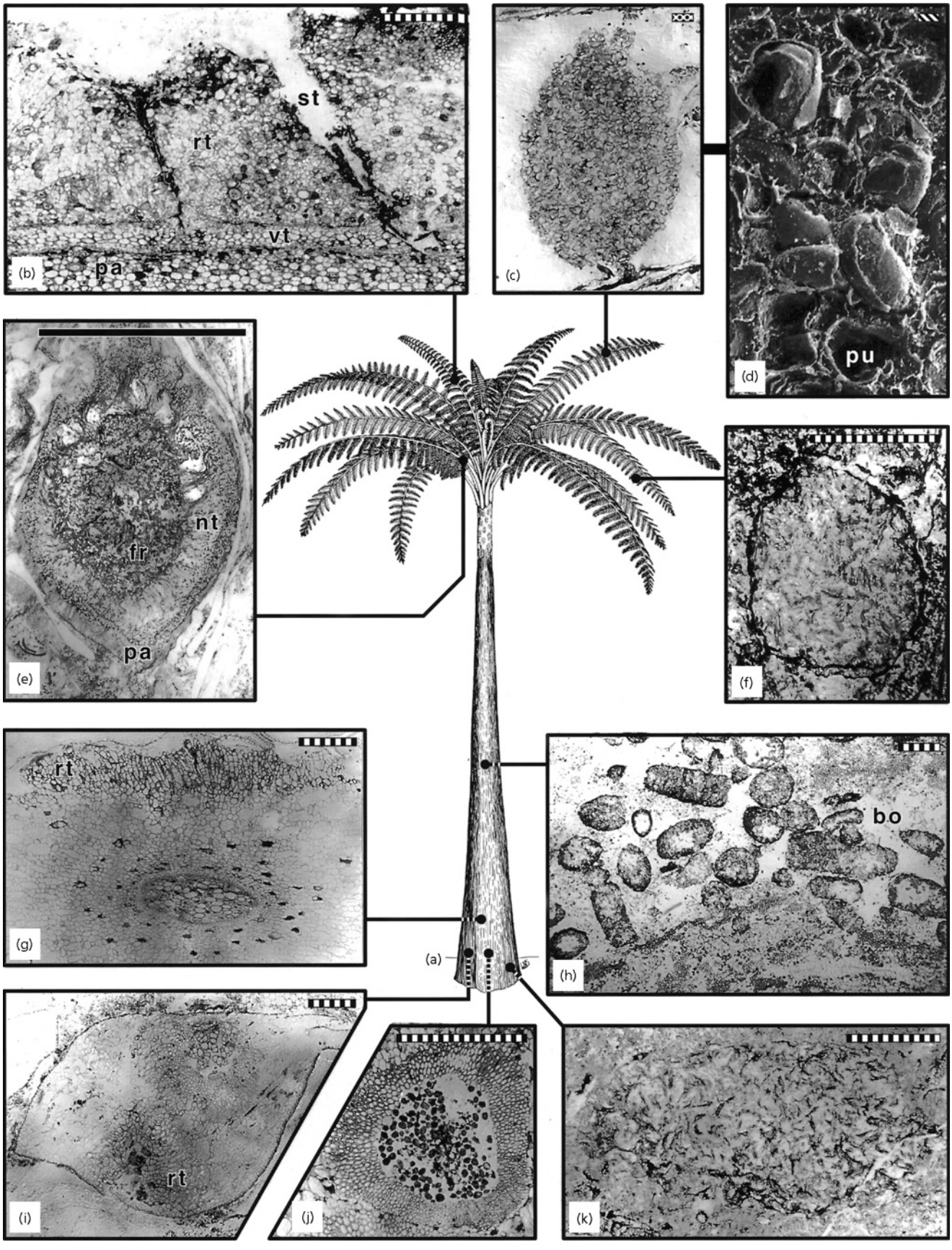
Virtually all understanding of Palaeozoic insects is based on their external morphologies and intragroup and intergroup taxonomic relationships. The ecological associations of Palaeozoic insects with other organisms, and their trophic roles in terrestrial ecosystems, are a more recent focus of research. The best-studied deposit for assessing Palaeozoic insect palaeoecology is the Calhoun Coal of the Mattoon Formation. Within this coal unit there are permineralized nodular structures that preserve swamp plants in exceptional anatomical detail, including cellular detail of tissues and the histological structure of organs, principally from the marattialean tree fern *Psaronius* and the seed fern *Medullosa*. Tissue damage patterns in these two arborescent plants provide a clear picture of how insect herbivores and detritivores trophically partitioned plant organs and reveal the spectrum of insect functional feeding groups that was present during the Late Carboniferous (Labandeira 1998).

At least seven distinctive insect functional feeding groups have been documented for *Psaronius* (Fig. 1.3.9.4a), collectively representing a community of consumers trophically dependent on a plant host, each using a stereotyped mode of feeding to target a particular tissue (Labandeira 1998). Mandibulate insects representing canopy herbivores fed externally on most foliar tissues (Fig. 1.3.9.4f); other mandibulate insects tapped sporangia collectively or spores individually for selective ingestion (Fig. 1.3.9.4c,d); a palaeodictyopteran insect with stylate mouthparts consumed xylem and phloem of petiolar vascular tissue by piercing and sucking (Fig. 1.3.9.4b); and a holometabolous larva encapsulated in petiolar inner parenchyma elicited a reciprocal host-plant response through galling (Fig. 1.3.9.4e). Evidence also indicates that this insect galler induced proliferation of a distinctive response tissue from *Psaronius* (Fig. 1.3.9.4e) and was targeting the basal frond petioles of only this species, indicating an intimate and host-specific association. Within the trunk and root system of *Psaronius*, three types of endophytic borers are known: an unknown herbivorous insect borer of parenchyma within exposed roots (Fig. 1.3.9.4i,k), and two detritivorous borers—a stem borer of soft parenchyma located between more indurated trunk tissues (ecologically analogous to certain modern cockroaches) (Fig. 1.3.9.4h), and a mite on the hard supportive tissue of the root mantle (Fig. 1.3.9.4j). Lastly there was an external grazer on root epidermis (Fig. 1.3.9.4g). With the exception of leaf mining, the earliest occurrence of which is Middle Triassic, the coarse spectrum of herbivore and detritivore functional feeding groups in this Carboniferous community is remarkably complete and modern, although the post-Palaeozoic counterparts of these feeding types were occupied by entirely different taxa.

Post-Palaeozoic developments

During the Permian there was gradual supplementation of typical Late Carboniferous insect taxa by basal

Fig. 1.3.9.4 (*Facing page*) The community of insect herbivores and detritivores on their late Pennsylvanian (300 Ma) host plant, *Psaronius*, a tree fern that dominated peat-substrate swamp forests of the Illinois Basin. Members of the *Psaronius* component community are inferred from patterns of host-plant tissue damage and associated coprolite contents. All interactions are from insects, except (j) which is a mite. Most of these associations indicate feeding on live plant tissue (herbivory) and are confined to the canopy or exposed roots at ground level; however, interactions indicated by (h), (j), and probably (k) are examples of detritivory. (a) Reconstruction of *Psaronius chasei* Morgan, a marattialean tree fern approximately 10 m tall, from the Mattoon Formation (Calhoun Coal) of the Illinois Basin. (b) Stylet tracks in a frond-bearing petiole, showing that vascular tissue (xylem and phloem) was being targeted by a piercing-and-sucking palaeodictyopterid insect. (c) Insect coprolite occurring in peat litter, consisting almost entirely of *Punctatisporites* spores from a *Psaronius* source plant. (d) SEM enlargement of section in (c) showing crushed and relatively intact spores that have passed through an insect's gut. (e) Gall from a frond petiole, showing a tunnelled centre replaced by insect frass, surrounded by a zone of nutritive tissue proliferation and normal outer parenchyma; the galler is a holometabolous insect. (f) Another coprolite from peat litter, containing leaf cuticle and trichomes borne by *Psaronius* foliage. (g) Surface grazing on a ground-level root, characterized by files of abnormally produced cells of reaction tissue. (h) An insect boring of stem tissue within the central trunk, displaying consumption of softer parenchyma but avoidance of more indurated root mantle, sclerenchyma, and vascular strands (outer root mantle is toward the bottom; inner stem tissues are at the top). (i) A boring of a surface root, showing a chamber filled with coprolites, surrounded by tufts of reaction tissue. (j) An example of mite consumption of woody tissue along the outer root mantle, indicated by very small coprolites occurring in the lumen of a mantle root. (k) An elongate coprolite wedged in peat litter, showing a distinctive texture of collapsed root epidermis, indicating consumption of a ground-level root. Abbreviations: bo, stem boring; fr, insect-associated frass; nt, gall-produced nutritive tissue; pa, parenchyma; pu, *Punctatisporites* spores as gut contents; rt, reaction tissue; st, stylet trace piercing outer parenchyma tissue; vt, vascular tissue (xylem). Scale bars: solid = 1.0 cm; striped = 0.1 cm; dotted = 0.01 cm; backslashed = 0.001 m.


st
rt
vt
pa
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lineages of hemipteroid and holometabolous insects. Although Late Permian insect faunas are poorly known, it is clear that the terminal Permian extinction had a profound effect on the course of insect evolution by extirpating most of the major Palaeozoic lineages. Those that survived into the Triassic were preferentially enriched in hemipteroid and holometabolous taxa. The spectrum of insect taxa from Late Triassic faunas is fundamentally modern in composition, containing few Palaeozoic lineages (Labandeira and Sepkoski 1993; Anderson *et al.* 1998). Importantly, this Modern Insect Fauna represents a separate macroevolutionary radiation into the same ecological roles previously occupied by the Palaeozoic Insect Fauna (Labandeira 1997).

During the preangiospermous Mesozoic, freshwater habitats were invaded by several insect clades, particularly Diptera (flies) and Trichoptera (caddisflies). Meanwhile, the diversification of many seed-plant lineages on land, such as conifers, seed ferns, cycads, bennettitaleans, and ephedraleans, resulted in a proliferation of associations with insects, including external feeders such as chrysomelid beetles, endophytic gallers, and leaf miners, in addition to pollination mutualisms such as those between cycads and weevils that persist today. The appearance of angiosperms during the Early Cretaceous offered new and diverse substrates for dietary partitioning (Labandeira 1997; Wilf *et al*. 2000), even though major feeding adaptations had occurred earlier on other seed-plant lineages. Later events of importance for insect evolution included the extensive diversification of placental mammals during the early Cenozoic, which offered new opportunities for colonization by endoparasitic and ectoparasitic insects, and the geographical spread of the grassland biome during the mid-Cenozoic, which induced specialization by numerous herbivorous insect lineages.

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1.3.10 Origin of Mammals

J.A. HOPSON

Introduction

Mammals have been major components of terrestrial and aquatic environments for only the past 65 million years, even though the first mammal, defined as the common ancestor of the living monotremes, marsupials, and placentals, appears to have lived some 150 million years earlier, during the Late Triassic. More distant antecedents of mammals, the non-mammalian synapsids or 'mammal-like reptiles', can be traced back an additional 100 million years, to the Late Carboniferous, when Synapsida and Sauropsida (the clade that includes living reptiles and birds) diverged.

The fossil record of synapsids is remarkable for its completeness in documenting the gradual evolutionary transition from ectothermic basal synapsids, or 'pelycosaurs', to fully endothermic mammals (Kemp 1982; Hopson 1994; Sidor and Hopson 1998). Synapsid diversification (Fig. 1.3.10.1) can be regarded as a series of adaptive radiations, each structurally closer to modern mammals: the Late Carboniferous–Early Permian pelycosaurs; the primarily Late Permian non-cynodont therapsids; the primarily Triassic non-mammalian cynodonts; the Late Triassic–Late Cretaceous basal mammals (non-therian mammaliaforms); and the Late Cretaceous–Recent therians (marsupials and placentals).

Interestingly, each of these radiations includes at least one long-surviving group that coexisted for a time with the succeeding, more mammal-like radiation. These long-lived taxa—caseid pelycosaurs, anomodont therapsids, tritylodontid cynodonts, and multituberculate mammals—were all herbivores whose survival may

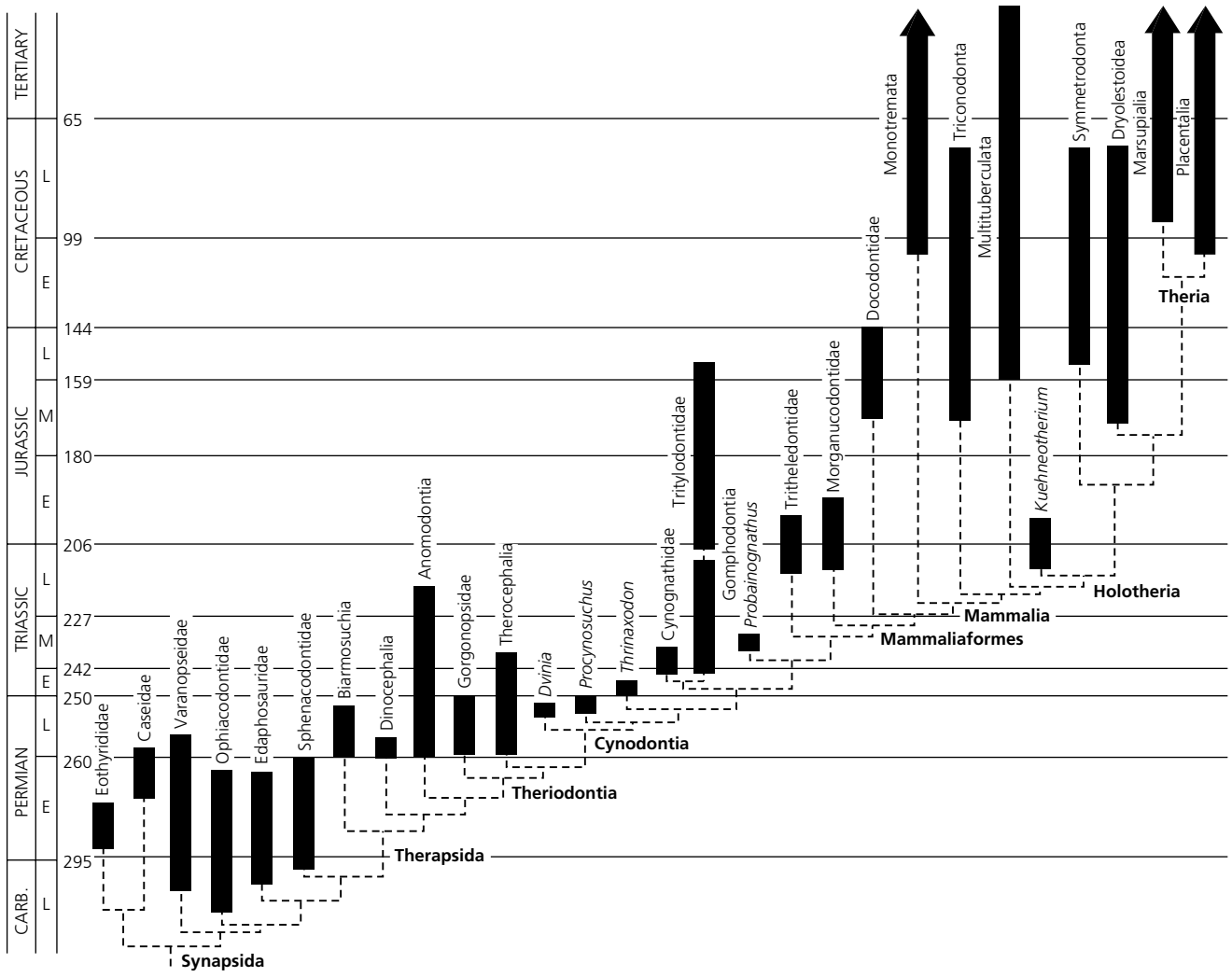


Fig. 1.3.10.1 Phylogenetic diagram of the major clades of Synapsida ('mammal-like reptiles' and mammals) on a geological time scale. Vertical bars indicate known taxon ranges. The ranges of Monotremata, Marsupialia, and Placentalia extend to the present. Divergence times of sister taxa, indicated by dashed lines, are hypothetical. Basal (non-therapsid) synapsids form a paraphyletic group informally called 'pelycosaurs'. Tritylodontidae is a terminal subgroup of Gomphodontia. Triconodonta, Multituberculata, and Holotheria form the Theriimorpha.

be explained by specialized trophic adaptations that allowed them to successfully compete with their more physiologically mammalian contemporaries. This also applies to the highly specialized invertebrate-eating monotremes, the only non-therian mammals to survive beyond the Eocene.

Comparison of basal synapsids with mammals

The magnitude of the differences in anatomy and physiology between a basal synapsid and a primitive living mammal may be inferred from an examination of their skulls (Hopson 1994). The pelycosaur (Fig. 1.3.10.2a) was an ectotherm, as are living reptiles, with a resting metabolic rate too low to generate sufficient heat to warm its body above ambient temperature. Therefore, its food and oxygen requirements were about one-tenth those of a mammal of comparable size. This is reflected in the simple dentition, adapted for capturing and holding prey items but not for breaking them down into small bits. Also, the internal nostrils, or choanae, lie near the front of the mouth, so that air had to traverse the oral cavity to deliver oxygen to the lungs; if food blocked the air passage, the animal was able to suspend breathing for a few minutes without ill effect.

Synapsid skulls are characterized by an opening behind the eye, the temporal fenestra, which in pelycosaurs is relatively small. An undifferentiated mass of jaw-closing muscles was restricted to the small space beneath the cheek, attaching primarily to the underside of the broad skull roof. As in all other non-mammalian tetrapods, the lower jaw of the basal synapsid consists of

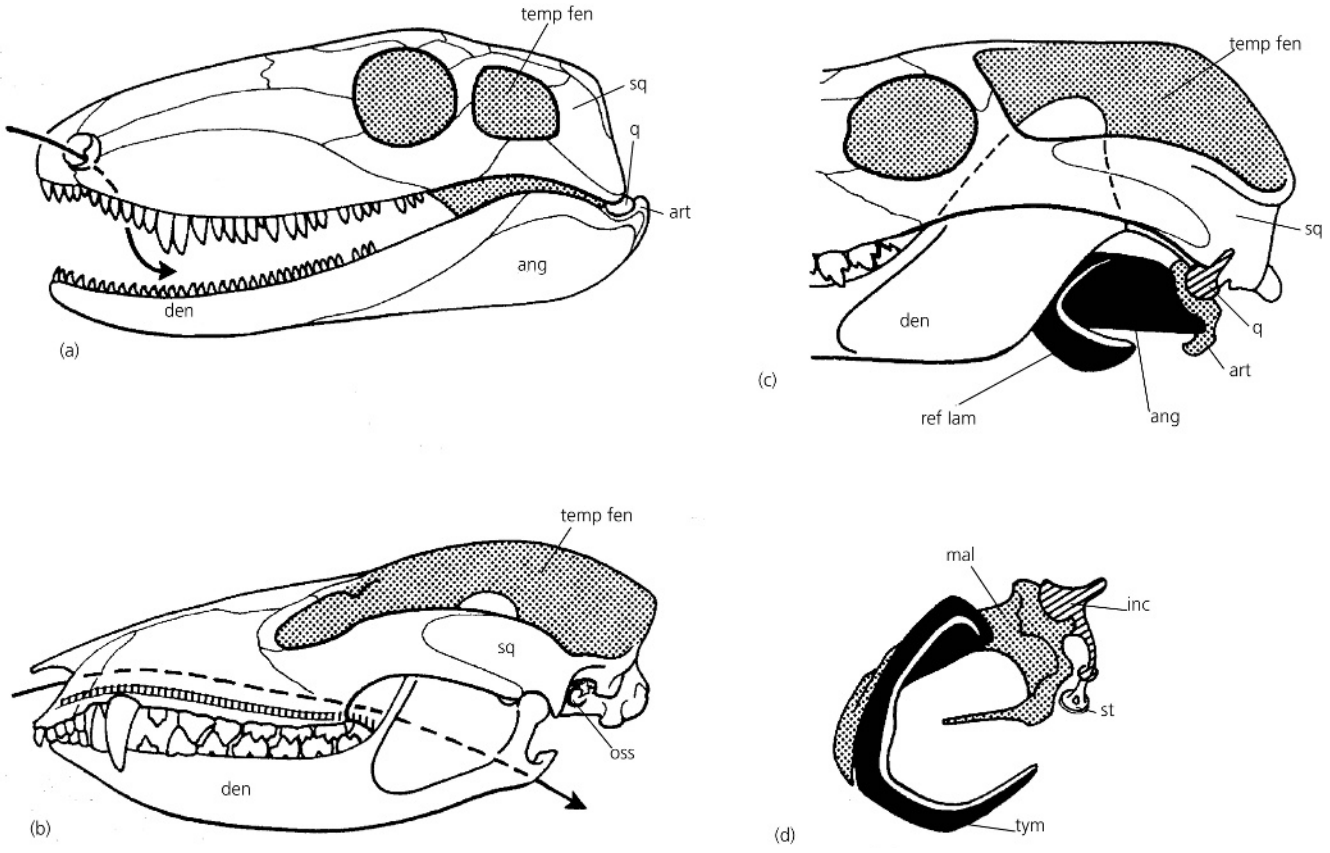


Fig. 1.3.10.2 Skulls of (a) an Early Permian basal synapsid, or 'pelycosaur' (based on the ophiacodontid *Varanosaurus*), and (b) a Recent mammal, the Virginia opossum (*Didelphis virginianus*), to show the craniodental differences between an ectothermic and an endothermic synapsid. Arrows indicate the path of inspired air; vertical hatching in (b) indicates the bony secondary palate. (c) Posterior half of the skull of an Early Triassic cynodont (*Thrinaxodon*). (d) Middle ear ossicles of a mammal (*Didelphis*). Patterning in (c) and (d) indicates homologous elements in the cynodont jaw and the mammalian middle ear. The eardrum of the mammal is held by the C-shaped tympanic bone; possibly the hook-like reflected lamina of the Triassic cynodont also held a tympanum in life. Abbreviations: ang, angular; art, articular; den, dentary; inc, incus; mal, malleus; oss, middle ear ossicles; q, quadrate; ref lam, reflected lamina; sq, squamosal; st, stapes; temp fen, temporal fenestra; tym, tympanic. (From Hopson 1994.)

a large number of bones behind the tooth-bearing dentary, with an articular bone forming a hinge-like jaw joint with the quadrate bone in the skull.

The opossum (Fig. 1.3.10.2b), like all mammals, is an endotherm, with an active metabolism generating sufficient heat to provide a constant high optimal body temperature, irrespective of ambient temperature. The mammalian dentition is differentiated into pointed incisors and canines in front for grasping and killing prey, and premolars and molars behind for breaking it down; this vastly increases the surface area available to digestive enzymes and thus increases the rate at which food energy is assimilated. The choanae no longer open directly into the mouth; rather, the air passage is separated from the oral cavity by a bony plate, the secondary palate. Thus, mammals have evolved special features for the rapid delivery of food energy and the uninterrupted delivery of oxygen to their body tissues, in order to maintain an endothermic metabolism.

The jaw muscles of mammals have increased both in mass and complexity, with one portion, the temporalis, attaching around the margins of a greatly enlarged temporal fenestra (now confluent with the eye socket) and a new external portion, the masseter, attached to the cheek bone (zygomatic arch). The lower jaw is formed entirely by the dentary, which bears a posterodorsal coronoid process for attachment of the temporalis and a posteroventral angular process for attachment of the masseter. These muscles aid in moving the lower jaw from side to side so that the molars can effectively slice and grind the food.

The mammalian jaw joint is a new structure, formed by the dentary with the squamosal bone of the skull. The quadrate and certain postdentary bones of the synapsid

lower jaw have been shifted into the middle ear (Fig. 1.3.10.2c,d) where they serve to transmit sound vibrations from the eardrum to the inner ear (Allin and Hopson 1992).

Comparison of the postcranial skeleton of early synapsids with that of mammals also permits inferences about differing activity levels. Pelycosaurs have relatively short sprawling limbs, with joint surfaces permitting only a restricted range of movements. Lateral bending of the trunk helped to increase stride length, but such side-to-side movement also interfered with ventilation of the lungs (Carrier 1987). Thus, pelycosaurs, like living reptiles, probably suspended breathing while running, relying on anaerobic muscle metabolism to sustain a short burst of speed. In contrast, mammals have a more upright stance and more mobile limb joints, permitting the long limbs to move with greater freedom in a fore–aft plane. The trunk bends in a dorsoventral plane, which both increases stride length and aids in ventilating the lungs. Thus, mammals increase respiratory rate with increasing speed and so are able to sustain high levels of aerobic activity over long periods of time.

Basal synapsids—'pelycosaurs'

The earliest undoubted synapsids are known from Late Carboniferous rocks, about 310 Ma. By the end of the Carboniferous, all major pelycosaur groups must have been in existence, though caseasaurs are first known from the Early Permian (Fig. 1.3.10.1). Pelycosaurs are extremely abundant in the Early Permian of North America and western Europe, diversifying into small to medium-sized hunters of arthropods and other small animals (eothyridids and varanopseids), large predators on vertebrates (ophiacodontids and sphenacodontids), and some of the earliest obligate herbivores among terrestrial vertebrates (edaphosaurids and caseids). Among pelycosaur-grade synapsids, only caseids and varanopseids survived into the early Late Permian to coexist with basal therapsids.

Sphenacodontids, which include the well-known 'sailback' *Dimetrodon*, as well as sail-less taxa, share many features with their more derived sister group, the Therapsida. Notably, they have enlarged canine teeth and a posteriorly notched keel on the angular bone of the lower jaw; this reflected lamina of the angular (Fig. 1.3.10.3a) provides the first hint of the mammalian tympanic bone.

Because of their sprawling posture and use of lateral undulation of the trunk in locomotion, pelycosaurs, like many living reptiles, probably ambushed prey, capturing them after a short dash fuelled by anaerobic muscle activity.

Therapsids

The earliest therapsids, known from the Kazanian of Russia, South Africa, and possibly China, belong to three major groups: Biarmosuchia, Dinocephalia, and Anomodontia. A fourth group, the Theriodontia, appears in slightly younger faunas. Biarmosuchians are very sphenacodontid-like in retaining a small temporal fenestra, though a slip of jaw musculature passed out through the fenestra to attach on its outer margin (Fig. 1.3.10.3b). The upper canine is very long and the reflected lamina of the angular is deeply emarginated. Dinocephalians and anomodonts have larger temporal fenestrae, with a greater mass of musculature attaching to the outer surfaces of surrounding bones.

Therapsids differ from pelycosaurs in having a more upright stance, with the limbs held closer to the body. The limb joints permitted greater freedom of movement and lateral undulation of the trunk was probably reduced. The changes in the locomotor apparatus suggest that therapsids may have actively foraged for food over much greater distances than was possible for pelycosaurs; this change in hunting behaviour would have selected for an increased ability of the respiratory and cardiovascular systems to sustain aerobic activity. Ultimately, selection for increased aerobic capacity led to the elevated metabolic rates associated with mammalian endothermy (Bennett and Ruben 1979).

The main predators of the Late Permian were the theriodonts, characterized by large serrated canines, a low skull with a large temporal opening, and a coronoid process on the dentary. Theriodonts include the primitive gorgonopsians (Fig. 1.3.10.3c), with a broad temporal roof, and the more derived therocephalians and cynodonts, grouped as eutheriodonts, in which the temporal fenestra is expanded medially to leave only a narrow roof, with a sagittal crest for muscle attachment. Therocephalians were a diverse group, including large predators and small, lightly built, insectivores; among the latter, Early Triassic bauriids paralleled cynodonts in developing expanded, occluding teeth and a secondary palate.

The earliest cynodonts, of very late Permian age, are *Dvinia* from Russia and *Procynosuchus* (Fig. 1.3.10.3d) from Germany and Africa, the latter corresponding closely to the common ancestor of all later cynodonts, including mammals. Their postcanine teeth have accessory cusps that give them a molar-like appearance. The zygomatic arches are flared out from the lower jaw, creating a gap through which a slip of undifferentiated jaw muscle, an incipient masseter, shifted to the outer surface of the coronoid process. In the palate, a pair of bony plates extends medially to form a partial secondary palate separating the air passage from the mouth. These specializations indicate that cynodonts were breaking

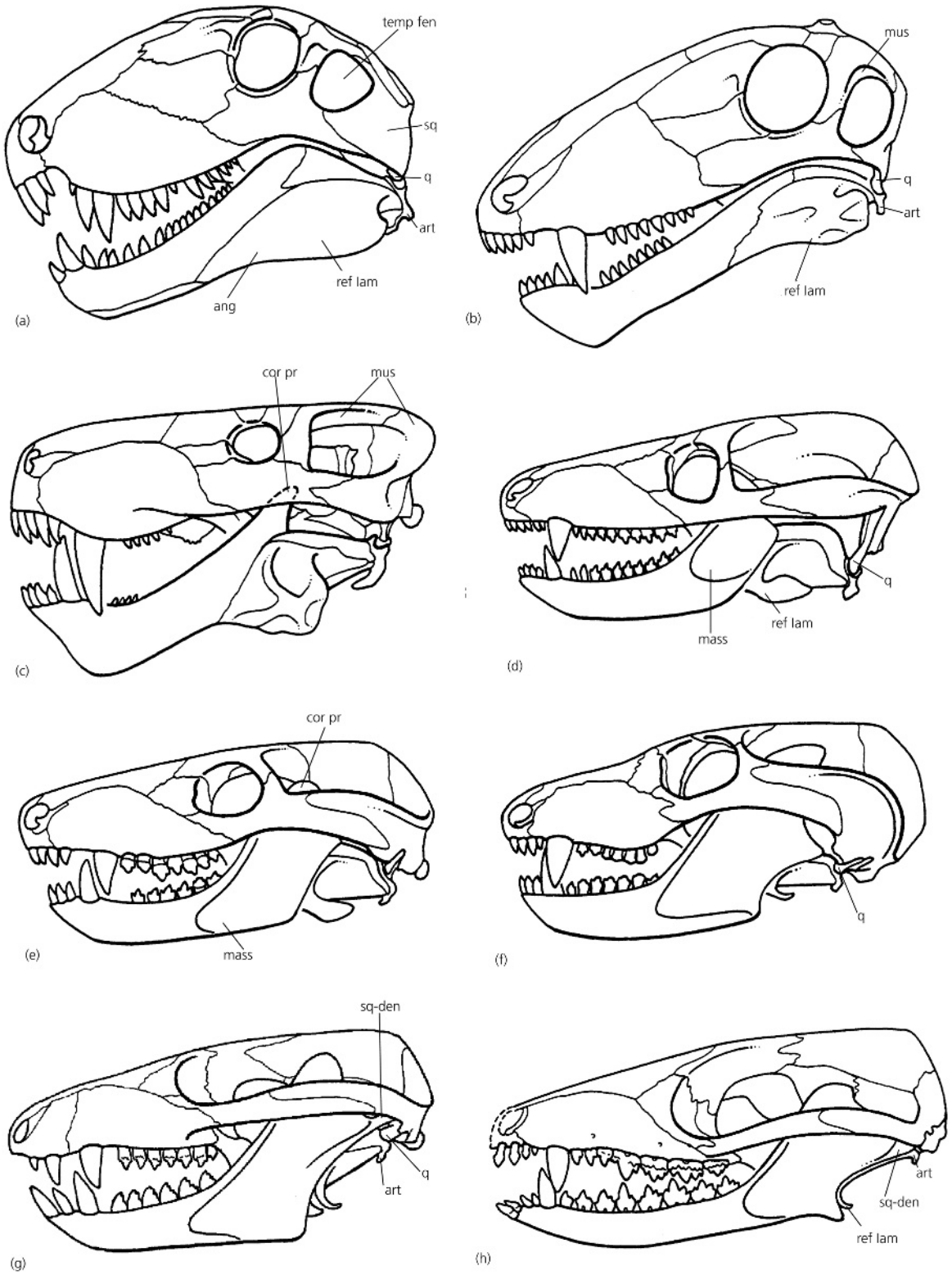


Fig. 1.3.10.3 Skulls of synapsids. (a) Sphenacodontid 'pelycosaur' *Dimetrodon*. (b) Basal therapsid *Biarmosuchus*. (c) Gorgonopsian *Leontocephalus*. (d) Late Permian cynodont *Procynosuchus*. (e) Early Triassic cynodont *Thrinaxodon*. (f) Middle Triassic cynodont *Probainognathus*. (g) Tritheledontid cynodont *Pachygenelus*. (h) Early mammaliaform *Morganucodon*. Abbreviations: cor pr, coronoid process; mass, area of attachment of masseter muscle; mus, muscle attachment site; sq-den, squamosal–dentary jaw contact. Other abbreviations as in Fig. 1.3.10.2. (From Hopson 1994.)

down food orally without interrupting the flow of oxygen to the lungs, features suggesting a more endothermic physiology than occurred in earlier therapsids.

Triassic cynodonts bridge the gap to mammals. The Early Triassic *Thrinaxodon* (Figs 1.3.10.2c, 1.3.10.3e) further enlarged the dentary and reduced the postdentary elements, including the reflected lamina. A fully developed masseter extended to the lower border of the jaw and a differentiated temporalis attached to a robust coronoid process. The cheek teeth are more complex, resembling those of early mammals, and the palatal plates join on the midline to form a complete secondary palate. In the Middle Triassic, more derived cynodonts, such as *Probainognathus* (Fig. 1.3.10.3f), have postdentary bones reduced to a slender rod and a large dentary closely approaching, though not contacting, the skull. This contact is seen in tritheledontid cynodonts, such as *Pachygenelus* (Fig. 1.3.10.3g), and near-mammals, such as *Morganucodon* (Fig. 1.3.10.3h), from the Late Triassic/Early Jurassic. In the latter, the rear of the dentary forms a knob, or condyle, which fits into a hollow, or glenoid, on the squamosal.

The postdentary bones of Triassic cynodonts show progressive reduction to a slender rod, with the reflected lamina becoming a delicate hook. The articular and quadrate are also reduced in size and the whole apparatus takes on the appearance of mammalian middle ear bones, though how it functioned is uncertain. Possibly the reflected lamina supported an eardrum, the vibrations of which caused the postdentary rod to move, thus conducting sound vibrations from the articular to the quadrate and thence, via the stapes (the reptilian ear bone), to the inner ear (Allin and Hopson 1992). Once the dentary contacted the skull and the new mammalian jaw joint took over, the postdentary sound-conducting apparatus was free to relinquish its dentary attachment and become firmly joined to the ear region of the skull. Fossil evidence indicates that separation of the ear ossicles from the dentary occurred independently in several groups of early mammals.

Mammaliaforms and mammals

The earliest true mammals are known from the Late Triassic (Norian), about 210 Ma. Appearing somewhat earlier are what might be called near-mammals, creatures which in life probably looked like mammals but which lie phylogenetically outside the Mammalia as currently defined (the common ancestor of monotremes, marsupials, and placentals and its descendants; McKenna and Bell 1997). The near-mammals are placed in a more inclusive taxon Mammaliaformes, which includes Mammalia plus the Late Triassic/Early Jurassic *Morganucodon* and related forms, as well as the Middle–Late Jurassic docodonts. Mammaliaforms are characterized by having molars with two roots and precise occlusion between matching shear surfaces on upper and lower teeth. Their molars are no longer replaced and the more anterior teeth have a single milk series that is replaced by a set of permanent teeth; limited replacement appears to be correlated with precise occlusion and contrasts with the unlimited replacement in the non-occluding teeth of earlier synapsids. Although basal mammaliaforms possess a dentary–squamosal jaw joint, they retain a functional articular–quadrate joint beside it.

Also known from the Late Triassic is *Kuehneotherium*, the earliest member of the Holotheria, the group including the living marsupials and placentals. Holotheres are characterized by molars in which the three main cusps, rather than lying in a fore–aft line (as in *Thrinaxodon* or *Morganucodon*), form a broad V, the apex of which points inward in the uppers and outward in the lowers; thus, the tooth rows form a zigzagging cutting surface. On this 'reversed triangles' molar pattern was based the enormous functional diversity seen in the molars of therian mammals.

Though not known with certainty prior to the Middle Jurassic, the other major mammalian clades—monotremes, triconodonts, and multituberculates—must have diverged from their common ancestor with the holotheres some time in the Late Triassic. The phylogenetic relationships of the egg-laying monotremes (the living platypus and echidnas of the Australian region) have long been a mystery because of their extremely specialized skulls, cynodont-like postcranial skeletons, and lack of adult teeth. Fossil monotreme teeth from the Early Cretaceous of Australia have suggested a special relationship with Late Jurassic holotheres (Kielan-Jaworowska *et al.* 1987). However, recent discoveries of complete triconodont, multituberculate, and basal holothere (symmetrodont) specimens demonstrate that these taxa all possess postcranial skeletons strikingly similar to those of living therians and much more derived than the Triassic-grade skeletons of living monotremes (Hu *et al.* 1997). Thus, triconodonts (Middle Jurassic–Late Cretaceous carnivores with blade-like molars) and multituberculates (Late Jurassic–Late Eocene rodent-like herbivores) form a clade with holotheres, the Theriimorpha, from which monotremes are excluded.

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1.4 Mesozoic Events

1.4.1 Mesozoic Marine Revolution

P.H. KELLEY and T.A. HANSEN

Introduction

Two hundred years ago, the debate between catastrophists and uniformitarians dominated the nascent fields of geology and palaeontology. Although modern palaeontologists are at least nominally uniformitarians, many would reject Lyell's view of slow and steady change for a more catastrophic view of the history of life as a series of revolutions.

A marked restructuring of shallow marine benthic communities occurred during the middle and late Mesozoic, which has been called the Mesozoic marine revolution (Vermeij 1977). The changes included the intensification of grazing and the diversification of durophagous (shell-destroying) predators such as teleost fish, decapod crustaceans, and carnivorous gastropods. As a result of the intensified predation and grazing, bioturbation and the frequency of infaunal life modes increased, stalked crinoids and brachiopods disappeared from shallow-water habitats, and increases occurred in prey shell sturdiness and the frequency of shell repair (Vermeij 1977).

Mesozoic increases in predation and grazing

Most molluscivores appeared or developed durophagous habits (such as crushing, hammering, or peeling the growing edge of a shell) in the Mesozoic, particularly the Jurassic and Cretaceous (Vermeij 1977, 1987). Cephalopods developed crushing abilities in the Middle Triassic; other Triassic crushers were marine reptiles, such as placodonts and the ichthyosaur family Omphalosauridae, and possibly pycnodontiform and semionotiform fishes. The Jurassic marked the origin of such shell breakers as the Heterodontidae (sharks), Batoidea (rays), Stomatopoda (crustaceans), Palinuridae (spiny lobsters), Nephropidae (lobsters), Brachyura (crabs), and Aves (birds); most of these groups developed durophagy by the Cretaceous. Drilling gastropods (Naticidae and Muricidae) also diversified in the Cretaceous, as did other predatory gastropods (e.g. Buccinidae, Fasciolariidae, Melongenidae, Volutidae, Olividae). Other important Cretaceous durophagous predators were the mosasaurid lizards and ptychodontoid sharks. The radiation of durophagous predators has continued through the Cenozoic (Fig. 1.4.1.1). Grazing also accelerated during the later Mesozoic with the expansion of teleost fishes and sea urchins (Echinoidea; Vermeij 1977). Both groups scrape algae and epifaunal animals from hard substrates and are important determinants of community structure today, especially in reef environments.

Community response to the Mesozoic marine revolution

Various changes in benthic communities have been attributed to the increase in predation and grazing during the Mesozoic marine revolution. Communities of the Palaeozoic and early Mesozoic were dominated by

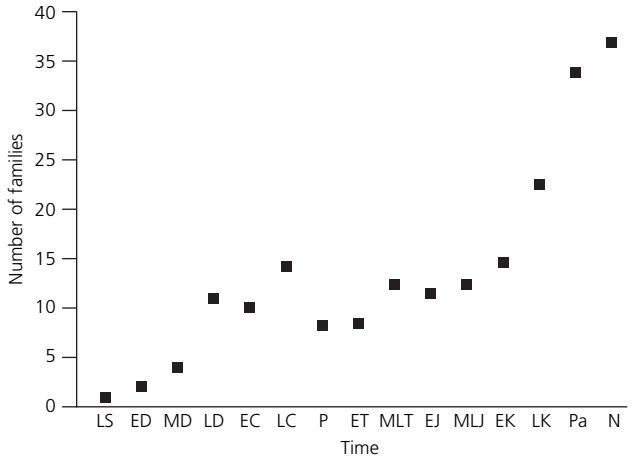


Fig. 1.4.1.1 Number of families of marine durophagous predators, including eurypterid and crustacean arthropods, cephalopod molluscs, and vertebrates. Abbreviations from left to right: LS, Late Silurian; ED, Early Devonian; MD, Middle Devonian; LD, Late Devonian; EC, Early Carboniferous; LC, Late Carboniferous; P, Permian; ET, Early Triassic; MLT, Middle–Late Triassic; EJ, Early Jurassic; MLJ, Middle–Late Jurassic; EK, Early Cretaceous; LK, Late Cretaceous; Pa, Palaeogene; N, Neogene. (After Vermeij 1987.)

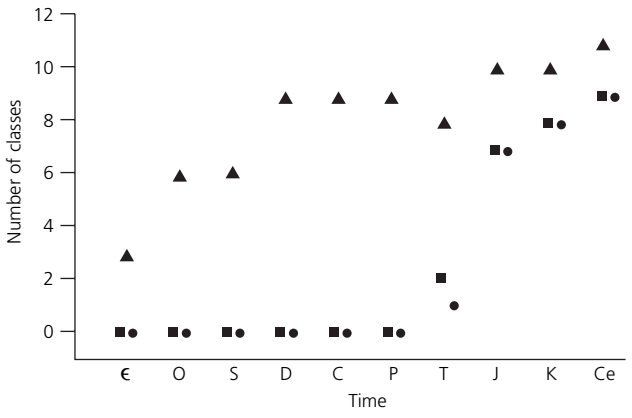


Fig. 1.4.1.2 Temporal changes in number of classes of bioturbating animals. Triangles, number of classes with bioturbating members; circles, number of classes with intensively bioturbating members (those that rework sediment at a rate of 10 cm^3/day); squares, number of classes with deeply bioturbating members (10 cm or more depth of bioturbation). (Modified from Vermeij 1987; data from Thayer 1983.)

epifaunal suspension-feeders, such as stalked crinoids, brachiopods, and epifaunal molluscs. In contrast, shallow-water soft-bottom communities of the later Mesozoic and Cenozoic were greatly impoverished in solitary epifaunal and semi-infaunal taxa. Both a retreat of epifaunal taxa to cryptic or deeper-water environments and infaunalization appear to have occurred.

Increased epifaunal predation and grazing apparently led to the displacement of stalked echinoderms and brachiopods to cryptic or deeper-water refugia and their replacement in shallow water by unstalked comatulid crinoids and byssally attached or cemented epifaunal bivalves (Vermeij 1977). The frequency of arm regeneration, and therefore predation, in modern Caribbean stalked crinoids is greater in shallower water, suggesting that increased predation pressure of the Mesozoic marine revolution caused the disappearance of stalked crinoids from shallow water and the consequent radiation of mobile comatulids. In addition, a statistically significant decrease of shallow-water dense ophiuroid populations ('brittlestar beds') occurred in the Early Cretaceous (Aronson 1989). The decline of these epifaunal suspension-feeding echinoderms is consistent with an intensification of predation and bioturbation during the Mesozoic marine revolution. The shift of such epifaunal taxa to deeper-water refugia reflects a general trend of onshore origination, followed by expansion (or retreat) to offshore habitats, which has been documented for several groups (Jablonski and Bottjer 1990).

A post-Palaeozoic increase in frequency of infaunal life modes among echinoids, gastropods, and especially bivalve molluscs has been noted (Stanley 1977). Although mantle fusion and the development of siphons permitted deeper and more rapid burrowing in the Bivalvia, widespread Mesozoic infaunalization has been attributed to increasing predation pressure (Stanley 1977). The role of predation is supported by the observation that extant epifaunal bivalves generally have traits that protect them against predation, such as thick shells, large size, commissural spines, ability to swim, or confinement to habitats in which predation is reduced. The replacement of epifaunal and semi-infaunal forms by infaunal taxa has been particularly marked since the Late Cretaceous (Vermeij 1977, 1987) or perhaps earlier. A significant increase in the percentage of shallow-burrowing to moderately deep-burrowing organisms, especially in shallow-shelf environments, began in the Middle Jurassic.

The trend of increasing infaunalization is consistent with a dramatic rise in bioturbation beginning in the Jurassic (Thayer 1983; Vermeij 1987) (Fig. 1.4.1.2), with drastic consequences for epifaunal attached and unattached organisms. Bioturbation may cause the burial of organisms that lie on the sediment surface; resuspended fine sediment may clog the filters of suspension-feeders. Increased bioturbation would thus have reinforced the role of predation and grazing in the Mesozoic elimination of epifaunal and semi-infaunal suspension-feeders from shallow-water habitats. Diversification of phytoplankton (coccolithophorids, dinoflagellates, and diatoms) in the late Mesozoic may also have been facilitated by the recycling of benthic nutrients, as bioturbators resuspended organic particles in the water column (Thayer 1983).

Changes in shell architecture also occurred during the Mesozoic marine revolution (Vermeij 1977, 1987). The incidence of mechanically sturdier, more highly armoured shells increased in the late Mesozoic, probably due to increased predation pressure. Among gastropods, shells with an umbilicus and planispiral or open coiling, which have little resistance to crushing predation, waned in importance after the early Mesozoic. For example, umbilicate species represented >25% of Palaeozoic and Triassic assemblages; after the Early Jurassic, such species never constituted more than 20% of warm-water faunas. Palaeozoic snails generally lacked nodes, spines, or ribs, whereas later Mesozoic taxa were characterized by sturdier, more highly sculptured shells resistant to breaking predation. In particular, the percentage of gastropod subfamilies with thickened or narrowed apertures increased steadily from zero in the Early Triassic to approximately 15% in the Late Cretaceous (and 20–30% in the Cenozoic). The ability to remodel the interior of the shell has allowed highly ornamented mesogastropods and neogastropods with apertures restricted by dentition to flourish since the Cretaceous. Elaboration of armour also occurred among cephalopods, bivalves, arthropods, and echinoderms, such as an increase in overlapping and crenulated shell margins among bivalves. However, locomotion may be more important than armour as an antipredatory defence for at least some members of these groups (Vermeij 1987).

A statistically significant increase in the frequency of repair scars, presumably caused by unsuccessful predation, is evident in the shells of Mesozoic gastropods from shallow-water soft-bottom assemblages (Vermeij 1987). In a Late Triassic assemblage, 18% of the abundant species had a frequency of shell repair >0.25; the corresponding value for the Late Cretaceous was 63%. Although an increase in sublethal attacks may have various causes (for instance, better-defended or older prey that accumulated a large number of scars), these data are also consistent with an increase in the abundance of shell-breaking predators during the middle Mesozoic.

Evolutionary dynamics, escalation, and the Mesozoic marine revolution

Although the rise in predation and the synchronous community restructuring and architectural changes of the Mesozoic marine revolution are generally accepted, the evolutionary dynamics of these changes are inadequately understood and their causes are debated. The Mesozoic decline of semi-infaunal, endobyssate taxa and their replacement by burrowing or epifaunal forms with antipredatory traits have been attributed to the differential extinction of species vulnerable to predation (Stanley 1977). This phenomenon has been referred to as 'species selection' or 'species sorting'. The Mesozoic marine revolution could represent the intensification of species selection or sorting by physical or geographical conditions of the Mesozoic that permitted synchronous changes in various groups (Vermeij 1977). For instance, biogeographical differentiation coupled with mild climate may have fostered the expansion of predators and well-armoured prey.

The Mesozoic marine revolution is one of several intervals during which both predation and the frequency of predation-resistant morphologies increased significantly. A similar radiation of durophagous predators and armoured prey occurred in the Middle to Late Devonian, termed the 'mid-Palaeozoic precursor to the Mesozoic marine revolution' (Signor and Brett 1984). Such results support a key role for biotic interactions, particularly predation, in evolution and form the basis for Vermeij's (1987) hypothesis of escalation. This hypothesis claims that, during the Phanerozoic, biological hazards (such as predation and competition) have increased and adaptations to these hazards have become better expressed. As a result, long-term trends have occurred in the morphology, behaviour, and distribution of organisms, such as those cited for the Mesozoic marine revolution. According to the hypothesis of escalation, these long-term trends have been driven by interactions with enemies (predators, competitors, and dangerous prey), which Vermeij views as the most important agents of natural selection. Escalation may involve coevolution, in which interacting species evolve reciprocally, if the species involved are mutual enemies (e.g. predators and dangerous prey). However, Vermeij argued that predators are more likely to respond evolutionarily to their own enemies (predators or competitors) than to antipredatory adaptation of benign prey. The extent to which such adaptation occurs within species or during speciation is unclear. Although intraspecific antipredatory adaptation has been reported in the bivalve prey of Miocene naticid gastropods (primarily increased shell thickness), Vermeij (1987) envisioned adaptation to enemies as occurring primarily during speciation and stated that differential diversification would lead to increased representation of species with antipredatory adaptations within a clade.

This view is consistent with the clade-level dynamics of aporrhaid gastropods, important prey taxa that diversified during the Mesozoic in two episodes, the Middle Jurassic and Late Cretaceous (Roy 1994). The initial radiation established two morphological groups, one with multidigitate, generally thin apertures, and the other with apparently sturdier, simpler apertures. The second radiation preferentially added species to the sturdier group with the apparently more predation-resistant architecture. Selection due to predation may have

created an origination bias in favour of the sturdier morphology; the sturdier taxa were also more widespread and thus more prone to speciation (Roy 1994).

Although interactions with enemies drive escalation, abiotic circumstances may produce episodes of escalation, such as the Mesozoic marine revolution. Vermeij argued that escalation of predator–prey or competitive relationships occurred episodically through the Phanerozoic and was fostered by intervals of climatic warming, transgression, and high productivity. Under such conditions, ecological limitations are relaxed and adaptive innovations can take hold. Episodes of massive submarine volcanism (such as during the later Mesozoic) raised water temperatures, caused transgression, and injected nutrients into the water column (Vermeij 1995). Productivity was enhanced by the warmer temperatures and higher nutrient levels. The warm temperatures and abundant and predictable resource supply allowed individual organisms to acquire more resources and permitted life modes requiring more energy (for instance, heavily calcified or mobile organisms with high metabolic rates). Such conditions also facilitated founder speciation (development of a new species by divergence of a small initial 'founder' population) by allowing the expansion of daughter populations. This scenario could account for the Mesozoic marine revolution, the early Palaeozoic development of predators, burrowers, and mineralized taxa, and possibly lesser episodes of diversification during the Phanerozoic (Vermeij 1995).

By the same argument, mass extinctions caused by cooling, drops in productivity, and/or regression should interrupt escalation (Vermeij 1987, 1995). Highly escalated species (those with antipredatory traits) should be particularly prone to extinction because of their higher metabolic requirements, whereas organisms with lower energy requirements are more likely to survive declines in productivity. According to the hypothesis of escalation, although mass extinctions apparently interrupted escalation, they did not undo the general trend of adaptation to enemies that pervaded the Phanerozoic (Vermeij 1995).

The occurrence of revolutions in the history of life, such as the Mesozoic marine revolution, is well documented. However, the broader but related concept of escalation remains controversial. Debate continues regarding the relative importance of biotic and abiotic factors in evolution, the reality of directional evolutionary trends, and the processes underlying the macroevolutionary patterns.

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1.4.2 Origin and Radiation of Angiosperms

E.M. FRIIS, K.R. PEDERSEN and P.R. CRANE

Introduction

Angiosperms (flowering plants) were the last major group of plants to appear in the fossil record; their first scattered occurrences are reported from the earliest Cretaceous. Angiosperms diversified and increased dramatically in abundance through the Cretaceous, and by the mid-Cretaceous they had attained ecological prominence in most parts of the world. The radiation of angiosperms in the Cretaceous led to profound changes in the composition of terrestrial plant communities, which included extinctions or marked declines in the diversity or abundance of many other groups of seed plants that had previously been important in Mesozoic vegetation, including Bennettitales, Cycadales, Ginkgoales, and, to a lesser extent, Gnetales. Conifers were also impacted by changes in Cretaceous ecosystems but several groups, for example Pinaceae, continued to diversify in parallel with the angiosperm radiation. In their rise to ecological dominance angiosperms exhibited extraordinary developmental and evolutionary plasticity, resulting in vegetative and reproductive

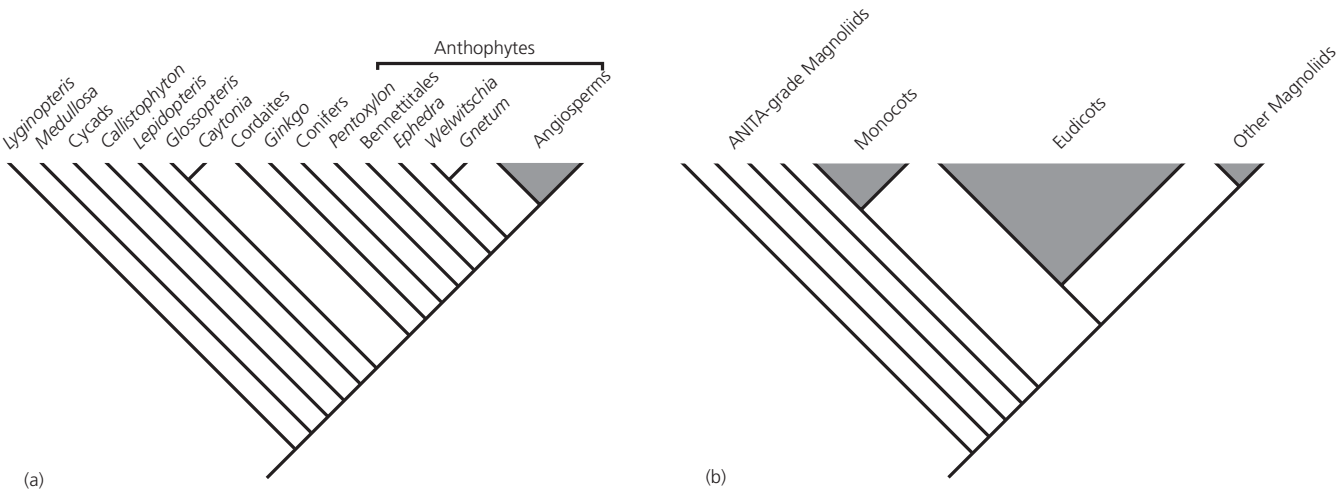


Fig. 1.4.2.1 Hypotheses of relationships among seed plants and angiosperms. (a) Cladogram showing one hypothesis of seed plant relationships where angiosperms are grouped with Gnetales, Bennettitales, and *Pentoxylon* in the anthophyte clade. (b) Cladogram showing relationships of angiosperms with monocotyledons and eudicotyledons nested in a paraphyletic magnoliid grade.

organs that are more diverse in structure than those of any other group of land plants.

Angiosperm origin

According to most traditional interpretations, as well as explicit phylogenetic analyses, angiosperms are a well-defined monophyletic group. Most morphology-based cladistic analyses including both extant and extinct taxa identify a monophyletic clade, often referred to as the anthophytes, comprising the angiosperms, Gnetales, Bennettitales, and *Pentoxylon* (Fig. 1.4.2.1a). Several molecular phylogenetic studies also place Gnetales as the closest living relatives to the angiosperms. The anthophyte concept has, however, been questioned by other analyses of which some resolve the conifers as most closely related to the Gnetales, and angiosperms as sister-group to all seed plants. Such discrepancies are most likely related to the relictual nature of living seed plants and the inherent difficulties of using molecular sequence data to resolve relationships among lineages that diverged long ago and have evolved independently since. Attempts to establish relationships among seed plants based on morphological data also confront substantial difficulties, particularly in establishing homologies among their vegetative and reproductive structures because of the incomplete knowledge currently available of the structural diversity in extinct taxa.

Although many theoretical models have been offered in attempting to reconcile the reproductive structures of angiosperms with those of other seed plants, many fundamental issues are still poorly understood, especially the derivation of the angiosperm carpel and the outer integument of the angiosperm ovule. Such uncertainties, combined with the substantial morphological gaps that separate angiosperms from other seed plants, greatly increase the difficulties of rooting the angiosperm tree, and establishing relationships among basal angiosperms. However, in general terms there is clear evidence that the subclass Magnoliidae comprises a paraphyletic basal grade of dicotyledons in which two major monophyletic groups, the monocotyledons and the eudicotyledons, are embedded (Fig. 1.4.2.1b). At the magnoliid grade there is also evidence that the extant taxa most likely to diverge at the very base of the angiosperm tree include Amborellaceae, Nymphaeaceae *sensu lato* (water lilies), Illiciales, Trimeniaceae, and Austrobaileyaceae (the so-called ANITA-grade; Fig. 1.4.2.1b).

Angiosperm characteristics

Angiosperms exhibit exceptional morphological diversity, particularly among their flowers, and this diversity is also manifested among plants at the magnoliid grade. Both large bisexual floral structures, consisting of numerous tepals, stamens, and carpels in a spiral arrangement (e.g. Magnoliaceae), and minute unisexual flowers consisting of just a single stamen or a single carpel (e.g. Chloranthaceae), occur among basal magnoliid angiosperms (Fig. 1.4.2.2). Unique defining characters that unite the angiosperms relate mainly to the reproductive system and include, most importantly, the presence of carpels enclosing the ovules, and stigmatic pollen germination that is often followed by growth of a pollen tube through the carpellary tissue. Most flowers

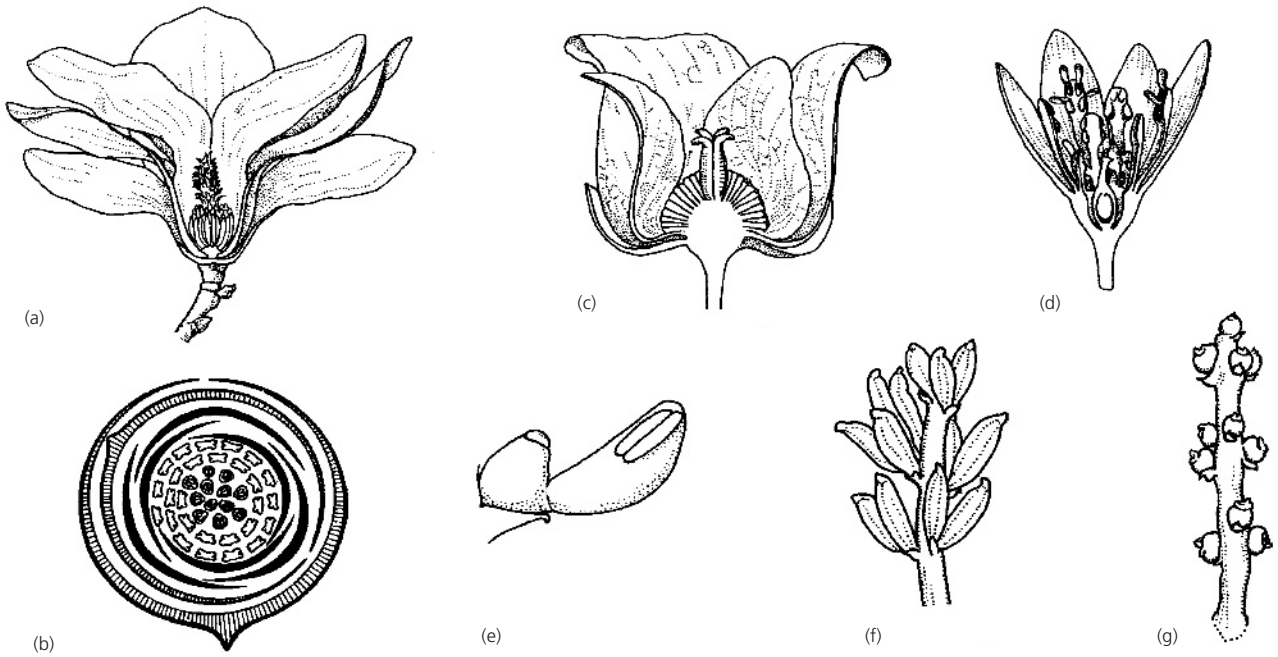


Fig. 1.4.2.2 Structural features of angiosperms (floral diversity in extant magnoliids). (a) Magnoliaceae. (b) Floral diagram of *Magnolia* flower. (c) Annonaceae. (d) Lauraceae. (e–g) Chloranthaceae; (e) bisexual flowers of *Sarcandra*; (f,g) unisexual flowers of *Ascarina*. (a,c–g, From Friis and Endress 1990; b, from Crane *et al*. 1995 with permission.)

are bisexual, with both carpels and stamens in the same flower, but unisexual flowers in which the stamens and carpels occur in separate flowers are also common in many widely scattered groups.

Angiosperm pollen grains also show much greater diversity in aperture configuration and wall structure than is seen in the pollen grains of other groups of seed plants. Angiosperm pollen grains are apparently distinguished from those of other seed plants by having a thin non-laminate inner layer of the pollen wall (endexine, Fig. 1.4.2.3f), while in other seed plants this layer is thick and laminate. Magnoliid angiosperms and monocotyledons typically have monoaperturate pollen grains with a single aperture (monocolpate, monoporate; Fig. 1.4.2.3d), a feature that they share with many non-angiospermous seed plants. In contrast, the pollen of eudicotyledons is distinguished from that of all other seed plants in having three or more apertures that are typically distributed in a radially symmetrical pattern around the equator (e.g. tricolpate, tricolporate, triporate; Fig. 1.4.2.3e,f). Among living seed plants, pollen with a reticulate–columellate pollen wall is restricted to the angiosperms. However, the interpretation of this feature as a defining characteristic of the group is complicated by the fact that it is not universally present in magnoliid angiosperms, and records of dispersed pollen from the Triassic (the Crinopolles-complex) indicate that reticulate and columellate pollen was perhaps also produced by non-angiospermous seed plants.

Angiosperm leaves typically have a broad leaf blade and a characteristic reticulate venation pattern formed by a hierarchical system of successively thinner veins and free ending veinlets (Fig. 1.4.2.3a). Reticulate venation also occurs in several other plant groups, but in these plants (except extant *Gnetum*) such venation is typically simpler and without free ending veinlets. Another vegetative feature characteristic of most angiosperms is the presence of vessels with scalariform or scalariform-derived pitting (Fig. 1.4.2.3b,c). The wood of most other seed plants lack vessels, as does that of a few living angiosperm taxa, but it is currently uncertain whether this reflects an ancestral or derived state in the context of angiosperms as a whole.

Timing of angiosperm origin and their first major radiation

The earliest angiosperm remains that can be recognized with certainty in the fossil record are dispersed, monoaperturate pollen grains with a reticulate–columellate outer pollen wall very similar to the pollen

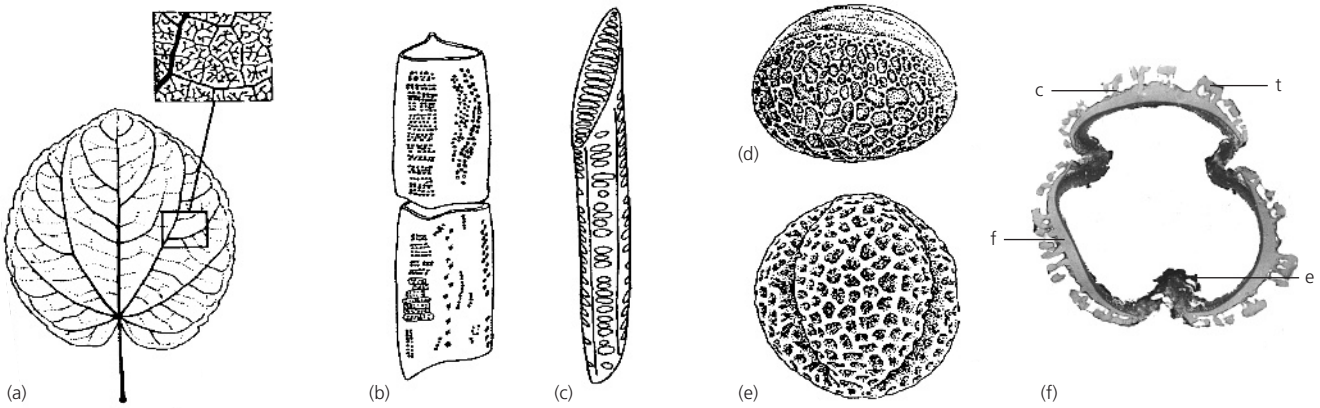


Fig. 1.4.2.3 Structural features of angiosperms (leaves, wood, pollen). (a) Leaf of *Cercidiphyllum* with hierarchical reticulate venation. (b,c) Vessel elements of angiosperm wood. (d,e) Angiosperm pollen with reticulate–columellate pollen wall; (d) monoaperturate grain of monocotyledon; (e) tricolpate grain of eudicotyledon. (f) Cross-section of tricolpate pollen grain showing pollen wall with tectum (t), columellae (c), foot layer (f), and granular endexine (e). (Line drawings by P. von Knorring.)

of living magnoliids and perhaps also certain monocotyledons. These pollen grains occur scattered in microfloras of Early Cretaceous age (Valanginian–Hauterivian). Angiosperm pollen is rare in these earliest microfloras, but has been reported over a wide geographical area extending from southern England to Italy, Morocco, and Israel, and perhaps to sites in Asia (Hughes 1994). By this time angiosperm pollen already shows considerable diversity in the form of the reticulum and tectum ornamentation (Hughes 1994). Currently there is no reliable evidence of angiosperms prior to the Cretaceous, and a reproductive structure with angiospermous features from northern China thought initially to extend the fossil record of angiosperms back to around the Jurassic–Cretaceous boundary now appears to be substantially younger (Barremian–Aptian).

The various phylogenetic models that have been put forward for angiosperm relationships all support the view that the lineage leading to angiosperms diverged prior to the Cretaceous. However, the firstmajor diversification and radiation of angiosperms clearly took place in the Early and mid Cretaceous. During this time interval the fossil record shows a marked increase in the diversity, structural complexity, and abundance of angiosperm pollen, leaves, and reproductive structures (Hickey and Doyle 1977; Crane *et al*. 1995; Friis *et al*. 1999).

Patterns of structural diversification — pollen and leaves

The earliest angiosperm pollen grains from Valanginian–Hauterivian microfloras all have a single aperture. The pollen wall typically has an outer reticulate layer supported by a layer of columellae (e.g. Hughes 1994). Among living plants this kind of pollen is known only from basal angiosperms at the magnoliid grade and monocotyledons. By the Barremian, monoaperturate pollen had diversified further, and the first appearance of pollen grains with three apertures (tricolpate) documents the establishment of eudicotyledonous angiosperms in Cretaceous vegetation (e.g. Hughes 1994). During the Aptian and Albian pollen of eudicotyledons diversified considerably, and by the end of the Cenomanian a variety of aperture types, including forms with three elongated apertures (tricolpate), three elongated apertures each with a central pore (tricolporate), and three pores (triporate) were widely distributed (Hickey and Doyle 1977).

The earliest scattered records of angiosperm leaves are from the Hauterivian–Barremian and Aptian. These leaf fossils are typically very small and simple with a disorganized venation pattern and often without a distinctly differentiated petiole. By the Albian, however, angiosperm leaves had attained considerable architectural diversity, typically with a regular and well-differentiated vein pattern and distinct petiole. Compound leaves also appear for the first time during the Albian (e.g. Hickey and Doyle 1977).

Patterns of structural diversification — floral structures

Numerous mesofossil floras with small well-preserved flowers, fruits, seeds, stamens, and other dispersed plant fragments have been discovered from Cretaceous strata in Europe, North America, Asia, and Antarctica (Knobloch and Mai 1986; Friis *et al*. 1994, 1999; Crane *et al*. 1995; Crepet 1996; Frumin and Friis 1998; Herendeen *et al*. 1999; Takahashi *et al*. 1999), mainly from Upper Cre-

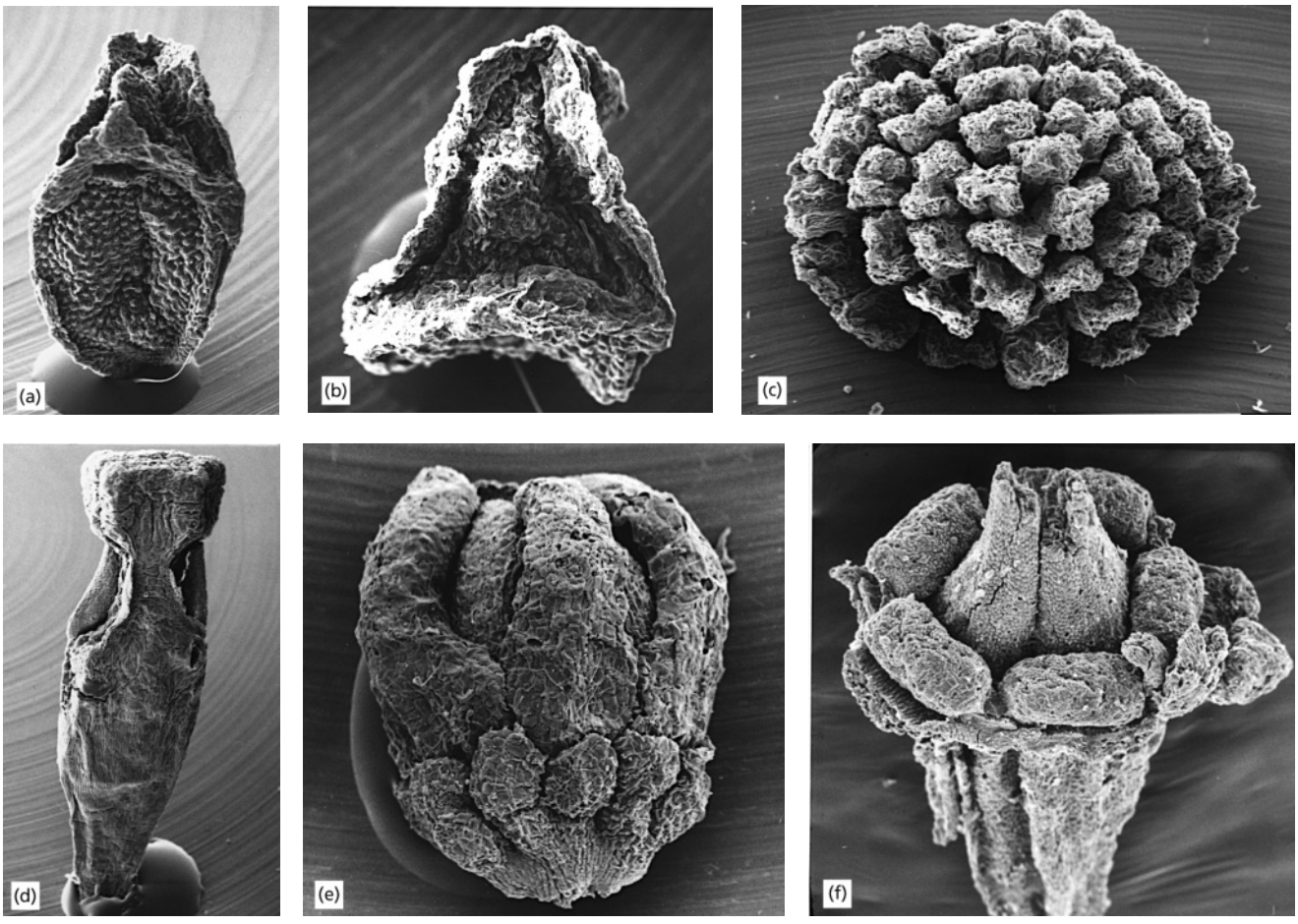


Fig. 1.4.2.4 Three-dimensionally preserved floral structures from the Cretaceous. (a,b) *Hedyosmum*-like female flower from the Barremian or Aptian of Portugal; (a) lateral view, ×54; (b) apical view, ×70. (c) *Hedyosmum*-like male inflorescence from the Barremian or Aptian of Portugal, ×65. (d) Isolated stamen from the Barremian or Aptian of Portugal with minute pollen sacs and a massive connective developed both between and apically to the pollen sacs, ×22. (e,f) Late Cretaceous flowers from southern Sweden; (e) *Scandianthus* showing calyx and corolla, ×70; (f) unnamed flower with distinct nectary, ×50. (All SEM-micrographs.)

taceous sediments, but several rich floras have also been discovered from Lower Cretaceous strata. The oldest abundant and well-preserved angiosperm mesofossils are in floras of Barremian or Aptian age from the Western Portuguese Basin (Friis *et al.* 1994, 1999). Many of these fossil angiosperm reproductive organs are charcoalified and retain their original three-dimensional shape and anatomical details (Fig. 1.4.2.4).

Studies of fossil flowers from the Cretaceous show that diverse kinds were established early in angiosperm evolution. With few exceptions, all floral structures, fruits, and seeds from the Cretaceous are very small, ranging from about 0.5 mm to 3–4 mm. Both unisexual and bisexual flowers are present in the earliest assemblages of fossil flowers. Early Cretaceous flowers are simple, typically with few floral organs, and either lack a floral envelope (perianth) or exhibit a perianth that is insignificant and poorly differentiated (Fig. 1.4.2.4a–c). Many stamens are characterized by having a poorly differentiated filament. Anthers often have small pollen sacs with valvate dehiscence and extensive sterile tissue between and above the pollen sacs (Fig. 1.4.2.4d). The ovary is formed from one or many carpels that are free from each other (apocarpous). Each carpel has a single or few ovules.

Several extant magnoliid taxa were established in the Early Cretaceous and some show a surprising lack of change in their floral organization. Most notably, flowers and dispersed pollen very similar to extant *Hedyosmum* (Chloranthaceae) occur abundantly in the Early Cretaceous (Fig. 1.4.2.4a–c) and appear to have remained unchanged for more than 100 million years after their first appearance in the Barremian–Aptian (Friis *et al.* 1999).

By the mid-Cretaceous the first angiosperm flowers with a well-differentiated floral envelope of sepals and petals, forming a calyx and a corolla respectively, are reported from fossil assemblages. The first records of flowers with an ovary of fused carpels and with nectaries also appear at the same time. The evolution of petals and the synorganization of carpels was a major step in the evolution of angiosperms and may have facilitated a further diversification among angiosperm subgroups through the Late Cretaceous and the early part of the Tertiary. To a large extent this Late Cretaceous–Tertiary diversification of angiosperms may have been closely linked to the evolution of more specialized pollination and dispersal syndromes involving coevolution with animal pollinators and dispersal agents. For example, many flowers from the Late Cretaceous have well-developed nectaries (Fig. 1.4.2.4f). Similarly, there is a clear increase in the maximum size of angiosperm fruits and seeds in the Early Tertiary.

By the end of the Cretaceous and Early Tertiary, many extant genera and families of angiosperms were already differentiated. However, major diversification in many of the most diverse groups of living angiosperms evidently continued through the Tertiary up to the present. Among these late radiating angiosperm groups are the grasses, and grass-dominated ecosystems were established in many parts of the world during the Miocene and Pliocene. The differentiation of other modern ecosystems, such as the tropical rain forests or boreal conifer forests, was apparently also mainly a Tertiary event.

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1.4.3 Rise of Birds

L.M. CHIAPPE

Introduction

'. . . if the whole hind quarters, from the ilium to the toes, of a half-hatched chicken could be suddenly enlarged, ossified, and fossilized as they are, they would furnish us with the last step of the transition between Birds and Reptiles; for there would be nothing in their characters to prevent us referring them to the Dinosauria.'
(T.H. Huxley 1869)

The origin of birds—Aves, the clade that originated from the common ancestor of *Archaeopteryx* and living birds—has been a matter of scientific debate and scrutiny throughout the history of taxonomy and evolutionary biology. In the eighteenth century, birds were placed immediately ahead of flying fishes in the 'chain of being'. With the establishment of evolutionary theories, more explicit hypotheses of relationships were formulated. During the nineteenth and twentieth centuries, birds were considered to be related to a variety of extinct and extant lineages of reptiles, including turtles, lizards, crocodylomorphs, pterosaurs, theropod and ornithischian dinosaurs, and a range of basal archosauromorphs (Witmer 1991) (Fig. 1.4.3.1).

Since J. Ostrom revitalized T.H. Huxley's hypothesis of the theropod origin of birds almost 30 years ago (Padian and Chiappe 1998), a large quantity of fossil documentation supporting a dinosaurian ancestry has been accumulated. Today, despite disagreement regarding the specific taxon phylogenetically closest to birds (e.g. dromaeosaurids, troodontids, oviraptorids), several lines of evidence converge to sustain the origin of birds

from maniraptoriform theropods (i.e. the common ancestor of *Ornithomimus* and Aves plus all its descendants; Fig. 1.4.3.1), no longer leaving any reasonable doubt that extant birds are short-tailed, feathered, maniraptoriform theropods (see also Section 4.1.13). (For other, less substantiated hypotheses of bird origins, see Witmer 1991 and Padian and Chiappe 1998.)

Evidence for the maniraptoriform origin of birds

The most visible evidence that birds are phylogenetically nested within maniraptoriform theropods is based on comparisons of their osteology, behaviour, oology, and integument with that of a variety of non-avian maniraptoriforms.

Osteology

A multitude of derived osteological characters are shared by all, or some, non-avian maniraptoriform theropods and birds. Comparisons between these taxa are greatly assisted by the many newly discovered basal birds (Padian and Chiappe 1998), which possess a skeletal morphology only slightly modified from the ancestral maniraptoriform condition. Some of these derived characters are the presence of rostral, dorsal, and caudal tympanic recesses (air spaces connected to the ear region), ventral processes on cervicothoracic vertebrae, ventral segments of thoracic ribs, forelimbs that are more than half the length of hindlimbs, a semilunate carpal bone allowing swivel-like movements of the wrist, clavicles fused into a wishbone, a pubic peduncle of the ilium longer than the ischiadic peduncle (these peduncles form the front and rear borders of the hip-socket), a vertically to caudoventrally orientated pubis ending in a boot-like expansion that projects only caudally, an ischium two-thirds or less the length of the pubis, and a femur with a feeble fourth trochanter (the attachment of the caudofemoralis longus muscle).

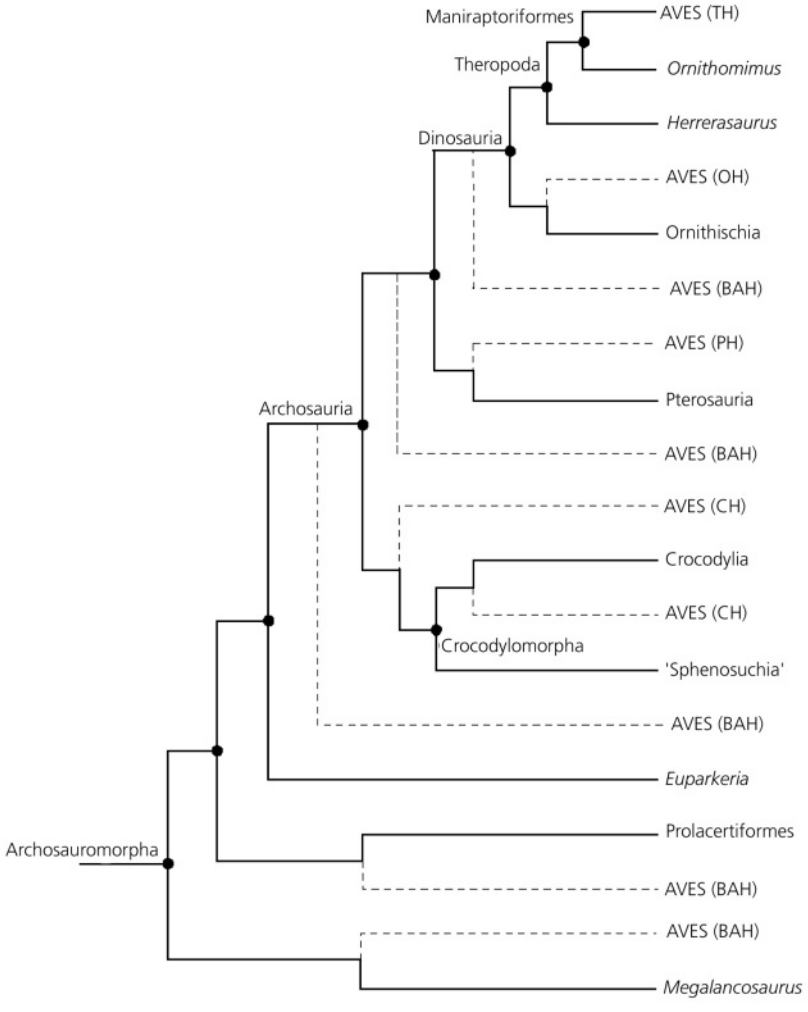


Fig. 1.4.3.1 Cladogram (derived from several cladistic analyses) depicting the phylogenetic relationships between various groups of archosauromorph reptiles and the diversity of hypotheses of bird origins advocated in the last three decades. BAH, array of often vague and somewhat different hypotheses that can be called the 'basal archosauromorph hypotheses'. CH, the initial 'crocodylomorph hypothesis' supported a close relationship between crocodylomorphs and birds; its current version places birds closer to extant crocodiles than to 'sphenosuchians'. OH, the 'ornithischian hypothesis'. PH, the 'pterosaur hypothesis'. TH, the 'theropod hypothesis' or, more properly, the 'maniraptoriform hypothesis'.

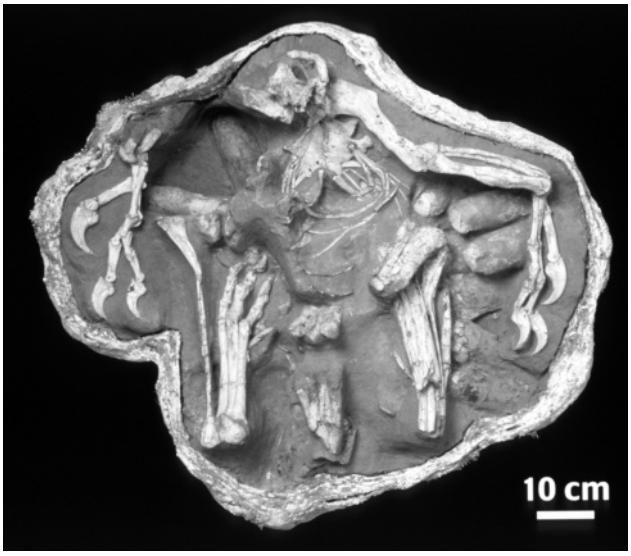


Fig. 1.4.3.2 Oviraptorid discovered on top of a clutch of oviraptorid eggs by the 1993 American Museum of Natural History–Mongolian Academy of Sciences expedition to Ukhaa Tolgod (Gobi Desert) (Clark *et al.* 1999). The behaviour inferred for this specimen, that of resting on top of presumably its own clutch of eggs, is a typical avian feature. (The specimen is IGM 100/979, Mongolian Institute of Geology, Ulan Bataar.)

Behaviour

Evidence of the behaviour of extinct organisms is rarely preserved in the fossil record. A handful of extraordinary discoveries, however, have shed light on the nesting conduct of certain non-avian maniraptoriforms. Several skeletons of Late Cretaceous oviraptorids from the Gobi Desert have been discovered on top of their clutches of eggs (Fig. 1.4.3.2). An oviraptorid embryo inside an egg of comparable morphology to those in these clutches strongly supports the idea that these specimens were brooding their own nest (Clark *et al.* 1999). A similar discovery of a Late Cretaceous troodontid skeleton from Montana in an identical brooding position suggests that, regardless of its specific function (e.g. protection, incubation), the typical avian nesting behaviour (i.e. adults sitting on top of their nests) was widespread among non-avian maniraptoriforms.

Oology

The general morphology and microstructure of calcified eggs is specific to certain groups of extant and extinct reptiles (Mikhailov 1997). Until recently, the precise characteristics of the eggshell microstructure of non-avian theropods remained elusive due to the absence of diagnostic embryonic material. The discovery of the Gobi oviraptorid embryo provided the first definitive evidence of a non-avian theropod egg (Clark *et al.* 1999). Since then, other non-avian maniraptoriform embryos have been found. Comparative studies between the eggshell microstructure of these eggs and those of extant birds have revealed features singular to the maniraptoriform type of eggshell, which define the ornithoid basic type (Mikhailov 1997). This basic type is unique in having shell units with at least two distinctly separated microstructural zones. The innermost zone is formed by a calcite crystalline structure that radiates from an organic core; the external zone has a scaly microstructural arrangement. In birds this external zone may grade into, or be completely separated from, a third, outermost zone. No other reptilian egg is known to have these microstructural characteristics (Mikhailov 1997).

Integument

Feathers have always been the quintessential bird feature. Unquestionable feathers are known in two maniraptoriforms, *Protarchaeopteryx* and *Caudipteryx*, from the Early Cretaceous of China (Ji *et al.* 1998). Down-like feathers are preserved covering portions of the several known specimens of these taxa. A fan-shaped cluster of pennaceous feathers (with a shaft and vanes) is attached to the distal part of the tail and symmetrically vaned feathers anchor to the distal portion of the forelimbs of *Caudipteryx*.

Initial cladistic analyses (Ji *et al.* 1998) placed *Caudipteryx* as the sister-taxon of birds, and *Protarchaeopteryx* in an unresolved trichotomy with velociraptorine dromaeosaurids and the clade formed by *Caudipteryx* and birds. Subsequent studies nested *Caudipteryx* within oviraptorosaurs. The fact that these two maniraptoriforms exhibit the primitive condition for several avian synapomorphies as well as for other synapomorphies diagnosing less inclusive clades of birds, makes it improbable that future cladistic analyses would nest them within birds.

Criticisms of the maniraptoriform hypothesis of bird origins

The 'temporal paradox'

Some critics of the maniraptoriform origin of birds (e.g. Feduccia 1996) have taken issue with the chronological gap between the oldest bird, the Late Jurassic *Archaeopteryx*, and the Cretaceous non-avian maniraptoriforms typically used in discussions of bird origins (e.g. *Deinonychus*, *Velociraptor*, *Oviraptor*). This criticism has become known as the 'temporal paradox' since it highlights the supposed inconsistency of arguing that birds evolved from creatures that lived several million years after their own origin. The 'temporal paradox', however, is meaningless because none of these Cretaceous dinosaurs has ever been regarded as the direct

ancestor of birds (Padian and Chiappe 1998). The maniraptoriform hypothesis postulates the existence of a most recent common ancestor of these Cretaceous dinosaurs and *Archaeopteryx* that obviously existed before the differentiation of the oldest of these taxa, *Archaeopteryx*. Advocates of the 'temporal paradox' often overlook the fact that Late Jurassic maniraptoriforms have been known for several decades (Padian and Chiappe 1998). Remains of putative maniraptoriforms (e.g. ornithomimids, therizinosaurids) were subsequently discovered in the Late Triassic of the USA and the Early Jurassic of China, suggesting that maniraptoriform theropods may have differentiated long before the known history of birds.

Embryology of the avian hand

Opponents of the dinosaurian origin of birds (e.g. Feduccia 1996; Burke and Feduccia 1997) often highlight the conflict between the identity of the avian wing digits, as suggested by embryological studies, and that indicated by the palaeontological evidence. Embryological investigations of extant birds have identified the digits of the hand as II, III, and IV of the pentadactyl limb and extrapolate this conclusion to include all birds. In contrast, the fossil record of non-avian theropods documents a reduction of digits IV and V throughout their evolution; these two digits disappeared prior to the differentiation of the maniraptoriforms (Padian and Chiappe 1998). Furthermore, the morphology, proportions, and phalangeal formula of the manual digits of certain maniraptoriforms (e.g. *Velociraptor*, *Deinonychus*) are remarkably similar to those of *Archaeopteryx*, indicating that the digits of the hand of *Archaeopteryx* are likely homologous to digits I, II, and III of the pentadactyl hand.

Despite the extrapolations made by critics of the maniraptoriform hypothesis, the real problem resides in whether the homology of the digits of *Archaeopteryx* is the same as that of modern birds, a difficult problem to address since the hand of modern birds is highly transformed and embryological data are unavailable for *Archaeopteryx*. Thus, even if the identity of the wing digits of modern birds is that indicated by the embryological data, the hand of *Archaeopteryx* may still have been formed by the same developmental trajectory of non-avian maniraptoriforms. The shift in this developmental trajectory may well have evolved after the differentiation of the lineage leading to *Archaeopteryx*. Consequently, the embryological research on the hand of extant birds (e.g. Burke and Feduccia 1997) is irrelevant to the understanding of bird origins; it bears only on their later evolution. Common usage notwithstanding, the extrapolation of the embryological pattern observed in modern birds to all birds (including *Archaeopteryx*) is unwarranted.

Lung structure and ventilation

Based on interpretations of soft structures alleged to be indicators of visceral compartmentalization and the morphology of the pubis, non-avian theropods have been reconstructed with a crocodile-like, hepatic-piston mechanism for lung ventilation (Ruben *et al.* 1997), in which lung inflation is a consequence of the liver being pulled by a series of muscles attached to the pubis. These authors argued that their interpretation of the lung structure and ventilation of non-avian theropods posited serious caveats to the theropod origin of birds. They contend that the transition from the crocodile-like pulmonary system of non-avian theropods to the flow-through lung system of birds would have required the evolution of an opening in the alleged partition between the thoracic and abdominal cavities of non-avian theropods, a diaphragmatic hernia (Ruben *et al.* 1997). Such a hernia would have compromised the efficiency of the pulmonary system of the transitional forms (Ruben *et al.* 1997).

The available osteological evidence of non-avian theropods, especially of non-avian maniraptoriforms, shows that several of the skeletal correlates of the avian flow-through lung were already present among those dinosaurs. Pneumatic foramina for the entrance of air-sac diverticula are widespread among the vertebrae of non-avian theropods. Intracostal articulations delimiting ossified costal and ventral ribs are known for dromaeosaurids and oviraptorids (Clark *et al.* 1999), and these and other maniraptoriforms have relatively large ossified sternal plates. The morphology of the ribs and sternum of these theropods suggests that the coordinated costal and sternal movements that ventilate the lungs of extant birds may have already been present in their maniraptoriform ancestors.

Non-avian theropods may have had a crocodile-like diaphragm dividing their visceral cavity (Ruben *et al.* 1997), but the presence in these dinosaurs of skeletal features correlated to the avian system of lung structure and ventilation is undeniable. Even if we were to reconstruct the lung ventilation system of non-avian theropods in a crocodile-like fashion, the alleged implausibility of this system evolving into the ventilatory mechanism of birds remains to be demonstrated.

Conclusion

In 1960, the origin of birds was thought to be largely a matter of deduction, with 'no fossil evidence of the stages through which the remarkable change from reptile to bird was achieved' (Swinton 1960). Since then, features that for decades highlighted the uniqueness of birds, from furculae and swivel-like wrists, to feathers and nesting behaviour, have been discovered among

non-avian maniraptoriform theropods. Specifics notwithstanding, the origin of birds from maniraptoriform dinosaurs is indisputable. Criticisms levelled by detractors are misleading. The main transformations from non-avian maniraptoriforms to modern birds are beautifully preserved in the fossil record.

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1.5 Cenozoic Events

1.5.1 Evolution of Modern Grasslands and Grazers

T.E. CERLING

Introduction

Grass-dominated ecosystems, and those where grasses make up a significant fraction of the flora, are globally widespread. Tropical savannahs make up more than half the land area at low latitudes, and grass-dominated ecosystems are abundant in parts of North America and central Asia. Modern grasses use two different photosynthetic pathways, the more ancient 'C_3 pathway' and the more recent 'C_4 pathway', where 'C_3' and 'C_4' refer to the number of carbon atoms in the first product during CO_2 assimilation. The C_4 pathway includes a CO_2 enrichment mechanism which is absent in the C_3 pathway. The study of carbon isotopes, which distinguish between the C_3 and C_4 photosynthetic pathways, has demonstrated that the rise of 'modern grasslands' (i.e. grasslands where C_4 grasses are significant) is much later than the rise of grasslands in general.

The traditional view of the rise of grasses and grasslands is closely tied to the observation that equids and other mammals developed hypsodont (high-crowned) teeth in the Early Miocene (Simpson 1951) in North America. This view is supported by observations that fossilized grass and grass pollen appear in the Miocene in some abundance and become more common from the Miocene to the present. This increase in hypsodonty in mammals occurred in the Oligocene in South America and therefore it is thought that grasses were significant somewhat earlier in South America and possibly Africa (Jacobs *et al.* 1999). Unfortunately, grasses are most abundant in settings that are not conducive to the preservation of fossil plants in the geological record; they are common in oxidizing and well-drained environments where they tend to be destroyed after burial. Stable isotopes offer a new view of the development of grasses and grasslands, especially those grasses that are found today in tropical to warm temperate environments.

Grasses belong to the family Poaceae and all are monocotyledons. Grasses, particularly C_4 grasses, have several properties that make them very different from C_3 dicotyledons: (1) they tend to have lower nitrogen contents which make them intrinsically less nutritious than dicotyledons; (2) C_4 and C_3 grasses rarely have secondary toxins, which are found in many C_3 dicotyle-

dons; (3) protein in C_4 plants is 'protected' in the bundle sheath cells, making them harder to digest than protein in the thinner mesophyll cells of C_3 plants (Ehleringer *et al.* 1997); and (4) grasses have higher silica contents than dicotyledons, making them more abrasive. This last property provided the supposed link between the increase in hypsodonty in mammals in the Early Miocene and the development of savannah and grassland ecosystems. Thus, the traditional view is that hypsodonty evolved so that mammals could take advantage of the new food source available, i.e. grasses (see Simpson 1951; MacFadden 1992).

The rise of modern C_4 grasslands

Stable isotopes apparently provide a test for the hypothesis that the increase in hypsodonty in the Late Miocene is linked with the spread of grasses. This is because C_3 plants (including grasses) have $\delta^{13}C$ values of about –26‰ while C_4 plants (which are mostly grasses) have $\delta^{13}C$ values of about –12‰. In the modern world, C_4 grasses are the dominant grass at latitudes less than about 40°. Fossil teeth record the proportion of C_3/C_4 biomass in diets, and palaeosol carbonates record the proportion of C_3/C_4 biomass in ecosystems. Thus, carbon isotopes should record when C_4 grasses became abundant. In several ways, dietary evidence is preferable to palaeosol evidence for studying global ecosystem changes: (1) the identification of fossils is less problematic than of palaeosols; (2) museums around the world have rich collections that can be studied; and (3) the selective nature of dietary preferences enhances the distinction between C_3 and C_4 biomass.

Unfortunately, the story is complicated by the presence of both C_3 and C_4 grasses. Most C_4 plants are grasses, and they are the dominant grass at low to intermediate latitudes; however, C_3 grasses are found in regions with cool growing seasons, such as are found at high latitudes, high altitudes, or in Mediterranean (i.e. winter-rain) climates. Therefore the isotope record documents only the increase in C_4 grasses, as opposed to the increase in grasses. C_3 grasses have the same $\delta^{13}C$ values as C_4 dicotyledons.

The carbon isotope record of equids from North America shows an abrupt increase in ^{13}C starting about 7 Ma (Fig. 1.5.1.1), corresponding to the time when equids began to have a significant component of C_4 biomass in their diets (Cerling *et al.* 1997). The isotope enrichment between diet and bioapatite is about 14‰, so that $\delta^{13}C$ values <–8‰ indicate a diet dominated by C_3 biomass while $\delta^{13}C$ values >0‰ indicate a diet dominated by C_4 biomass. This diet change occurred millions of years after hypsodonty appeared and equids became diversified (Fig. 1.5.1.1). In North America not all equids changed from a C_3 diet to C_4 grasses at this time: in more northern latitudes and along the Pacific Coast the advent of C_4 grasses in the diet was much delayed or absent altogether. Only in the southern USA and in Mexico did some equids become sole C_4 consumers. At the end of the Miocene (≈7–5 Ma), in southern Asia (Pakistan) and in Africa (Kenya) equids changed from being predominantly (>90%) C_3 consumers to predominantly (>90%) C_4 grazers (Cerling *et al.* 1997). Equids were not present in South America at this time, but other hypsodont mammals show an expansion of C_4 biomass at the end of the Miocene. Therefore, the carbon isotope record from

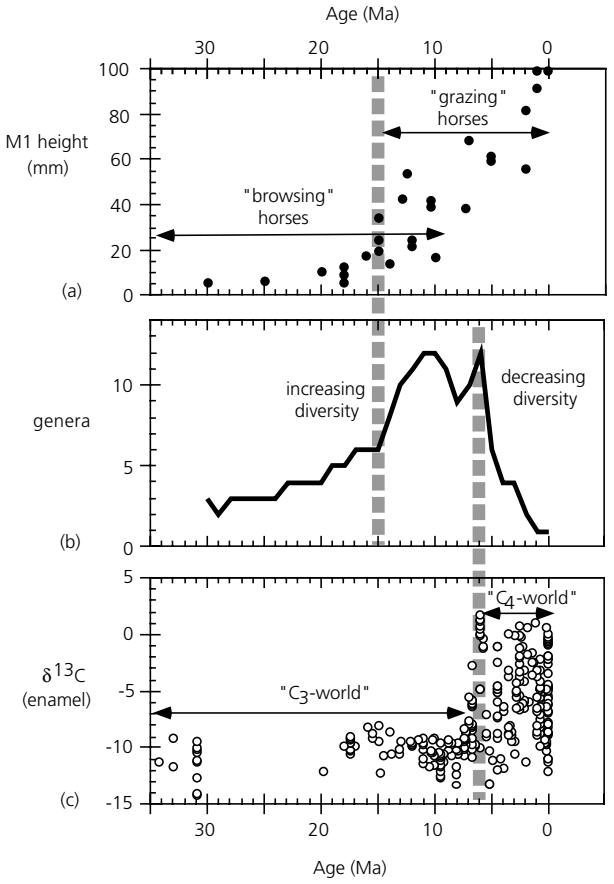


Fig. 1.5.1.1 (a) Development of increasing hypsodonty in North American equids; M1, first upper molar tooth. (b) Increasing diversity of equids between 20 and 15 Ma; the simultaneous increase in hypsodonty and diversity has been generally taken to indicate the expansion of grasses in the Early Miocene in North America. (c) North American equids underwent a significant dietary change beginning about 7 Ma when they began to eat C_4 grasses; this coincides with a significant decrease in the diversity of equids. Dashed lines show that increasing hypsodonty and diversity are correlated in time, and that the rise of C_4 grasses correlates with the decrease in equid diversity. (a, Modified from Wang *et al.* 1994; b, data from MacFadden 1992.)

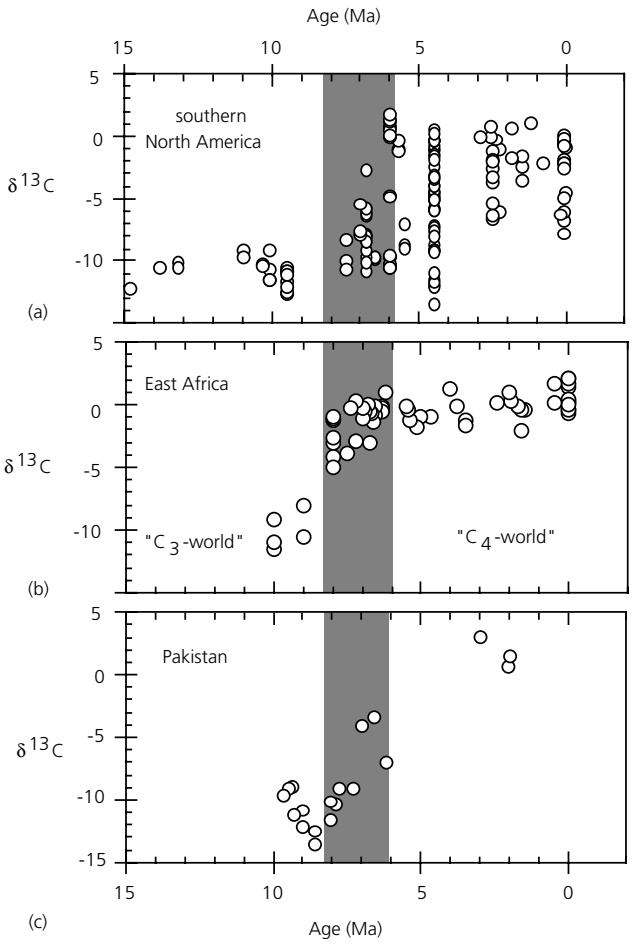


Fig. 1.5.1.2 $\delta^{13}C$ values for equids in: (a) southern North America (Florida, Texas, Arizona, Mexico); (b) Africa; (c) Pakistan. All show an abrupt increase in $\delta^{13}C$ in the Late Miocene, indicating that in all regions C_4 biomass became an available food resource. The details of the relative timing of the C_4 biomass expansion is under study. Equids immigrated from North America to the Old World at about 10.5 Ma. These first immigrants to the Old World had C_3 diets as shown. (Data from Cerling *et al.* 1997.)

four continents indicates that C_4 grasses underwent significant expansion at the end of the Miocene—a time of significant faunal change on each of these continents, including Europe. The carbon isotope record from Europe, however, does not show significant C_4 biomass at any time. The post-Miocene C_3 signal for equid diets in Europe could be due either to browsing of C_3 dicotyledons or to a diet of C_3 grass. The isotope record cannot distinguish between grazers and browsers when C_3 grasses are the dominant grass.

The $\delta^{13}C$ isotope record clearly shows a global increase in C_4 biomass at the end of the Miocene (Fig. 1.5.1.2). Major faunal turnover of mammals occurs on most continents at this time. The inception of modern grasslands, which are dominated by C_4 grasses at low to intermediate latitudes, began in the Late Miocene and developed fully in the Early to Middle Pliocene. It is still reasonable to assume that grasses developed in the Early Miocene, but it is now clear that modern grasslands developed much later. The grassland and savannah ecosystems of today (i.e. dominated by C_4 grasses) are of Late Miocene origin.

The conditions that favour C_4 photosynthesis are high temperatures and low concentrations of atmospheric carbon dioxide; these conditions promote photorespiration in C_3 plants. C_4 monocotyledons have a higher quantum yield than C_3 monocotyledons or dicotyledons above about 20–25°C for atmospheric CO_2 levels of 350 ppm (Ehleringer *et al.* 1997). The crossover temperature, where C_4 monocotyledons have a higher quantum yield than C_3 monocotyledons and dicotyledons, occurs at higher temperatures at higher CO_2 levels; the crossover at 500 ppm CO_2 is about 28–33°C. Because growing temperatures rarely exceed ≈ 35°C anywhere on Earth, 500 ppm CO_2 may represent the upper limit for ecosystems where C_4 plants would be more competitive than C_3 plants.

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1.5.2 Radiation of Tertiary Mammals

C.M. JANIS

Introduction

The Tertiary Period was the time when mammals radiated into the great variety of body sizes and morphological diversities seen today. However, the Tertiary represents only about one-third of the total time of mammalian existence (see Section 1.3.10). The first mammals appeared in the latest Triassic, but during the Mesozoic they were all of small body size (the largest was about the size of a house cat) and mostly of generalist insectivorous/omnivorous adaptations. Although it seems unlikely that Mesozoic mammals were in direct competition with dinosaurs, not until the latter's demise at the end of the Cretaceous did mammals diversify into a broader variety of ecomorphological types.

The Tertiary is traditionally divided into the earlier Palaeogene and the later Neogene (Fig. 1.5.2.1). However, the mammalian faunas better reflect the division between the 'hot house world' of the earliest Tertiary (Paleocene and Early Eocene), a continuation of the warm global temperatures and ice-free world of the Mesozoic, and the 'ice house world' of the later Tertiary to Recent. The end of the Early Eocene represents the point of highest mean annual temperatures in higher latitudes, which subsequently plummeted to levels resembling those of the present day (with some amelioration during the Miocene). The Antarctic ice cap first appeared in the later Eocene, and the Arctic ice cap was established by the Pliocene. The generic diversity of mammals tracks the palaeotemperature curve, with an initial peak in the Early/Middle Eocene (and subsequent Late Eocene extinctions), and a second peak in the Middle Miocene (followed by Late Miocene extinctions) (Fig. 1.5.2.1). The well-known Late Pleistocene mammal extinction was less extensive than these earlier events and primarily affected larger mammals.

The evolutionary history of many mammalian lineages is from small, relatively unspecialized forms in the early Tertiary to the larger, more specialized Recent forms. This is exemplified by the famous textbook *'Eohippus'* to *Equus* story of horse evolution, where the morphological changes are usually interpreted as progressive moves to a fitter, 'better adapted' type of animal. However, the history of Tertiary mammals is better understood in the context of changing global climates and environments, brought about by shifting continents and tectonic events (see Janis 1993; Bernor *et al*. 1996). In this view, the early horse *Hyracotherium* (='*Eohippus*') is interpreted as well adapted to the global tropical-like forests of the Early Eocene. The replacement of early horses by later forms of larger body size, better adapted for eating grasses and running on the plains, reflects the cooling and drying of higher latitude environments, with temperate woodlands and grasslands replacing the tropical forests. Had North America (the site of horse evolution) been connected to South America during the early Tertiary, then *Hyracotherium*-like horses might have been able to migrate with their original habitat toward the equator and survive today, in a fashion similar to the mouse deer (tragulids) of the Old World tropics.

The role of continental drift and the isolation of mammalian faunas

Much of Tertiary (and modern) mammalian diversity is related to the isolation of different founder groups of mammals on different continents, and subsequent convergent evolution of similar ecomorphological types. The most obvious example today is the separate nature of the Australian marsupials, with their own iteration of various adaptive types such as 'moles', 'anteaters', and 'wolves', etc. Later Tertiary dispersals have muted or obliterated many differences in mammalian faunas between different continental blocks—only Australia has retained its relative isolation. The fauna of South America has some unique elements today, such as edentates (sloths, anteaters, and armadillos) and opossum-like marsupials, but around half the modern genera are derived from Northern Hemisphere immigrants that arrived when the Isthmus of Panama formed around 2.5 Ma. A large diversity of original endemic forms, most notably a great variety of ungulates (hoofed mammals) and large marsupial carnivores (borhyaenids), are now extinct (although their demise was not directly related to the arrival of the Pliocene immigrants).

The break-up of Pangaea began in the middle Mesozoic, and some workers have suggested that the global distribution of mammalian stocks was related to a vicariance event with the Cretaceous isolation of continents (Hedges *et al*. 1996). However, the more traditional view, and that supported by the fossil record, is that the Tertiary distribution of mammals is largely explained by dispersal events. Considering again the isolated nature of the Australian mammal fauna, the unique presence of monotremes (egg-laying mammals such as the platypus and echidna) may reflect vicariance. (Note, however, that the discovery of a platypus in the Paleocene of southern South America hints at an originally broader, Gondwanan distribution.) However, the Australian marsupials clearly arrived by dispersal from the Americas. The earliest marsupials are known from North America, and fossils from Antarctica support the hypothesis that they dispersed via a southern route prior to the complete isolation of Australia. The oldest Tertiary

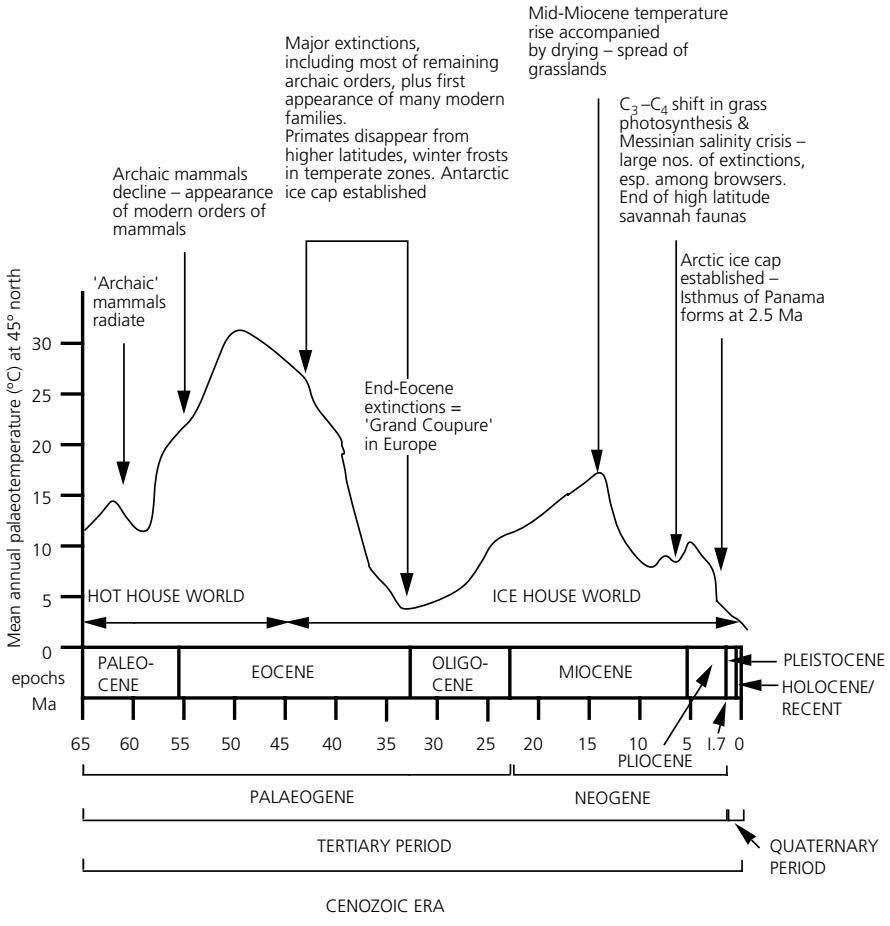


Fig. 1.5.2.1 Important events in Tertiary mammal evolution, related to palaeoclimatic curves for the Northern Hemisphere. (Palaeotemperature data from Burchardt 1978.)

fauna of Australia (Early Eocene) contains not only marsupials but also a single tooth of a placental, with its tantalizing suggestion that both marsupials and placentals initially dispersed to Australia but that only the former prevailed.

The island of Madagascar today provides a wonderful example of evolution in isolation: while many of its organisms represent a vicariance event since its Mesozoic split from Africa, its unique mammalian fauna (including lemurs, civet-like carnivores, and tenrec insectivores) was clearly derived from dispersal events, either from the African mainland or from Asia. Africa also contains a number of old endemic mammals, such as elephants, hyraxes, and aardvarks. Their original isolation may represent early vicariance, but most of the modern African fauna was obtained by dispersal from Eurasia, especially when Africa docked with Asia during the Oligocene.

Tertiary radiations and changing global climates

The mammals of the Paleocene largely represent 'archaic' groups. The majority of extant orders, most notably Primates, Cetacea (whales), and the ungulate orders Artiodactyla (pigs, camels, antelope) and Perissodactyla (horses, rhinos) date from the earliest Eocene. Rodents and bats are known from the Late Paleocene. Much information on the early Tertiary comes from the Northern Hemisphere. In the global tropical-like forests of the Paleocene the arboreal mammals were the squirrel-like plesiadapiform 'pro-primates', opossum-like marsupials, and the rodent-like multituberculates (an extinct subclass of mammals, holdovers from the Mesozoic). Terrestrial herbivores were primitive ungulates ('condylarths'), and forms of uncertain taxonomic affiliation (such as taeniodonts and pantodonts). The teeth of most of these animals suggest an omnivorous diet. Folivorous (leaf-eating) mammals were not apparent until the Eocene, perhaps reflecting a more deciduous type of vegetation associated with a more seasonal climate. Early carnivores were either the mesonychid 'condylarths' (which included the ancestors of whales) or the creodonts. These predators were all heavily built ambushers. The modern order Carnivora also appeared in the earliest Tertiary, but the earliest members ('miacoids') were small generalists and did not assume the role of larger predators until the Late Eocene.

Although many more modern groups of mammals first appeared in the Late Paleocene or Early Eocene, the more archaic groups did not immediately become extinct; their demise seems more related to the declining temperatures and changing vegetation of the later Eocene, which also affected some of the early modern types such as the higher-latitude lemuriform primates. The major extinctions occurred in the late Middle Eocene in North America, and close to the Eocene/Oligocene boundary in Europe (the 'Grand Coupure'). Dispersal of Asian mammals to Europe, following the drying up of the Turgai Straits at the end of the Eocene, may also be related to the magnitude of this extinction event. Evidence for Late Eocene mammalian extinctions elsewhere in the world is equivocal. A Grand Coupure event appears to have occurred in Asia (Meng and McKenna 1998), but critical faunas are missing in southern continents. Despite the more southerly Eocene position of Australia, a Grand Coupure type of replacement of an early Tertiary tropical-like fauna with one more adapted to cooler, drier conditions (e.g. containing kangaroos) is not apparent until the Pliocene.

Oligocene faunas represent a rather depauperate world without much diversification. By this time South America had received its faunal elements of rodents and monkeys, probably arriving from Africa by chance rafting. The major vegetation in the higher latitudes was now temperate woodland, perhaps with some arid patches. Grasslands were unknown, as were Arctic types of vegetation such as tundra and taiga. The major types of modern mammals are represented by extinct families belonging to modern orders, such as amphicyonids ('bear dogs') and nimravids ('false sabre-tooths') among the carnivores. By the Miocene, the higher-latitude temperatures started to rise again, to reach a Neogene maximum in the middle of the epoch. By the late Early Miocene, most Oligocene lineages were extinct, or on the wane, and the fauna began to take on a more modern aspect, dominated by members of extant families.

By the Middle Miocene, grasslands were spreading across the higher latitudes, and with them appeared mammals with adaptations for grazing, such as hypsodont (high-crowned) cheek teeth. Late Miocene faunas in Argentina and on the Great Plains of North America approached the ecomorphological diversity of mammals on the East African savannahs today, although of different taxonomic affiliations. For example, in North America a diversity of horses, camels, and pronghorns stood in for the African diversity of antelope. It is a popular notion that these new, longer-legged herbivores evolved in association with pack-hunting carnivores, but the fossil evidence shows that pursuit-type long-legged carnivores did not appear until the Pliocene. The longer legs of these Miocene ungulates were probably an adaptation for traversing a broader foraging territory in the drier, less productive environments (Janis and Wilhelm 1993).

This later Miocene spread of grasslands was traditionally attributed to Neogene mountain uplift (e.g. Rockies, Andes, Himalayas), which resulted in a rainshadow drying effect. However, the floral changes may have been driven by declining levels of atmospheric carbon dioxide, with a major shift in the carbon cycle biochemistry of grasses (from C_3 to C_4) at around 7 Ma in the latest Miocene (e.g. Cerling *et al*. 1998) (see Section 1.5.1). Drying was certainly an environmental factor, as evidenced by the latest Miocene desiccation of the Mediterranean sea (the Messinian salinity crisis). Whatever the reasons, major Late Miocene extinctions affected the high latitude mammal faunas as the savannah-like treed grassland habitat gave way to prairie (see Janis *et al*. 2000). Grazers were affected as well as browsers; in North America a diversity of over a dozen sympatric genera of grazing horses in the Late Miocene was reduced to a single genus in the Late Pliocene.

By the start of the Pliocene, an Arctic ice sheet was established, and tundra and taiga vegetation were present. A slight warming in the Early Pliocene was followed by a profound cooling at 2.5 Ma, resulting from changes in ocean currents following the establishment of the Isthmus of Panama. South American faunas were changed forever with the immigration of northern forms, while some southern forms (e.g. armadillos, opossums, monkeys) entered North America. Other late Tertiary dispersals resulted in present-day distributions of mammals: the dispersal from North America to the Old World of dogs, derived horses, and camels; the dispersal from the Old World to North America of deer, microtine rodents, and (in the Pleistocene) bovids (e.g. bison); and the dispersal of rodents from Asia to Australia (an event that had surprisingly little effect on the native fauna). In East Africa, the tropical forests gave way to savannahs at this time, resulting in the diversification of modern groups such as the bovids (antelope) and the emergence of humans (see Section 1.5.5).

Understanding Tertiary environmental changes provides the key to understanding mammalian evolution. Differences between early Tertiary and present-day mammals are largely the result of a change from equable, globally tropical conditions to a cooler, drier, and more climatically zoned world. Eocene-like mammals remain in the restricted equatorial forests (e.g. lemurs and mouse deer), but grazers have diversified in the grasslands (e.g. modern horses and antelope), and temperate woodland mammals in the higher latitudes (e.g. deer and bears), while some extreme specialists have evolved adaptations to environmental conditions unique to the past few million years (e.g. polar bears in the Arctic and camels in the desert).

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1.5.3 Rise of Modern Land Plants and Vegetation

M.E. COLLINSON

Introduction

Plants are primary producers—photoautotrophs which manufacture metabolites via photosynthesis—and are therefore at the base of the food chain for most life (except chemoautotrophic microbes). Vegetation forms the framework and provides the niches for other organisms (both above and below ground level). Plants and vegetation are therefore critical for understanding the history of life on land and the origin and evolution of modern land biomes.

The earliest modern biome?

Amongst modern land biomes tropical rain forests are familiar because of issues involving their fate due to human impact. However, asking palaeobiologists 'When was the earliest tropical rain forest?' may yield answers ranging from the Upper Carboniferous to only a few thousand years before present. None of these answers is incorrect, but all require further explanation.

In the Upper Carboniferous, peat (ultimately coal)-forming and clastic swamp forests existed in equatorial latitudes, so these indeed were equatorial wet areas with trees (i.e. 'tropical rain forest'). These forests included tall trees of various canopy heights, with understorey, scrambling plants, climbers, and epiphytes like modern tropical rain forests (see Section 1.3.8). However, their diversity was very low compared to modern tropical rain forests and the dominant plants (e.g. arborescent lycophytes and other spore bearers, seed ferns) and animals were utterly different in their taxonomy and functional biology from those that dominate the modern tropical rain forest biome (Krings and Kerp 1999). At the other extreme, the suggestion of a very recent origin assumes that tropical rain forest biotas, identical to those of the present day, could not have originated until after the influence of the last glaciation on global climates. A more appropriate approach is to evaluate the origin of modern biomes from the time when the dominant groups of organisms today first became dominant in the past.

The rise to dominance of modern land life

With the exception of moss-lichen tundra, and boreal conifer forests (taiga), most of the land surface today is dominated by flowering plants, even in lakes and in the seagrass banks of shallow seas. Numerous specializations of the reproductive (closed carpels, receptive stigma, double fertilization, faithful pollination, fruit variety and dispersal strategies) and vegetative (broadly laminate leaves, vessels in woods) organization of flowering plants distinguish their functional biology from that of other plants (Collinson 2000). Therefore, the rise of modern land vegetation must be considered to have begun after the rise of flowering plants. The means by which the fossil record of flowering plants is interpreted in terms of ancient vegetation is explained elsewhere (Collinson 2000).

Flowering plants appeared and diversified rapidly during the mid to Late Cretaceous. They rose to dominance in the rock record by about 90 Ma and in the Late Cretaceous a number of modern flowering plant families can already be recognized (Wing and Boucher 1998; Lupia *et al.* 2000). However, major modernization of flowering plants only occurred with their second radiation during the latest Cretaceous and early Cenozoic (Palaeogene) (Collinson 1990, 2000). This radiation resulted in numerous trees, shrubs, and lianas belonging to a high diversity of modern flowering plant families and genera (many represented by reconstructed whole plant fossils). Important plants included the para-

phyletic magnoliid dicotyledons (magnolias, bays, custard apples, water lilies), the dicotyledon subclasses Hamamelidae (planes, birches, walnuts, beeches, elms, casuarinas) and Rosidae (legumes, dogwoods, maples, grape vines), and monocotyledons (some herbaceous) of the subclasses Alismatidae (many lacustrine and pond plants such as pond weeds), Arecidae (palms and aroids), and Zingiberidae (gingers and bananas) (Collinson 2000).

Until the terminal Cretaceous extinctions the dominant groups of land vertebrates were the dinosaurs and pterosaurs. The mammals and birds did not rise to dominance until the early Cenozoic (Palaeogene), and many insect groups, which interact with plants in modern vegetation, were also unimportant until the Palaeogene (Friis *et al.* 1987; Collinson and Hooker 1991; Benton 1993). Therefore, the rise of modern land biomes is essentially an early Cenozoic phenomenon.

Tropical forests

The Early Eocene London Clay Flora of southern England, and similar floras elsewhere, can be reconstructed as Eocene tropical to paratropical forest. (Paratropical is similar to tropical but with fewer canopy layers.) The floras are diverse (up to 350 species) and include a wide range of flowering plant trees, shrubs, and lianas, the nearest living relatives of many of which are important in, or exclusive to, modern tropical rain forests (e.g. members of the families Arecaceae [palms], Anacardiaceae [cashew nut family], Anonaceae [custard apples], Burseraceae [sources of myrrh and frankincense], mastixioid Cornaceae [mastic trees], Dilleniaceae [Dillenias], Icacinaceae [Icacina vines], Lauraceae [cinnamon and bay trees], Menispermaceae [moonseed vines], Sabiaceae [*Sabia* and *Meliosma* trees and shrubs], and Vitaceae [grape vines, virginia creeper]). Physiognomic signatures from woods and leaves support the reconstruction of megathermal or warm mesothermal, broadleaved, evergreen vegetation, with tropical to subtropical climate regimes (Collinson 2000). (Mean annual temperatures (MAT) greater than 20°C sustain megathermal vegetation; MAT is 13–20°C and below 13°C for mesothermal and microthermal vegetation, respectively.) This vegetation was probably emplaced following increased humidity after the Cretaceous/Tertiary transition. Although there are flowering plant trees from at least three subclasses of dicotyledons in the Late Cretaceous, these are only known from low palaeolatitudes and their wood physiognomy does not indicate a rain forest setting. At the Eocene thermal maximum, the first extensive warm interval since their emplacement, the Eocene tropical forests spread up to palaeolatitudes ranging between 55 and 65° N and S. Their subsequent range restriction, both to lower latitudes and limited geographical areas (e.g. South-East Asia) was a consequence mainly of climatic change, especially global cooling, initiated in the Late Eocene and enhanced by terminal Eocene events (Collinson 2000).

The framework of Eocene tropical forests was formed by a high diversity of flowering plants, including trees, shrubs, and lianas, and their animal life was dominated by mammals and insects, as in modern tropical rain forests. Near living relatives of many of the Eocene biotic elements, and animal–plant interactions also documented in the Eocene, occur in tropical rain forests today and some are unique to this biome (Collinson 1990, 2000; Collinson and Hooker 1991). However, there are also differences. In European Eocene tropical forests the very limited occurrence of Dipterocarpaceae (a single macrofossil) is a major difference from modern South-East Asian rain forests (Collinson 2000). Furthermore, flowering plant epiphytes, so common in modern rain forests, lack a Palaeogene macrofossil record (Collinson 2000). Dipterocarp-dominated tropical rain forests like those of the present day in South-East Asia are considered to have developed during the Miocene (Morley 2000).

Mangroves

A *Nypa*-dominated mangrove (*Nypa* is a palm with a creeping stem) with subordinate occurrences of the mangrove family Rhizophoraceae (e.g. *Ceriops*) is reconstructed as the Early and Middle Eocene coastal vegetation of the former English, French, and Belgian North Sea coastlines (Fig. 1.5.3.1a,b) (Collinson 2000). Modern *Nypa*-dominated mangroves are common in South-East Asia (Collinson 2000). The *Nypa*-dominated mangrove may have been in place at low latitudes in the Late Cretaceous but during the Eocene thermal maximum it had expanded to palaeolatitudes approximately 55–65° N and S (Collinson 2000). A fossil record based largely on pollen grains indicates Middle Eocene occurrences for other mangroves (such as *Sonneratia*, *Brownlowia*, and *Oncosperma*) (Morley 2000).

Deciduous forests

The *in situ* tree stumps and litter layers of the Eocene fossil forests of Axel Heiberg Island (Canadian Arctic Archipelago, palaeolatitude 75–80°N) represent an excellent example of the Paleocene and Eocene vegetation of the high northern palaeolatitudes which has been termed polar broadleaved deciduous forest. These polar deciduous forests were of relatively low diversity and dominated by wind-pollinated, dry fruited, deciduous trees of the flowering plant families Betulaceae (birch trees), Cercidiphyllaceae/Trochoden-

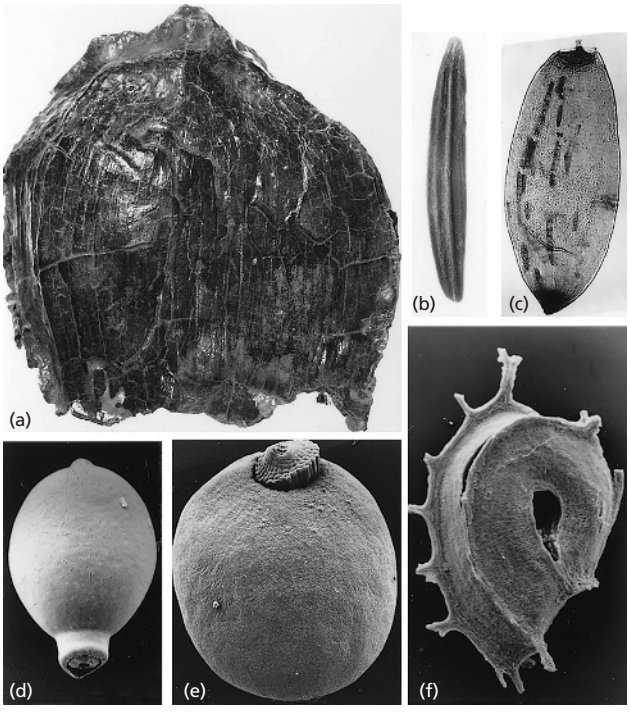


Fig. 1.5.3.1 Fossil fruits and seeds of flowering plants representative of *Nypa*-dominated mangrove (a,b) and freshwater marsh (c–f) in the Eocene. (a) Fruit of *Nypa* (mangrove palm), ×0.5. (b) Viviparous embryo of *Ceriops* (mangrove of the Rhizophoraceae family), ×1.5. (c) Seed of *Typha* (bulrush), ×35. (d) Seed of *Aldrovanda* (water wheel), a free-floating insectivorous plant with traps like those of Venus fly trap, ×15. (e) Seed of *Brasenia* (red water lily), ×20. (f) Fruit of *Potamogeton* (pond weed), ×40. See Section 4.1.18 for references to further details. (a,b, Reflected light micrographs; c, transmitted light micrograph; d–f, scanning electron micrographs.)

draceae (katsura and *Trochodendron* trees), Juglandaceae (walnuts and wingnut trees), Platanaceae (plane trees = sycamores in North America), and Ulmaceae (elm trees), as well as the *Ginkgo* (maidenhair tree) and conifers of the Taxodiaceae (swamp cypresses). The climate is judged to have been free from severe frost and with mild moist summers; deciduousness resulted from a lack of winter light rather than cold. All forest belts were shifted polewards at the Eocene thermal maximum but at other times (e.g. Late Paleocene) similar vegetation extended down into northern mid-latitudes (Alberta, Canada) where it existed as a deciduous forest colonizing open, disturbed areas of floodplains. There is no modern homologue of the polar deciduous forests because tree-dominated vegetation no longer exists at polar latitudes and this, albeit recent, biome is now extinct. However, the plants which once grew in the polar deciduous forests occur today in mesothermal to warm microthermal, broadleaved deciduous and mixed conifer/broadleaved deciduous forests in mid-latitudes in various parts of the world (Collinson 2000). Other elements in these modern deciduous forests may have originated in upland areas during the Eocene. Microthermal, broadleaved deciduous forests similar to those of the present day occupied mid-latitudes following the terminal Eocene temperature decline, though some mesothermal elements persisted in places. More arid floral elements appeared in continental interiors and forest canopies were lost, resulting in an opening of habitats which intensified during the Miocene (Collinson 1990, 2000; Wing 1998).

Conifer forests

Modern conifers are known in Mesozoic and Cenozoic floras but conifer forest comparable to the taiga in the boreal realm today (very low diversity to monotypic) is not documented in Palaeogene floras. Pinaceae conifers increased in the Late Eocene to Oligocene floras of northern high latitudes (see deciduous forests above) and through the Neogene conifers became increasingly important in these forests (Collinson 1990, 2000); boreal conifer forest is documented in the latest Pliocene of North America (Wing 1998).

Wetlands

Peat-forming, tree-dominated wetlands (swamp forests), like those of the present day in south-eastern USA, dominated by Taxodiaceae (swamp cypresses), occurred in the Late Cretaceous and early Tertiary (Collinson 1990). In the Miocene the peat-forming habitats which produced the extensive European brown coals included several distinguishable modern subcommunities, such as *Taxodium* swamp, *Nyssa* swamp, and *Cyrilla* shrub (Collinson 2000). Herb-dominated wetlands, with many floral similarities to those of the southern USA today, are also documented in the latest Paleocene and Eocene. These are especially well known in the English Late Eocene and included modern wetland associations such as a *Typha* (Fig. 1.5.3.1c) and *Acrostichum* (bulrush and leather fern) marsh, as well as marginal, open-water rooted, and free-floating aquatics such as water lilies (Fig. 1.5.3.1e), pond weeds (Fig. 1.5.3.1f), water wheel (Fig. 1.5.3.1d), water soldier, bur read, arrowheads, sedges, and water ferns with distinctive subcommunities at different sites (Collinson and Hooker *in* Friis *et al.* 1987; Hooker *et al.* 1995).

Herb-dominated (non-aquatic) vegetation

Although early flowering plants are considered to have been herbs or shrubs (Wing and Boucher 1998), these were very different from modern examples like the grasses and meadowland herbs. Important groups of

flowering plant herbs, such as subclasses Liliidae (lilies), Asteridae (e.g. daisies), and Caryophyllidae (e.g. pinks), and also several groups of Dilleniidae (cresses, umbellifers), show evident diversification only in the late Neogene or later (Collinson *et al. in* Benton 1993; Collinson 2000). Herb-dominated vegetation is a Late Miocene to Pliocene or Pleistocene development. Boreal forests persisted in many areas (e.g. borders of the Arctic Ocean) until the Pleistocene; tundra and true open grassland probably never existed in the Neogene (see Section 1.5.1) (Wing 1998; Collinson 2000).

Overview

The rise of modern land biomes, dominated by flowering plants, mammals, birds, and insects, is essentially a Cenozoic phenomenon. Modern herbaceous vegetation (including grasslands), and modern low-diversity to monotypic, boreal, conifer forest (taiga), had their origins in the late Neogene or later. Neogene vegetation contained plant subcommunities which can still be recognized at the present day. Palaeogene vegetation, in contrast, often contained combinations of plant genera whose nearest living relatives are now segregated in different geographical areas, and/or have small relict distributions, due to later Cenozoic climate change (especially global cooling). An important Eocene vegetation, polar broadleaved deciduous forest, is now extinct but near relatives of its component plants survive (alongside other taxa) in modern, mid-latitude, deciduous forests. Eocene tropical forests and *Nypa*-dominated mangroves extended to around 55–65°N and S. The tropical forests shared many features with the vegetation of modern tropical rain forests, but differed in the apparent absence of flowering plant epiphytes and in the lack of some key plant taxa. Eocene *Nypa*-dominated mangroves, and freshwater wetland swamps and marshes, were very similar to comparable modern vegetation.

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1.5.4 Early Primates

K.D. ROSE

Introduction

Living primates include monkeys, apes, and humans (grouped as anthropoids), and their primitive cousins the lemurs, lorises, and tarsiers (prosimians). This arrangement is gradistic but only partly phylogenetic: Anthropoidea are considered monophyletic, whereas prosimians are not. Consequently, many authorities employ the cladistic terms Strepsirrhini for lemurs + lorises (= Lemuriformes), and Haplorhini for Tarsiiformes + Anthropoidea (Fig. 1.5.4.1). A sister-taxon relationship between tarsiers and anthropoids is supported by genetics, placentation, cranial anatomy, and other criteria (Martin 1993; Kay *et al.* 1997; Fleagle 1999). However, other evidence has been adduced that strepsirrhines might be closer to anthropoids (Fleagle 1999). The closest relative of Anthropoidea thus remains one of the most contentious issues in primate systematics.

Undoubted forerunners of living primates—the oldest known strepsirrhines and tarsiiforms—can be traced back to the beginning of the Eocene (55 Ma). Equivocal

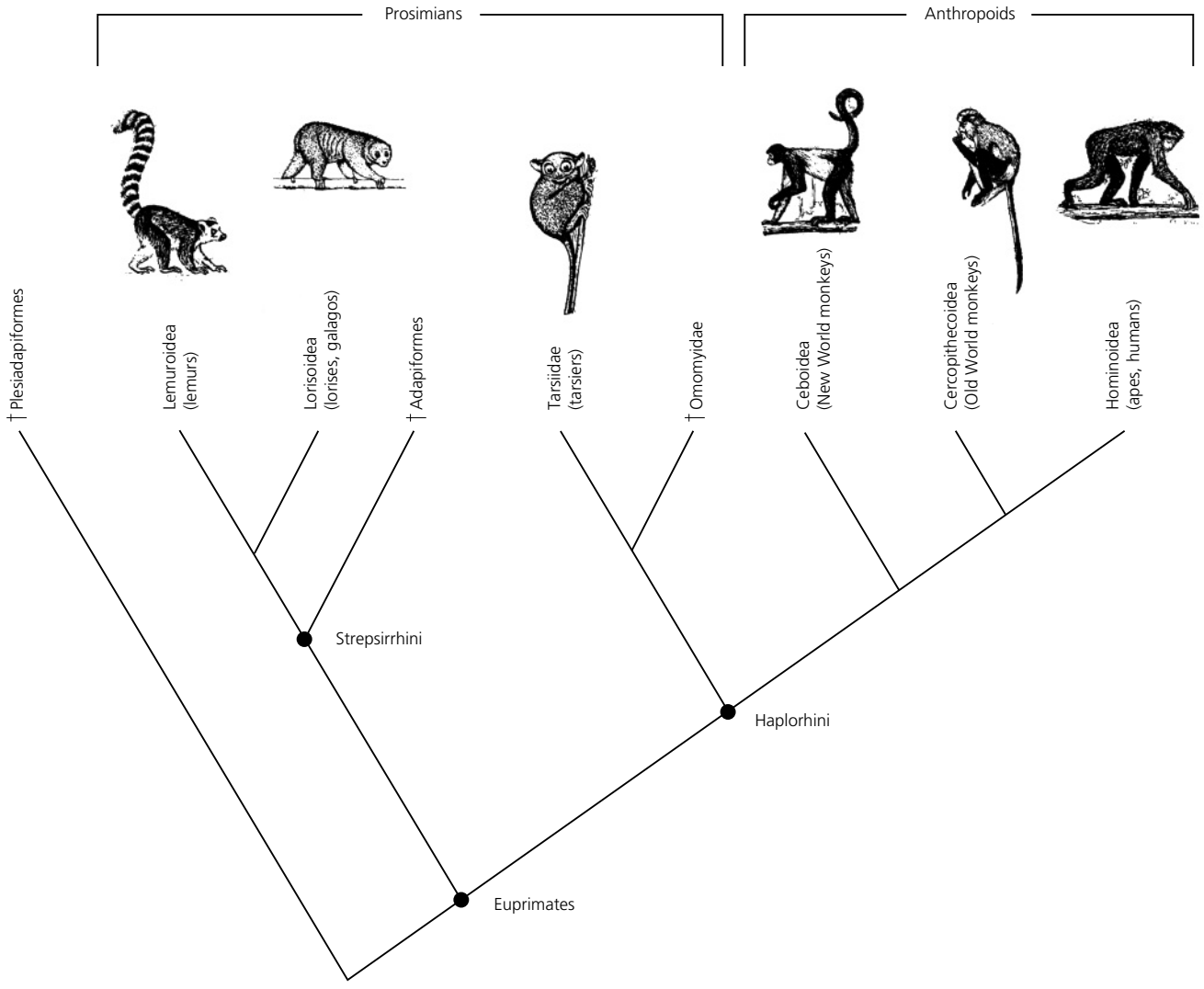


Fig. 1.5.4.1 Cladogram of relationships of the principal groups of living and extinct (†) primates.

primate relatives, comprising the order or suborder Plesiadapiformes, date back to the Early Paleocene (65 Ma).

Origin of Primates

Whether the order Primates is restricted to extant forms and their undisputed extinct relatives (= Euprimates), or encompasses Plesiadapiformes as well, the origin of the group is enigmatic. The oldest euprimates appear abruptly in the fossil record in basal Eocene deposits of North America and Europe (slightly later in Asia), with no clear indication of either their phylogenetic or geographical source. They seem to be part of an immigration event, also involving the ungulate orders Perissodactyla and Artiodactyla, that characterizes the Paleocene–Eocene boundary across Holarctica; but where these animals immigrated from is unknown. Because two euprimate clades are already present, a Paleocene or earlier origin of the order is indicated. Fragmentary dentitions of putative Late Paleocene euprimates are known from Morocco (*Altiatlasius*) and Mongolia (*Altanius*), but their relationships to other euprimates are controversial, and neither provides additional insight into euprimate origins (Rose 1995).

Early Eocene euprimates already possess anatomical traits diagnostic of living primates (Fig. 1.5.4.2b,c). The most important of these are a relatively large brain, a bony postorbital bar (a continuous bridge of bone around the lateral side of the eye socket), an auditory bulla (the thin, bubble-like, bony structure surrounding the middle ear cavity) composed of the petrosal bone, an opposable hallux (big toe), and digits with nails rather

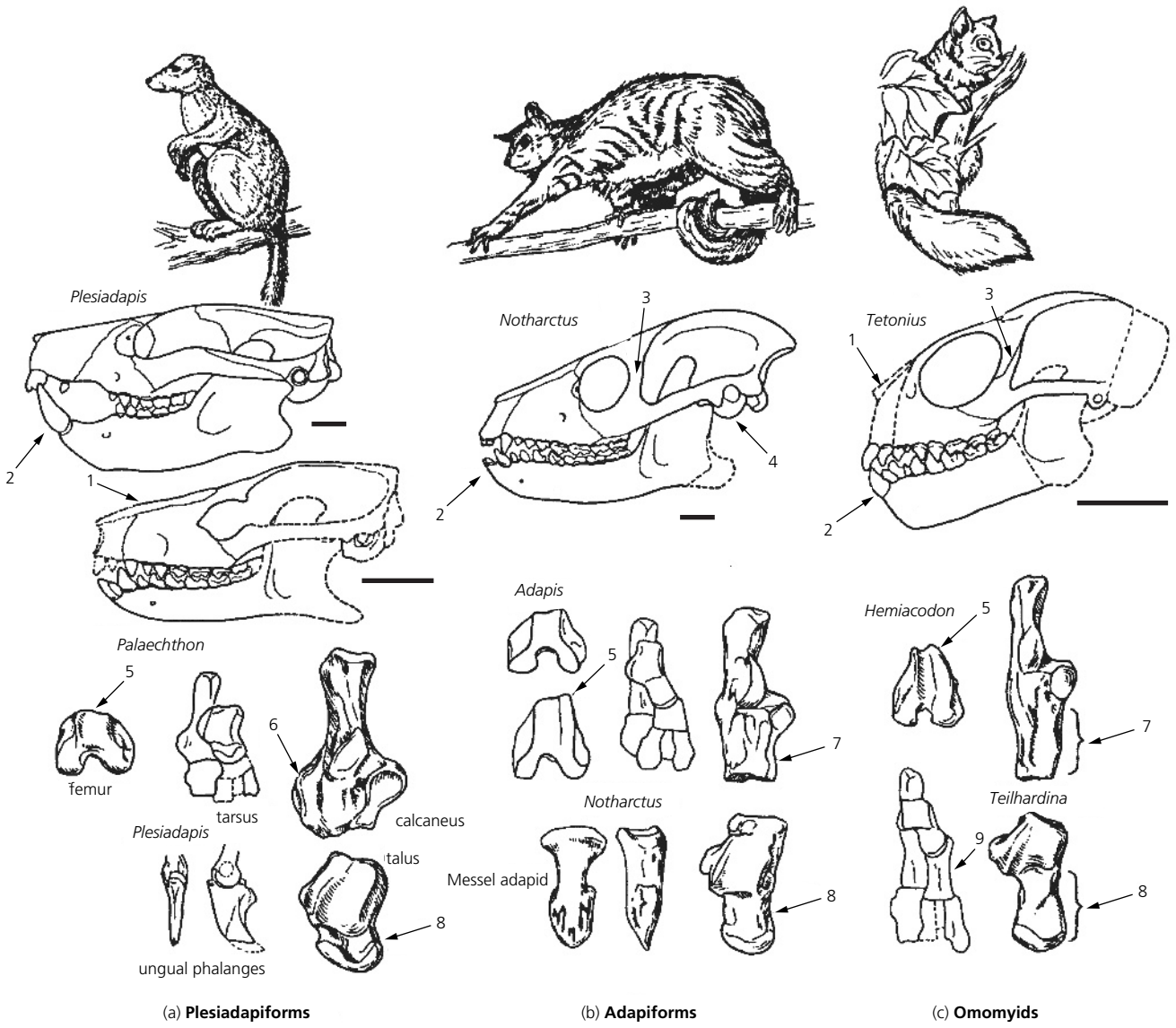


Fig. 1.5.4.2 Principal skeletal differences among: (a) plesiadapiforms; (b) adapiforms; and (c) omomyids. Lower drawings compare aspects of the distal femur, tarsus (ankle, with two ankle bones, the calcaneus and talus, enlarged), and ungual phalanges (terminal finger or toe bones, in dorsal and lateral view). Drawings in (a) are of *Plesiadapis*, except for lower skull (*Palaechthon*); those in (b) are mainly *Notharctus*, except for upper femur (*Adapis*) and ungual phalanges (unidentified adapid); in (c), skull and restoration represent *Tetonius*, lower left drawings are of *Hemiacodon*, and lower right drawings are of *Teilhardina*. Arrows highlight characteristics of each group: in the skull these include (1) snout length, (2) incisor size and form, (3) presence of postorbital bar, and (4) structure of auditory bulla; postcranial features include (5) configuration of patellar groove (the joint surface on the distal femur for the patella, or knee cap), (6) size of calcaneal peroneal tubercle (a bony process on the heel bone), and distal elongation of ankle bones, calcaneus (7), talus (8), and navicular (9). Scale bars for skulls = 1 cm. (From Rose 1995; reprinted by permission of Wiley-Liss, Inc., a subsidiary of John Wiley & Sons, Inc.)

than claws. These features probably arose as adaptations to arboreal life, and perhaps to visually orientated predation, but the exact explanation is not understood, and transitional stages that would document how they evolved from more generalized states are unknown.

The only Paleocene mammals that show modifications in the direction of primates are Plesiadapiformes, so-called 'archaic primates'. Plesiadapiforms have conventionally been included in Primates, usually as a suborder (Rose 1995; Fleagle 1999). Their precise relationship to euprimates is unknown, however, and some experts dispute any special relationship at all.

Postcranial specializations for arboreality and modifications of the molar dentition similar to those of Eocene euprimates are often cited as evidence of common ancestry. Undeniably derived dental resemblances do exist, including low cusps and trigonids (the anterior half of the lower molars, consisting of three cusps), broad basined talonids (the posterior half of lower molars), expanded lower third molars, and narrow stylar shelves (the region of the upper molars between the two main external cusps and the buccal border of the tooth). Functionally, this dental complex suggests a shift from insectivory to a more omnivorous or herbivorous diet. However, some of the closest dental similarities exist between plesiadapiforms and euprimates that cannot be directly related—an indication that these resemblances arose through evolutionary convergence. Furthermore, the oldest euprimates retain four lower premolars, whereas all except the two most primitive known plesiadapiforms (*Purgatorius* and *Anasazia*) have lost the first premolar. Thus only these two plesiadapiforms could be directly related to the origin of Euprimates. In addition, the fact that plesiadapiforms (Fig. 1.5.4.2a) lack many of the diagnostic traits of Euprimates (Fig. 1.5.4.2b,c) has led to an increasing rejection of their inclusion in Primates (Martin 1993).

The origin of Plesiadapiformes is also obscure, because most are known only from dentitions, and knowledge of potential Cretaceous precursors is so limited. Dental morphology suggests affinities with erinaceomorph insectivorans, which differ from other insectivores in having lower-crowned teeth with less acute cusps and broad talonid basins. Other anatomical evidence does not support this relationship, however, leaving the question of plesiadapiform origins unresolved.

Plesiadapiformes

Plesiadapiforms were mouse- to marmot-sized arboreal animals that were among the most successful Paleocene–Eocene mammals. They were especially common and diverse in western North America, and are also known from Eurasia. Plesiadapiforms occupied an ecological niche approximating to that of Eocene rodents and euprimates. All three groups coexisted in the Eocene, but plesiadapiforms were considerably less speciose and abundant then than during the Paleocene, a decline attributed to competition with rodents (Fleagle 1999).

Early Paleocene *Purgatorius* (Fig. 1.5.4.3a) from western North America is the oldest and most primitive plesiadapiform. Only its dentition is known, which resembles that of later plesiadapiforms in the characters listed earlier, except for having sharper cusps. The lower dental formula—3 incisors, 1 canine, 4 premolars, and 3 molars (abbreviated as 3-1-4-3)—is the most primitive known for Plesiadapiformes. (Almost all later plesiadapiforms lost at least one incisor and one premolar.) *Purgatorius* or a similar form probably lies near the ancestry of all other plesiadapiforms (Rose 1995; Fleagle 1999).

There are 10 families of plesiadapiforms, six of

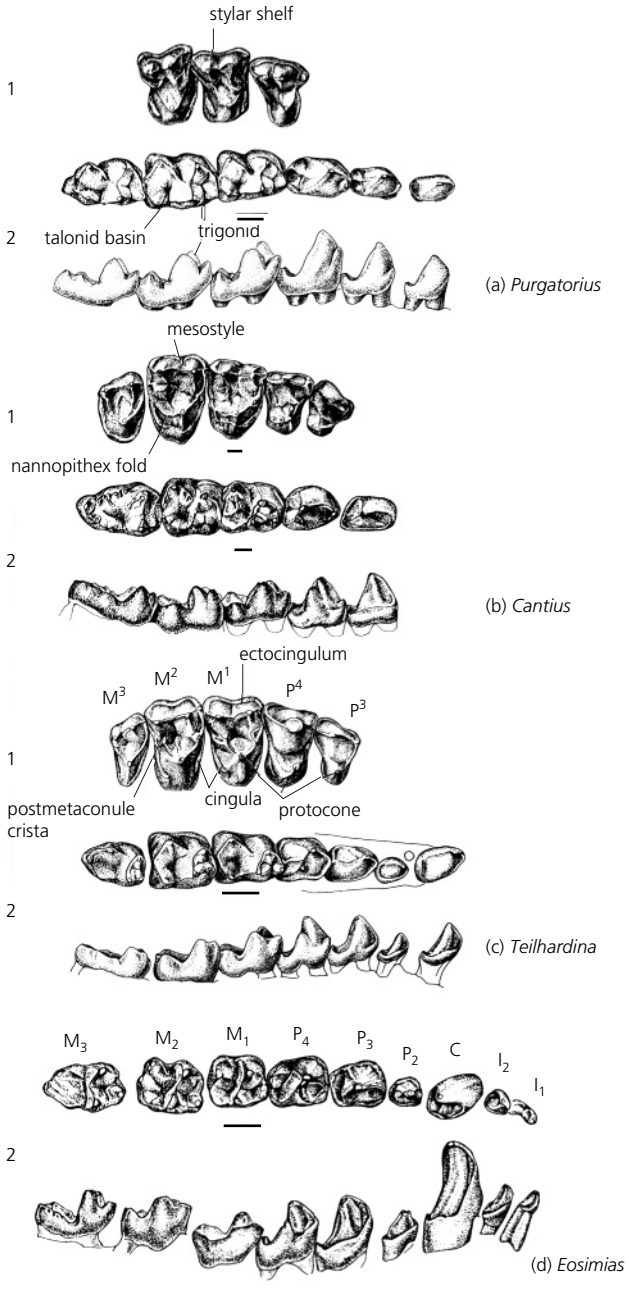


Fig. 1.5.4.3 Comparison of right upper (1) and left lower (2) dentitions of: (a) *Purgatorius* (plesiadapiform); (b) *Cantius* (adapiform); (c) *Teilhardina* (omomyid); and (d) *Eosimias* (anthropoid). Scale bars = 1 mm. (Modified from Rose 1995; reprinted by permission of Wiley-Liss, Inc., a subsidiary of John Wiley & Sons, Inc.)

which were established by the late Early Paleocene (Torrejonian North American Land-Mammal Age). Besides Purgatoriidae, they include Palaechthonidae, Plesiadapidae, Carpolestidae, Paromomyidae, and Picrodontidae. Four additional families appear in Late Paleocene or Early Eocene sediments: Saxonellidae, Micromomyidae, Microsyopidae, and Picromomyidae. Most of the more than 90 species and 40 genera are known solely or primarily from dentitions. Plesiadapiforms ranged in size from shrew-sized *Picromomys* (10 g) to marmot-sized larger species of *Plesiadapis* (3–5 kg).

The skull tends to have a long snout, laterally directed orbits, no postorbital bar, and a small braincase (Fig. 1.5.4.2a). Composition of the auditory bulla is difficult to establish with certainty, but in *Ignacius* (Paromomyidae) it seems to consist of the entotympanic bone, in contrast to the petrosal bulla of euprimates (Martin 1993). The endocranial arterial pattern also differs from that of the euprimates (and resembles that of Dermoptera) in lacking any significant blood supply from the internal carotid artery. Most plesiadapiforms had conservative molars and many had specialized antemolar dentitions. All had a pair of enlarged, procumbent (inclined) lower central incisors, which typically occluded with large, multipronged upper incisors. Parallel dental specializations were common. Reduction in the number or size of anterior teeth behind the incisor occurred in several lineages, and some (Plesiadapidae, Paromomyidae) developed an edentulous diastema (gap) between the incisor and posterior premolars. An enlarged, pointed, last lower premolar (P_4) evolved independently in paromomyids and micromomyids, and a bizarre, multicusped premolar blade arose separately in carpolestids (where it was P_4) and saxonellids (P_3). Sharp molar cusps and crests and the diminutive body size of some plesiadapiforms suggest they were insectivorous, whereas larger species (Plesiadapidae) have dental modifications indicative of omnivory or herbivory (including fruit and seed-eating). In other lineages (Paromomyidae, Picrodontidae, Picromomyidae), flatter molars coupled with procumbent incisors suggest gum feeding.

The postcranial skeleton is known in only three families (Plesiadapidae, Paromomyidae, and Micromomyidae), and only for *Plesiadapis* is it almost completely known. *Plesiadapis* had a relatively robust skeleton bearing the anatomical hallmarks of arboreal adaptation (strong crests and processes on limb elements, mobile elbow and ankle joints, sharp, laterally compressed claws). The lack of further specializations indicates that *Plesiadapis* was a non-acrobatic arboreal quadruped.

In contrast, paromomyids and micromomyids had more delicate limb bones with modifications of ankle, wrist, and digits that resemble those of living dermopterans and suggest the presence of a patagium, or gliding membrane. These and certain cranial features have been considered synapomorphies linking these families with Dermoptera (Beard 1993). This hypothesis has been challenged, however (see Martin 1993). Among conflicting evidence is the fact that paromomyid and micromomyid dentitions differ significantly from those of extant dermopterans. The controversy is likely to persist until there is more compelling evidence for or against a plesiadapiform–dermopteran relationship.

Euprimates

The oldest unequivocal primates appear suddenly at the beginning of the Eocene in Europe and North America. They already represent two major prosimian clades, Adapiformes and tarsiiform Omomyidae, which reflect the primary euprimate dichotomy into Strepsirrhini and Haplorhini (Fig. 1.5.4.1). Early euprimates were common mammals in Eocene assemblages. About 65 genera and 150 species of adapiforms and omomyids are currently recognized—triple the number of taxa of extant prosimians. Eocene euprimate lineages provide some of the best documentation known for gradual evolution (Rose 1995; Fleagle 1999).

Adapiformes

Among the best known of all fossil primates, adapiforms are represented by dozens of skulls, several nearly complete skeletons, and thousands of jaws. Anatomical evidence indicates that Adapiformes is the sister-group of living Strepsirrhini. Eocene representatives belong to two holarctic families: the lemur-like Notharctidae (best known from North America); and the somewhat lorislike (mainly European) Adapidae. Most of the more than 30 genera and 75 species of adapiforms are now regarded as notharctids, and European species outnumber North American ones; adapiforms are also known from Asia and North Africa (Godinot 1998).

Skeletons of notharctids, best known for North American *Notharctus* (Fig. 1.5.4.2b) and *Smilodectes* and European *Europolemur*, resemble in size and anatomy those of extant leaping arboreal lemurs. The hindlimbs were markedly longer than the forelimbs, the joints very flexible, and the feet adapted for grasping (with an opposable hallux and nails rather than claws). *Adapis* and *Leptadapis*, the best-known adapids, lack leaping specializations and instead show limb modifications that indicate either slow arboreal progression (like lorises) or perhaps quadrupedal running. The skull of most adapiforms was long-snouted, with small orbits, suggesting diurnal activity patterns. Short-snouted *Pronycticebus* had larger orbits, however, suggesting nocturnality (Godinot 1998). Some types were sexually dimorphic, judging by the strong sagittal crest and large canine teeth

of some specimens (presumably males). Most adapiforms weighed 1–5 kg, though some species were smaller than 100 g and others as large as 7 kg (Godinot 1998; Fleagle 1999).

European *Donrussellia* and Euramerican *Cantius* (Fig. 1.5.4.3b) are the most primitive known adapiforms. Like many other adapiforms, they retain a primitive dental formula (2-1-4-3). Adapiform molars had either low, rounded cusps adapted for frugivory, or sharp crests specialized for leaf-eating. Some small species had sharper cusps and must have been partly insectivorous. Adapiforms had small, vertical or somewhat inclined incisors and projecting canines (Fig. 1.5.4.2b; they lacked the lower toothcomb characteristic of living strepsirrhines.

Tarsiiformes

The Omomyidae, consisting of about 35 genera and 80 species, were the most successful and diverse radiation of tarsiiform primates. They are generally considered to be closely allied with, or ancestral to, Tarsiidae. Omomyids flourished in the Eocene and were most common and diverse in North America, but they also lived in Europe, Asia, and North Africa. Most omomyids were an order of magnitude smaller than contemporary adapiforms, weighing 100–500 g, but a few species reached 1–2 kg (Fleagle 1999).

The most primitive omomyids, Euramerican *Teilhardina* (Fig. 1.5.4.3c) and North American *Steinius*, had the same lower dental formula as in basal adapiforms (2-1-4-3), and the teeth show only subtle differences from those of *Donrussellia*, corroborating close common ancestry. Other omomyids lost at least the first premolar. Here, too, parallelism was common, and many lineages independently evolved enlarged, procumbent medial incisors, and tall, pointed lower fourth premolars. Based on small size and moderately sharp molar cusps, as in *Tarsius*, most omomyids are inferred to have been partly insectivorous. Some species probably also consumed gum, and larger species with more rounded cusps or crenulated enamel were presumably frugivorous or folivorous.

Although most omomyid species are represented only by dentitions, skulls are known for a few genera (*Tetonius*, *Shoshonius*, *Necrolemur*). They had short faces and distinctly larger orbits than adapiforms (but much smaller than *Tarsius*), suggesting nocturnality (Fig. 1.5.4.2c). Late Eocene *Rooneyia*, however, had relatively smaller orbits and was probably diurnal. The few known postcranial remains indicate that omomyids were active arboreal leapers with tarsal elongation comparable to that of living galagos, rather than the extreme elongation of *Tarsius* (Fig. 1.5.4.2c).

Two omomyid genera, *Necrolemur* and *Shoshonius*, have been considered particularly close to tarsiid origins, but dentitions recently discovered in China demonstrate that tarsiids very similar to extant *Tarsius* existed by Middle Eocene time (Beard *et al.* 1994). Hence Tarsiidae may be as ancient as Omomyidae and Adapiformes.

Origin of Anthropoidea

The source of Anthropoidea is an issue of intense debate, fuelled by exciting new fossil evidence from North Africa and China. Specialists are divided as to whether Anthropoidea are more closely related to Adapiformes or Tarsiiformes. Anatomical features can be cited in support of either argument, but a truly compelling case that would exclude one of these alternatives has yet to be made. It is also possible that anthropoids represent a third major clade tracing back to the origin of Primates. One conclusion that seems indisputable is that Anthropoidea evolved much earlier than previously thought.

The richest record of early anthropoids comes from Late Eocene–Early Oligocene deposits of Egypt, which have produced 10 genera of primitive anthropoids, including *Aegyptopithecus*, *Apidium*, and *Catopithecus* (Simons 1995; Fleagle 1999). Teeth, skulls, and postcranial skeletons confirm their anthropoid status, and also demonstrate that anatomical features diagnostic of Anthropoidea evolved in mosaic fashion. These early anthropoids were diurnal arboreal quadrupeds that fed on fruits and seeds. *Apidium* was also adapted for leaping (Simons 1995).

Discoveries in Algeria (*Algeripithecus*) and China (*Eosimias*, Fig. 1.5.4.3d) potentially push back the record of Anthropoidea 10 myr to at least the Middle Eocene (Martin 1993; Beard *et al.* 1994). Although these animals possess certain anthropoid features, they are decidedly more primitive in other traits. Confident assessment of their relationship to Anthropoidea must await more complete fossils; existing data suggest that *Eosimias* is the sister-taxon either of Anthropoidea or of Haplorhini.

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1.5.5 Hominid Evolution

B.A. WOOD

Introduction—Man's closest relatives

There is anatomical, molecular, and genetic evidence that the close relatives of modern humans are *Pan* (chimpanzee) and *Gorilla*. More detailed analyses of the DNA in both the nucleus and the mitochondria have revealed many similarities between the genomes of *Homo sapiens* and *Pan*, and an increasing number of researchers are convinced that *Homo* and *Pan* share a common ancestry to the exclusion of *Gorilla* (Ruvolo 1997). Most mutations are neutral, and if it is assumed that these neutral mutations have been occurring at the same rate in closely related lineages, then the degree of molecular difference can be used as a 'clock' to estimate the time elapsed since any two lineages separated. When this is done for the molecular differences between modern humans and the living African apes, it has been estimated that the human and chimpanzee lineages separated between 8 and 5 Ma (Fig. 1.5.5.1). Animals that are judged to be more closely related to modern humans than to the apes are called 'hominids'. What is known about the emergence and subsequent evolutionary history of this lineage?

Ancestral differences

The list of morphological differences between modern humans and the chimpanzee is an impressive one, but the differences between the earliest hominids and the Late Miocene ancestors of the living great apes are likely to have been a good deal more subtle. Those who study human evolution have to focus on the features that distinguish modern humans and the living apes and then trace these back into human prehistory. Some of these features, such as those linked with bipedalism, can be traced back a long way. Others, such as the relatively diminutive jaws and chewing teeth of modern humans, were acquired more recently, and thus cannot be used to discriminate between early hominids and potential ape ancestors. The presumption has been that ape ancestors will be quadrupeds with projecting faces accommodating elongated jaws, bearing relatively small chewing teeth and large, sexually dimorphic, canine teeth. Early hominids, on the other hand, will be distinguished by cranial and other skeletal adaptations to a predominantly upright posture, and skeletal and other adaptations for a locomotor strategy that includes substantial bouts of bipedalism, together with a masticatory apparatus which combines relatively large chewing teeth and modest-sized canines. However, these are hypotheses which may have to be revised as more fossil evidence is recovered from the 8–5 Ma interval.

Ardipithecus—the earliest hominid?

The hominoid fossil record for the period 8–5 Ma is poor, consisting of isolated specimens, most of which are too fragmentary to provide any reliable evidence about taxonomic affinity. The first creature with a more comprehensive fossil record, and which shows at least some rudimentary human specializations, is *Ardipithecus ramidus*, the 4.5 Ma remains of which were recovered at a site called Aramis, Ethiopia, in 1992 and thereafter. The fossils share some features with living species of *Pan*, others with the African apes in general, and, crucially, several features of the skull and teeth with later hominids. The material was initially allocated to an established genus, *Australopithecus*, but its describers have subsequently assigned it to a new genus, *Ardipithecus*. It is claimed (White *et al.* 1994) that the canines of *A. ramidus* are relatively larger, the crowns of the first deciduous molars are less complex, the articular eminence is flatter, the enamel is thinner, and that both the upper and the lower premolar crowns are more asymmetric, and thus more ape-like, than the equivalent morphology in *Australopithecus afarensis*, the taxon that was previously believed to have been the most primitive hominid. *Ardipithecus ramidus* should be excluded from the apes because of the relatively small upper central incisors, the lack of a well-defined canine honing mechanism, the broad mandibular molar crowns, and because the foramen magnum is situated too far anteriorly.

Judging from the size of the shoulder joint, *A. ramidus* weighed ≈ 40 kg. Its chewing teeth were relatively small and the position of the foramen magnum (the opening for the spinal cord) was close to the centre of the skull, suggesting that the posture and gait of *A. ramidus* were, respectively, more upright and bipedal than is the case in the living apes.

The context of *A. ramidus* suggests that the bones were buried close to, if not actually within, woodland. Neither the size of the brain, nor the nature of the posture and locomotion are yet known. The thin enamel covering on

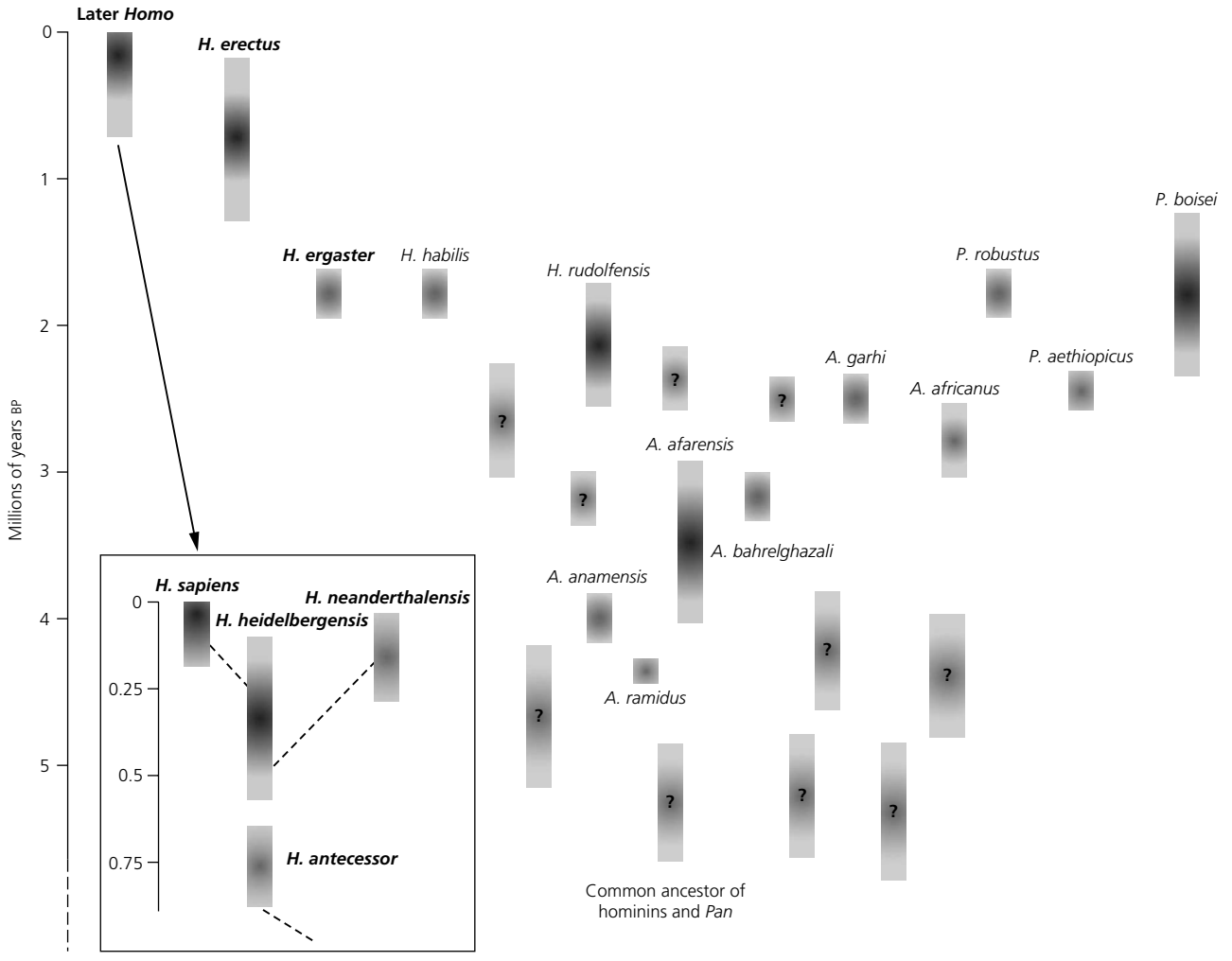


Fig. 1.5.5.1 Phylogram showing the species of hominids. Many now place these taxa in the tribe Hominini, instead of the family Hominidae (see Table 1.5.5.1). Thus the species are referred to as hominins, as opposed to chimpanzees and their direct ancestors, or panins. The horizontal axis spreads the species out according to the relative size of their chewing teeth and brain size; taxa with large molar and premolar crowns are to the right, and those with smaller postcanine teeth are to the left. Of the early taxa, the best evidence for brain enlargement comes from *Homo habilis*. The brain of *H. ergaster* (≈ 850 cm^3) is absolutely, but not relatively, larger than *H. habilis* (≈ 550 cm^3) because the former is estimated to have a larger body mass. Recently, it has been suggested that *H. habilis* and *H. rudolfensis* are more closely related to *Australopithecus* than to *Homo*, thus the genus *Homo* should probably be restricted to the taxa in **bold** type. The hypothetical taxa are a reminder that the period between 2 and 6 Ma is relatively poorly sampled, and that, if the experience of the Pleistocene is repeated, the numbers of species and genera will almost certainly increase. For generic abbreviations, see Table 1.5.5.1.

the teeth suggests that the diet of *A. ramidus* may have been closer to that of the chimpanzee than is the case with any of the other early hominids.

Australopithecus

Approximately half a million years later in time, also from east African sites, there is much better preserved evidence of another primitive hominid, *Australopithecus afarensis*. This was the name given in 1978 to hominid fossils recovered from Laetoli, in Tanzania, and from the Ethiopian site of Hadar. Since then further evidence of *A. afarensis* has been found at other localities in Ethiopia, and in Kenya. The majority of this evidence is dated to between 4 and 3 Ma.

The fossil record of *A. afarensis* includes a well-preserved skull, substantial portions of several others, many lower jaws and limb bones, as well as just less than half of an adult female skeleton. The picture that emerges is of a species that ranged in body mass from about 25 kg for a small female, to more than 50 kg for a large male. This is a substantial size range for an animal

so small, and some workers have revived the suggestion that *A. afarensis* may consist of the remains of more than one species of early hominid.

The brain volume of *A. afarensis* was between 400 and 500 cm^3, but relative to its estimated body mass the brain is no larger than that of the chimpanzee. However, the chewing teeth—the premolars and molars—are relatively larger than those of the contemporary apes.

Reconstructions of the habitat of *A. afarensis* suggest that it lived in an 'open' woodland environment. The appearance of the pelvis and the lower limb suggests that, although *A. afarensis* was capable of bipedal walking, it was not adapted for long-range bipedalism. This indirect evidence for the locomotion of *A. afarensis* is complemented by the discovery, at Laetoli, of several trails of fossil footprints. These provide direct evidence that *A. afarensis* was capable of bipedal locomotion. The size of the footprints and the length of the stride provide corroboration for estimates of stature derived from the limb bones of *A. afarensis*. These suggest that its standing height was between 1 and 1.5 m.

Fossils dating to between 4 and 4.5 Ma have been found at Kanapoi in northern Kenya. In some ways these resemble *A. afarensis*, but in others they are more primitive, and they have been placed in a separate species, *Australopithecus anamensis*. A third species, *Australopithecus bahrelghazali*, was introduced for 3.5 Ma hominid remains from Chad, in north central Africa, and the most recent evidence for *Australopithecus* in east Africa are the 2.5 Ma remains of *A. garhi* (Asfaw *et al.* 1999).

Discoveries in southern Africa

Nearly 50 years before the discovery of *A. afarensis*, a child's skull was found in 1924 at the Buxton Limeworks in Taung, southern Africa. The exact geological age of the find was not known, but it was more primitive than any of the hominid remains that had been recovered previously in Europe, Java, or China. In 1925 the new hominid was named *Australopithecus africanus*, which literally means the 'southern ape' of Africa.

Since the Taung discovery, the remains of *A. africanus* have been found at other cave sites in southern Africa, at Makapansgat and Gladysvale, but at present these sites can only be dated by comparing the remains of the mammals found in the caves with the mammalian fossils found at the better-dated sites in east Africa. In this way the *A. africanus*-bearing cave breccias have been estimated to be between 2.4 and 3 Ma.

Males and females of *A. africanus* probably did not differ in body size to the degree they did in *A. afarensis*. The physique of *A. africanus* was much like that of *A. afarensis*, except that its chewing teeth were larger and the skull was not as ape-like. The brain was larger than that of *A. afarensis* and the postcranial skeleton suggests that, although *A. africanus* was capable of walking bipedally, such a gait would have been relatively inefficient. The other animal remains found with *A. africanus* suggest that its habitat was a combination of grassland and trees, comparable to modern open 'bushland'.

Paranthropus—a genus of large-toothed hominids

Just as there are east and southern African regional variants of *Australopithecus*, there are two regional variants of another hominid genus called *Paranthropus*. They are often referred to as 'robust' australopiths because they have more massive faces and lower jaws than *Australopithecus* species.

Remains of the southern variety, *Paranthropus robustus*, come from caves at Swartkrans, Kromdraai, Gondolin, and Drimolen and are dated to between 2 and 1.5 Ma. The face and chewing teeth are larger than those of *A. africanus*, yet the incisor teeth are smaller, suggesting that there were dietary differences. What little is known of the postcranial skeleton suggests that it was similar to *A. africanus*. Some workers point to differences between the fossils from Swartkrans and Kromdraai, and allocate the former material to a separate species, *Paranthropus crassidens*.

The east African 'species' of *Paranthropus* probably consists of not one but two species (Table 1.5.5.1). Both have large jaws and large chewing teeth, and the later species is very sexually dimorphic; the earlier species dates from 2.5 to 2.3 Ma, and the later one between 2.3 and 1.4 Ma. The earlier and more primitive species, *Paranthropus aethiopicus*, is known from a handful of specimens including a well-preserved cranium. It has a smaller brain, around 400–450 cm^3, a more ape-like face, and larger anterior teeth than does the later species, *Paranthropus boisei*. The type specimen of *P. boisei* is the OH 5 cranium; it was originally referred to the genus *Zinjanthropus*. The relatively large chewing teeth in the two species have prompted the suggestion that they were specialist feeders on a diet that required heavy mastication. What little information there is about their postcranial skeleton suggests that it was much like that of *Australopithecus*.

The inclusion of the one southern African and two east African 'robust' species in the same genus, *Paranthropus*, reflects the consensus that they resemble each other because they inherited their wide face, large jaws, and large chewing teeth from a common ancestor. What prompted the appearance of these large-toothed creatures first in east Africa, and then in southern Africa? Some palaeontologists point to analogous changes occurring in the masticatory apparatus of other large mammals, and have suggested that the common 'cause' may be a general shift to a drier climate that occurred

between 3 and 2 Ma. This 'climatic' explanation has been linked to a global cooling phenomenon, superimposed on the effects of 'local' uplift of the land surface in the two regions (Partridge *et al.* 1995).

Table 1.5.5.1 Classification of fossil hominids. There is no 'official' hominid taxonomy. Some researchers prefer to recognize more, rather than fewer, species. Other researchers set their species boundaries at a higher level of variation; these interpretations would not recognize the species marked in **bold** type. The genera, and the species names within each genus, are listed in order of their publication. Species not in their original genus are marked with an asterisk. Traditional classifications of the higher primates place the non-human taxa in the family Pongidae, and modern humans and their ancestors in a second family, the Hominidae. Hence apes were referred to as 'pongids', and humans and their ancestors as 'hominids'. Given the compelling molecular evidence that chimpanzees are more closely related to modern humans than they are to gorillas, a new classification was required that interprets Hominidae more inclusively. In one version of such a classification, the orangutan and gorilla both have their own subfamily, Ponginae and Gorillinae. Modern humans and chimpanzees make up a third subfamily, Homininae, that consists of two tribes, Panini for the chimpanzees, and Hominini for modern humans and their ancestors. Hominini is divided into two subtribes, Australopithecina and Hominina, the details of which are given below. In this scheme the taxa we now refer to as hominids would be 'hominins'.

Hominoidea
- Hominidae
  - Hominini
    - Australopithecina
      - *Australopithecus*
        - ***A. afarensis***
        - *A. africanus*
        - ***A. anamensis***
        - ***A. bahrelghazali***
        - *A. garhi*
      - *Paranthropus*
        - *P. robustus*
        - *P. boisei**
        - ***P. aethiopicus****
      - *Ardipithecus*
        - *A. ramidus*
    - Hominina
      - *Homo*
        - *H. sapiens*
        - ***H. neanderthalensis***
        - *H. erectus*
        - ***H. heidelbergensis***
        - *H. habilis*
        - ***H. ergaster***
        - ***H. rudolfensis****
        - ***H. antecessor***

Early *Homo*, or its precursors?

When Louis and Mary Leakey discovered the OH 5 cranium at Olduvai Gorge in 1959, it was perhaps natural to assume that hominids like OH 5 made the stone tools found in the same sediments, but discoveries made in the same year, and in the 1960s, challenged this assumption.

The new material included parts of the vault, or roof, of a skull, a fragment of lower jaw, and parts of a hand, foot, and lower leg. Although these specimens are fragmentary, researchers were convinced that the larger cranial capacity, smaller tooth size, and what were interpreted as advanced features of the limb bones made this hominid a stronger contender for the role of toolmaker than OH 5. Therefore, Louis Leakey and colleagues proposed that the new material be included within the genus *Homo*, as a new species, *Homo habilis*, which means 'handy man', or 'maker of the tools'. They justified the inclusion of *H. habilis* in *Homo* because, they claimed, it departed significantly from the morphology of *Australopithecus* and *Paranthropus* in the direction of later *Homo*. That consensus has since broken down in the face of convincing demonstrations that the cranium and postcranial skeleton are less human-like than the original researchers had concluded.

Specimens resembling the Olduvai *H. habilis* remains have since been recovered from the site of Koobi Fora, in northern Kenya. As this evidence accumulated, it became apparent that *H. habilis* was more variable than would be expected for a single species. This led to the proposal that part of the *H. habilis sensu lato* hypodigm belonged to a second species of 'early *Homo*', and this was called *Homo rudolfensis* (Wood 1992).

Present evidence suggests that *H. habilis sensu stricto* dates from just less than 2 Ma to around 1.6 Ma, whereas *H. rudolfensis* dates from perhaps as early as 2.5 Ma to 1.8 Ma. In the two 'early *Homo*' species the opening for the spinal cord is closer to the middle of the skull, and compared with *Australopithecus* the skull base is reduced in length and increased in width. The two 'early *Homo*' species differ in the form of the face. In *H. habilis sensu stricto* the face is reduced in width and the opening of the nose is sharply defined. The brain volume of *H. habilis* is around 500–700 cm^3, whereas the estimated brain volume for *H. rudolfensis* is in the order of 700–800 cm^3, with an average of 750 cm^3.

Overall, the case for including *H. habilis sensu stricto* and *H. rudolfensis* within *Homo* has weakened since *H. habilis* was first announced. However, by around 1.9 Ma there is good evidence from East Africa of an early hominid that is a much stronger candidate for inclusion in *Homo* (Wood and Collard 1999).

Homo emerges in Africa

The painstaking excavation of a juvenile male skeleton, KNM-WT 15000, from one-and-a-half million years old sediments at West Turkana (Brown *et al.* 1985), had a significant effect on the interpretation of the early stages of the genus *Homo*. Over the previous decade, similar-looking skulls, jaws, and limb bones had been recovered from Koobi Fora, on the east side of Lake Turkana (Wood 1991). Although they resembled *Homo erectus* remains from Asia and elsewhere in Africa (see below), it was not until the discovery of KNM-WT 15000 that their affinities with each other and with *H. erectus* could be confirmed. Although the age of the West Turkana skeleton is ≈1.5 Ma, other remains attributed to the same species are as old as 1.9 Ma. Some workers have given the species a new name, *Homo ergaster*, while others refer to it as 'early African' *H. erectus*. Why are researchers more confident that these remains should be included in the genus *Homo*?

Homo sapiens differs from *Ardipithecus*, *Australopithecus*, and *Paranthropus* in four main ways. First, our brains are larger, both in absolute size and when they are related to the size of the body. Second, our jaws and teeth are generally smaller when related to body mass. Third, while it is apparent that the early hominids were capable of standing and even walking bipedally, the shape of their skeleton suggests that they could also still climb using all four limbs; they were not committed to bipedalism. Modern humans, on the other hand, only move from one place to another on all fours in childhood; adult modern humans are not only habitually upright in their posture, but they can only cover distances effectively if they are bipedal. The fourth distinction between modern humans and the early hominids, and particularly *Australopithecus*, is that whereas the early hominids and the apes accomplish their development relatively quickly, modern human infants are relatively helpless for longer, their locomotor skills take longer to acquire, and their molar teeth erupt later. This prolonged period of dependence, together with improved dexterity, is believed to have been important for the transfer of complex skills.

The remains of *H. ergaster*, or 'early African' *H. erectus*, satisfy most of these criteria. The lengths of the long bones of the skeleton from West Turkana confirm that this hominid species had a body shape and limb proportions more like those of modern humans. When the jaws and teeth of *H. ergaster* are related to body mass, they are no larger than those of African and Australian samples of modern humans. Likewise, the timing and pattern of tooth development in *H. ergaster* is much closer to that in modern humans than is the case for any of the other early hominid species. The cranial capacity of *H. ergaster*, between 800 and 900 cm^3, is greater than that of *H. rudolfensis*, but its relative size compared to body mass is similar.

Thus, the overall body plan of *H. ergaster* shows clear and strong links with modern humans. These resemblances are sufficient evidence to make *H. ergaster*, or 'early African' *H. erectus*, the first and earliest species which can confidently be placed within *Homo* (Wood and Collard 1999).

Homo expands beyond Africa

The first hominid species for which there is compelling evidence outside Africa is *Homo erectus*. More than a century ago Eugene Dubois reported the discovery of a skull and femur on the bank of the Solo River, at Trinil, in what is now Indonesia. Since then, similar-looking remains have been located elsewhere in Indonesia, mainly from the Sangiran region where the Solo River cuts through Pliocene and Pleistocene sediments.

Due to intensive cultivation, the exact location of many of the finds is difficult to pinpoint, and the paucity of volcanic ash and the weakness of the magnetic signals in the sediments means that accurate dating is difficult. There is, however, evidence that some of the finds at Sangiran may be around 1 Ma, and fossils from at least one of the sites may be ≈ 1.8 Ma (Swisher *et al.* 1994). The first hominids must have left Africa before this, and the first species to do so was likely to have been a *H. ergaster*-like hominid, or a more primitive precursor.

What prompted this first exodus from Africa? The larger bodies of *H. ergaster* would have provided improved tolerance to heat stress and to dehydration, and the more sophisticated stone 'tool kits' that make their first appearance around 1.7 Ma may have contributed to the ability to tolerate a wider range of landscapes and climates. There is archaeological evidence that hominids had occupied Europe and the Near East by just less than one million years ago, and perhaps as early as 1.6 Ma, and at the southern African site of Swartkrans there is evidence of an 'early *Homo*'-like hominid at ≈ 1.5 Ma. Remains of *H. erectus* persist in the Far East, at the Chinese site of Zhoukoudian (formerly Choukoutien) near to Beijing, as late as 200 Ka. Thus, *H. erectus* remained in at least one region while hominids closer in appearance to modern humans were making their appearance in other parts of the world.

Precursors of modern humans

There is no designated type specimen of *H. sapiens*, and because it is a 'polytypic' species (i.e. it incorporates a relatively large range of variation), a spectrum of skull shapes and limb proportions have to be taken into account when considering whether fossils can be

assigned to *H. sapiens*. However, the variation is not random, and a good deal of it is related to climate. For example, modern human populations follow Allen's Rule which stipulates that populations in warmer climes will have longer extremities, while those in colder climates will have shorter, stockier limbs. Head shape responds in the same way, with long heads linked to warm climates, and round heads and larger noses more common in colder climates. Thus, some of the morphological characteristics of 'anatomically modern' *H. sapiens* differ according to the predominant climate.

However, there are fossils which are more modern human-like than *H. erectus*, yet not fully modern in appearance. Such material is known from Africa (at Ndutu and Kabwe, for example), Europe (at Mauer and Arago), and China (at Dali and Jinnuishan). Perhaps the best-known material in this 'archaic *Homo*' category are the remains which have been attributed to *Homo neanderthalensis* (see Section 1.5.6). This species has a characteristic appearance which includes a large, globular-shaped cranium, jaws and teeth which are set well forward in the face, particularly robust limb bones with large joint surfaces, and DNA that is distinct from modern *H. sapiens* (Krings *et al.* 1997). There is soundly dated fossil evidence for specialized Neandertals by ≈ 125 Ka, and fossil evidence from sites in France and Germany (Biache and Ehringsdorf) may confirm the presence of Neandertals as early as 200 Ka. However, some of these Neandertal specializations can be seen in fossils from the Spanish site of Sima de los Huesos that date from ≈ 300–400 Ka, and researchers have even suggested that Neandertal-like morphology can be detected in the collection of fossils from the Gran Dolina, also in Spain, that dates from ≈ 700–800 Ka. The geologically most recent Neandertals are dated to ≈ 27 Ka.

Neandertals are confined to Western Europe, the Near East, and adjacent parts of Asia. For much of this period the climate in Europe oscillated between cold, glacial phases and shorter, warmer, interglacial periods. The short stature and robust limb bones of the Neandertals are the body shape predicted in colder regions by Allen's Rule.

Populations of 'archaic *H. sapiens*' peoples from other regions are not so characteristic in their appearance, but all have some distinguishing features. The ones from Europe, and adjacent areas, have been assigned to their own species, *Homo heidelbergensis* (Rightmire 1998). There is less of a consensus about the taxonomy of the archaic *Homo* remains from Africa. It is the extent to which regional characteristics persisted in modern populations that lies at the root of debates about the origin of anatomically modern humans.

Modern human origins

There are two competing hypotheses for the origins of modern humans. One, the 'out of Africa' or 'Noah's Ark' hypothesis, suggests that the genetic modifications that were responsible for the shift from an archaic to an anatomically modern morphology occurred only once, and in Africa. The rival 'multiregional' hypothesis proposes that the shift to an anatomically modern human morphology occurred several times, but only once in each region. A modification of these main hypotheses allows for gene flow between the regions, but maintains that it was not sufficient to obscure regionally distinctive morphologies (Brauer 1992).

Evidence about modern human origins comes from the fossil record, and the pattern of modern human variation. The 'out of Africa' hypothesis predicts that adaptively neutral variation in the genotype would be greatest in Africa, where modern human populations have existed for the longest time. Analysis of the variation in mitochondrial DNA, the Y chromosome, and in other systems suggests that this is the case. However, there are explanations other than the antiquity of the regional gene pool, such as drastic reductions in population size and geographical restrictions on the exchange of genes between Africa and the rest of the world, for these results.

The earliest fossil evidence of hominids with a skull, jaws, teeth, and limb bones equivalent to those of contemporary humans comes from Africa. Remains from Klasies River Mouth, southern Africa, from the Omo in Ethiopia, from Lake Turkana in Kenya, and from the Skhul and Qafzeh caves in the Near East all date to ≈ 100 Ka and earlier. However, while this evidence is consistent with the 'out of Africa' hypothesis, it does not 'prove' it. Some regions do not have fossils of this antiquity so that their 'modernity', or lack of it, cannot be judged. The old adage 'absence of evidence is not evidence of absence' means that, while the case for an African origin for early modern humans is a strong one, it is as yet unproven.

Peopling the planet

Anatomically modern humans were dispersed across the Old World by 25–35 Ka. By that time, and perhaps as early as 50–60 Ka, they had also managed to cross from the Asian mainland to Australasia. Reductions in sea level during times of maximum glaciation would have shortened any sea crossings, but the colonizers of Australia must have been able to make a raft, or its equivalent. Archaeological evidence suggests that the occupation of the New World did not take place until 10–12 Ka. Modern humans could have entered the New World across the land bridge that was established

between Siberia and Alaska around 70–20 Ka, but the earliest archaeological evidence of modern human occupation of Siberia dates from just 20–30 Ka. A provocative recent theory suggests that at least one early (≈ 10–12 Ka) ingress of modern humans may have been via the Atlantic to the Eastern seaboard. This suggests that despite the presence of the land bridge, the inclement climate of the latest ice age deterred potential migrants until the climate warmed around 15–13 Ka. Thus by ≈ 13 Ka all the major land masses, except Antarctica, had been populated by *Homo sapiens*.

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1.5.6 Neandertals

L.C. AIELLO

Introduction

The Neandertals are arguably the best-known members of the human evolutionary tree. There are a number of reasons for this. They were the first hominids to bury their dead; burial protects remains from scavengers and the Neandertals are among the first of the early human ancestors for whom relatively good samples of articulated skeletons from individuals of all ages are known. Secondly, Neandertals lived quite recently in time; they first appeared as a species distinct from earlier ancestors at about 125 Ka and did not disappear from the fossil record until ≈ 27 Ka. They also occupied Europe and adjacent areas of Eurasia; as a result, their remains were the first to be found and recognized as human ancestors by European scientists who had been stimulated by the Darwinian revolution in the second half of the nineteenth century.

Who were the Neandertals?

The first two Neandertals found (Engis, Belgium 1829; Gibraltar 1848) remained unrecognized as early humans until after the discovery of the well-known Neandertal skeleton in the Neander Valley (Germany 1856). These early finds were followed by others at La Naulette (1866) and Spy (1886), both in Belgium, and a plethora of material from the Dordogne region of southern France (e.g. La Chapelle-aux-Saint 1908; La Ferrassie 1909–10; La Quina 1908–20; Le Moustier 1908, 1914). Throughout this time, Neandertals were characterized as brutish, with a stooped posture and habitually bent knees.

Neandertals are now known to be much more modern in their body form and behaviour than was first appreciated. The bodies of Neandertals were short, stocky, and robust and have their closest analogue among living peoples such as the Inuit who are physically adapted to living under arctic conditions. Like these living peoples, the Neandertals had relatively short distal extremities (lower legs and lower arms) and relatively wide bodies that serve to maximize internal body volume in relation to surface area, and therefore conserve body heat. This cold-adapted body form may have evolved during Oxygen Isotope Stage 6, the long period traditionally known as the Riss Glaciation (≈186–128 Ka). Probable ancestors of the Neandertals living in Europe, such as Boxgrove (England, 500 Ka) and Sima de los Huesos (Atapuerca, Spain, ≈ 300 Ka), were bigger, although still very robust people (Stringer *et al.* 1998).

Neandertals were not just modern humans adapted to a cold climate. They had wider bodies than today's cold-adapted people and weighed 10% or so more than modern people of equivalent stature. Consistent with their wide bodies were very wide and robust pelves, with unusually shaped, long, and narrow superior pubic rami (bones that form the front of the pelvis). They also had long collar bones, unusually proportioned fingers and toes, extremely robust extremities, and scapulae with details that indicate upper arm strength and shoulder stability. This must reflect adaptively important differences to modern humans in mobility, upper limb loading intensity, and behavioural patterns. Neandertals also had unusually thick cortical bone throughout the skeleton, but particularly in their arms.

The craniofacial skeletons of Neandertals were also unique (Fig. 1.5.6.1). Their faces were very large, with cavernous noses and eye orbits. They had a marked degree of midfacial prognathism, with an associated swept-back, streamlined cheek morphology, a long and relatively flat cranial base, and an elongated foramen magnum. The rear of the skull protruded in an occipital bun. They had large brain sizes that, in absolute terms, exceed the average of modern humans. In relation to inferred body mass, however, their relative brain sizes were marginally lower than those found in modern humans (Ruff *et al.* 1997).

Neandertal adaptation

Some of the Neandertal morphology may have been a direct consequence of living in cold conditions (Churchill 1998). One hypothesis suggests that their short and squat bodies were the result of an endocrine shift during ontogeny, where heightened levels of androgens promoted rapid somatic growth, muscle development, and early closure of the epiphyses (termination of long bone growth), resulting in a short and stocky body. High levels of androgens could also be related to general bone thickness, browridge, nasal, alveolar, and sinus development, and molar taurdontism (a characteristic expansion of the pulp cavities in the molar teeth). Selection may also have favoured large and robust babies, able to withstand the relatively cold conditions. Accelerated growth in the cartilaginous precursors of bone, particularly in the cranial base, during late fetal development could have contributed to the unusual cranial morphology of Neandertals (Smith 1991). This accelerated development is also consistent with other evidence suggesting that dental and brain development was marginally more rapid in Neandertals than in modern European children (Stringer *et al.* 1990).

Other early hominids share some of the robusticity of Neandertals, suggesting that at least some unique features of Neandertal morphology may have more complicated causes than a simple endocrine adjustment to cold weather conditions. Neandertal upper limb robusticity, as well as features such as the orientation of their joints, might reflect the need for strength and endurance under difficult foraging circumstances. This is consistent with the fact that the Mousterian tool industry, with which the majority of the Neandertals are associated, implies: (1) close-contact hunting using short-range weapons; and (2) high reaction forces in the upper limb during, for example, flint knapping, woodworking, and other subsistence activities.

There is considerable evidence for a difficult and strenuous Neandertal life. Age at death suggests not only a high level of mortality at all ages but also a particularly high level of mortality among young adults. There

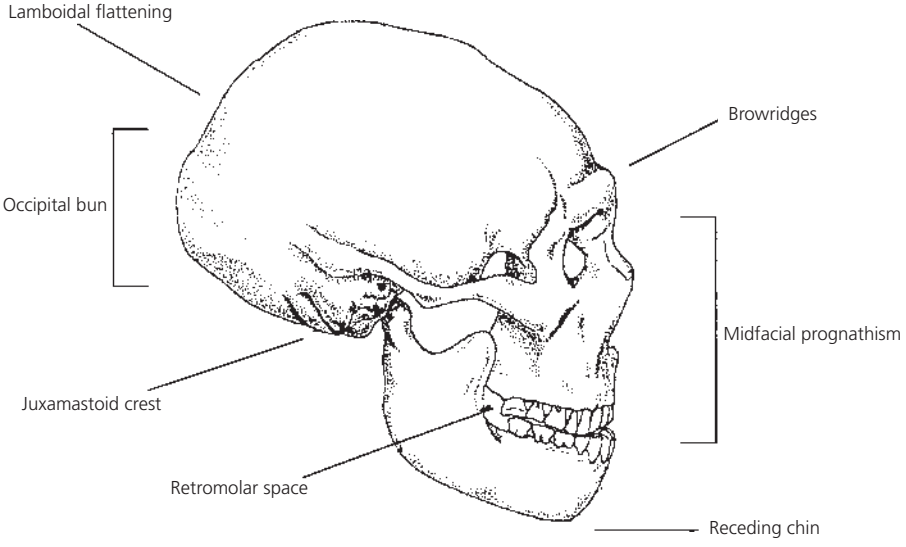


Fig. 1.5.6.1 Reconstruction of Neandertal skull from Shanidar, Iraq, illustrating some characteristic cranial features.

are high levels of enamel hypoplasia (malformation of dental enamel) that seem to indicate particular stress around the time of weaning. The great majority of adult Neandertal skeletons also show indications of trauma and/or infection.

Neandertal cognitive abilities

There is debate over the cognitive abilities of the Neandertals. Some archaeologists suggest that Neandertals lacked concern for the visual appearance of the tools they made. This is because the Mousterian tools seem to grade into one another without clear-cut typological divisions (Mellars 1998). This lack of patterning in the stone tools might suggest that Neandertals lacked a highly structured vocabulary for the different artefact types. The absence of complexity in many aspects of Neandertal culture also suggests that they may have had limited capacity to organize and structure their activities. This contrasts with the Upper Palaeolithic cultures of anatomically modern humans who entered Europe ≈ 40 Ka. The greater degree of both chronological and spatial variation in technology associated with these modern humans suggests that they might also have had more sharply defined ethnic divisions. This contrast between the Neandertal Mousterian culture and the modern human Upper Palaeolithic cultures may also reflect fundamental linguistic differences; language is used to transmit tightly defined rules of complex behaviour and is a catalyst to the emergence of sharply defined cultural traditions.

The suggestion that the Neandertals may not have had a system of vocal communication characterized by any or all of the symbolic and syntactic features which define modern human language is surprising in the context of other evidence. Neandertals had large and energetically expensive brains and also would have had a vocal apparatus entirely compatible with the production of the full range of human speech sounds (Aiello 1998). Toward the end of their known existence (≈30–36 Ka), Neandertals in France are found with the more advanced Chatelperronian culture (at Arcy-sur-Cure and St Cesaire) characterized by simple bone tools, red ochre, perforated animal teeth, and other forms of personal decoration, in addition to more elaborate stone tools. These cultural aspects are otherwise associated only with anatomically modern humans. It is a matter of debate whether the Neandertals copied these traits from contemporary modern human populations or invented them independently as these populations were entering and dispersing across Europe (d'Errico *et al.* 1998).

This is all the more interesting because the last surviving Neandertals apparently occupied the Iberian peninsula south of the Ebro river for at least 5000–10 000 years after the arrival of modern populations in the adjacent parts of northern Spain and the Mediterranean coast, at ≈ 40 Ka. These isolated, remnant Neandertal populations show no indication of the more elaborate cultural elements found in the Chatelperronian sites further north.

The apparent difference between the archaeological remains of Neandertals and anatomically modern humans, and the complexities surrounding their inferred linguistic and cognitive abilities, are particularly relevant in the context of mitochondrial DNA evidence (Krings *et al.* 1997). This suggests that Neandertals are genetically distinct from all modern humans and that the two lineages had separate evolutionary histories for about 500 kyr. This would have been sufficient time to allow different cognitive processes, possibly including language, to develop in both lineages.

The question of differences in Neandertal cognitive abilities remains unanswered. The best evidence to date suggests that modern humans had arrived in the Near East by ≈ 100 Ka but penetrated no further north or west at this time. Like the Neandertals, these early modern people used Mousterian tools and may simply not have had the behavioural sophistication to compete with the Neandertals, who were biologically adapted to the ice-age conditions of Europe. In fact, these early moderns disappear from the Near East ≈ 80 Ka, leaving Neandertals as the sole occupants of the area until the moderns return ≈ 40 Ka with their more sophisticated Upper Palaeolithic tool culture. Whether the evolution of Upper Palaeolithic cultures implied significant advances in cognitive evolution amongst these modern humans relative to the Neandertals has not been established. The Chatelperronian culture suggests that Neandertals had the necessary cognitive capability to make and use more elaborate tools and symbolic artefacts. If so, the evolution of the Upper Palaeolithic may have had more to do with the social and/or environmental pressures on early modern humans than with any major cognitive differences between them and the Neandertals.

Conclusion

Neandertals are best interpreted as an extinct subspecies of archaic *Homo sapiens* which had been largely isolated from mainstream human evolution in Africa and Asia for at least the latter half of the Middle Pleistocene and the early part of the Upper Pleistocene. They were biologically well adapted to the glacial conditions of northern Europe, but there is also evidence that their life was hard. Modern humans arrived in Europe with their more sophisticated Upper Palaeolithic culture at ≈ 40 Ka when the climate was deteriorating towards the last glacial maximum. In the context of deteriorating environmental

conditions, competition with the better equipped early moderns could only have put increasing pressure on the Neandertals, pushing them into more peripheral environments, increasing their levels of mortality, and ultimately driving them to extinction.

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