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MAJOR EVENTS IN THE HISTORY OF LIFE



The Jurassic pterosaur *Pterodactylus kochi* from Solnhofen Limestone preserving impressions of the wing membranes, $\times 0.84$. (Photograph courtesy of J.M.V. Rayner.)

1.1 Origin of Life

C. R. WOESE & G. WÄCHTERSCHÄUSER

Introduction

The origins of man and his fellow creatures are concerns perhaps as old as man himself. However, before the nineteenth century these could not be given scientific form. The prescientific notions of life's beginnings were an incongruous amalgam of biblical thought, philosophy, alchemy and folk wisdom. The Bible taught that all life arose through special acts of divine creation during the first days of the Earth's existence. Commonplace experience showed, however, that life can also arise spontaneously, as maggots seemed to, for example, from rotting meat. And vitalism saw life as an ever-present non-material property of the universe.

In the nineteenth century four great scientific achievements laid the groundwork for making the origin of life a scientific problem: (1) The realization that the cell was the fundamental unit of biology introduced an enormous gulf between the living and non-living worlds; (2) Darwin's theory of evolution implied that all life came from some distant universal ancestor; (3) Pasteur painstakingly and convincingly refuted the claims of spontaneous generation (of microscopic life); so that, if life had arisen spontaneously on this planet, it must have done so under conditions no longer present and probably long gone; and (4) Mendel discovered genetics, whose origin is to this day one of biology's great mysteries.

The picture we now have of life's origin, though scientific, is based upon very few facts. It derives mainly from metaphysical assumptions, cultural images we take for granted. Consequently, it is likely to share features with the prescientific accounts of life's origin which go unrecognized and unchallenged. The present discussion of origins is framed along historical lines, a format that generally helps to reveal prejudices that impede or sidetrack the development of a scientific picture.

The conventional primitive ocean scenario

Darwin apparently gave little thought to the origin of life; he understood the problem to be intractable in his time. However, his casual 'warm little pond'

allusion has had a significant impact on later thinking, undoubtedly far more than its author intended or would have liked. Oparin (1924 *in* Bernal 1967) and Haldane (1929 *in* Bernal 1967) are generally credited with formulating the issue scientifically; not because they were the first to attempt it, but because their origin scenarios were more comprehensive than those of their predecessors. The details of these theories need not concern us; for they often reflected misconceptions, for example as to the nature of genes, viruses, and protoplasm, and how they replicate. However, in their general aspects the theories are of great interest, for, remarkably, these half century old proposals still remain the foundation of our understanding of life's beginnings.

The Oparin ocean scenario has by now become almost catechismal. It begins with a primitive anoxic atmosphere, comprising gases such as carbon dioxide or methane, nitrogen or ammonia, hydrogen sulphide, water, and hydrogen. Current thinking invokes the less reduced forms of these elements, the fully reduced forms being postulated earlier, by Urey (1951) and others, on the mistaken assumption that the nascent Earth possessed an atmosphere similar to those found on the large gaseous planets. Miller (1953) was the first to put such models to scientific tests when, as a student in the nineteen-fifties, he demonstrated that electrical discharge acting on Urey's atmosphere produced a conglomeration of organic compounds that included many of the familiar amino acids. The many experiments that followed showed that not only amino acids, but also a variety of organic compounds of biological interest, can be produced by a variety of energy sources under a variety of conditions (providing that oxygen is absent). So today we believe that some anoxic, slightly reducing atmosphere, acted upon by ultraviolet light and/or electrical discharge, served as a continual source of the simple reactive organic chemicals needed to begin and sustain the evolutionary process.

The products of this atmospheric chemistry ended up in the primitive ocean, which over time became a vast repository of reactive organic chemicals. Oparin's and Haldane's primitive ocean was a 'hot

dilute soup' (Haldane's phrase); hot on the mistaken assumption (common in the nineteen-twenties) that the Earth had arisen as a fragment of the Sun. With the later acceptance of a cold accretion model for the Earth's formation (also incorrect), the oceanic soup was cool from the start. The primitive ocean, then, was a 'vast chemical laboratory', a cosmic retort in which the great alchemist Nature sought to concoct the first living cell.

The most important but weakest element in the ocean scenario is the transition from prebiotic chemistry to actual living, self-replicating entities. The early models necessarily resorted to hand waving arguments — interactions occurring among the reactive chemicals in the primitive ocean led to ever more complex structures, to more and more complicated aggregates, that ultimately somehow became self-perpetuating. Later proposals, drawing upon the structure of nucleic acid, refined this notion to that of macromolecular templating.

As Haldane (1929) put it, in the ocean 'the first precursors of life found food available in considerable quantities'. Therefore, there was no need for them to evolve the capacity to produce these metabolites, and so they did not. The aboriginal organisms were total heterotrophs. This seldom questioned assertion determines the subsequent evolutionary course. A heterotrophic life style will necessarily (and rather quickly in evolutionary terms) deplete the oceanic stores of nutrients. If organisms are then to survive, they must evolve an intermediary metabolism and eventually learn to transduce other forms of energy (light or chemical) into biochemical energy.

The current explanation for how intermediary metabolism arose in the aboriginal heterotrophs was fashioned by Horowitz (1945). When the oceanic supply of a particular amino acid, for example, became exhausted, the supply of its immediate chemical precursor, for example an hydroxy acid (for which organisms previously had had no need), still remained untapped. Were the organism to evolve an enzyme that converted this precursor to the needed amino acid at this point both the organism and its progeny would survive. When, sometime later, the supply of the precursor also became exhausted, the process would repeat — the organism evolving another enzyme to catalyse synthesis of the precursor from its own (previously unutilized) precursor; and so on. In this manner all intermediary metabolism arose, the pathways evolving 'backward', one step at a time.

Neither Oparin nor Haldane initially postulated

cellular entities as a starting point for evolution, although Oparin did so later, with his coacervate model. There has been no subsequent consensus as to when cellularity arose.

Criticisms of and refinements to the standard model

The essence of the primitive ocean scenario (i.e. its metaphysics) has never been seriously questioned. However, many weaknesses in its details have come to light over the years. In each case the tendency has been to correct the problem by adding some new feature to the model. As a result today's origin scenario is a Ptolemaic hodgepodge of *ad hoc* assumptions. There is little point any longer in criticizing the standard model simply in the standard way, adding another *ad hoc* feature to remedy each new difficulty. The basic (implicit) assumptions of the model must be questioned.

Cultural roots of the primitive scenario. Although the Oparin ocean scenario was developed as a scientific alternative to the prescientific versions of the process, its similarity to the Garden of Eden myth should be worrisome. An oceanic 'paradise' is postulated in which organisms can develop safely in the midst of plenty. In addition to having 'food available in considerable quantities', the first organisms 'had no competitors in the struggle for existence' (Haldane 1929). Scientists have tended to see the first organism as arising through a series of highly unlikely events; discussions centre about improbable happenings that, given long times and enormous numbers of trials, eventually come to pass. (Remember that before the discovery of microfossils the Earth was generally thought to have been sterile for most of its existence, allowing billions of years for key events to happen.) Yet none of this is regarded as miraculous!

One can even detect something akin to the biblical banishment in the scientific account: because organisms ultimately destroyed their oceanic paradise (by consuming the store of biochemicals), they were thrust into a harsh world where they had to fend for themselves by developing intermediary metabolism, autotrophy, and eventually phototrophy. This was the dog-eat-dog world of competitive existence: 'The further life progressed the less nutrient substances were available to the organisms and the more strongly and bitterly the struggle for existence was waged' (Oparin 1924). Its truth aside, the Oparin ocean scenario seems a prime example of culturally

determined imagery shaping a scientific concept. The sooner these cultural influences are recognized and understood, the sooner a proper scientific picture of the origin of life will emerge.

With a need for major restructuring in mind, let us analyse the main elements in the standard scenario in detail.

Energy sources, the multi-theatre assumption, and the ocean repository. The ultraviolet light or electrical discharge invoked by the standard scenario to create the initial simple reactive compounds are so energetic that they produce indiscriminate bond ruptures, ionizations and free radicals. These would be entirely destructive of any larger (organic) compounds, not to mention living systems. This dilemma forces the standard scenario into a 'two-theatre' assumption: the initial simple reactive compounds produced in one theatre (the atmosphere) are subsequently quenched and protected in a second theatre (the ocean), where they accumulate and further react to produce more complex structures, and ultimately living systems.

The need for two widely separated theatres seems to underlie a pernicious paradox in the standard scenario: the notion of reactive chemicals is at odds with their transport over great distances, from the high atmosphere to the ocean. The ocean must accumulate reactive chemicals over long times because distance necessarily translates into dilution. A protracted accumulation (and storage) in turn is at odds with the reactivity of these chemicals and their rapid removal by hydrolysis or sedimentation.

In retrospect it is strange that all attempts to correct the difficulties with this oceanic chemical repository—reaction pot have never questioned its underlying multi-theatre assumption. Rather, difficulties were overcome by invoking *additional* theatres. Mineral surfaces, particularly clays, were seen by Bernal (1967) as a vehicle for concentrating and reacting organic chemicals. He pictured the dilute organic compounds in the ocean becoming concentrated in the froth that forms on its surface, the froth being driven shoreward, to end up in estuaries — where the already concentrated compounds became even more so in the oozes that formed there. Organic compounds adsorbed in high concentrations on clay sediments (and perhaps oriented and/or activated in the process) might then undergo spontaneous condensations, to produce biopolymers, and so on. Considerable experimental work has been done, e.g. by Katchalsky (1973) and co-workers, on the properties of clay

minerals *vis-à-vis* the adsorption and reactivity of organic compounds. We shall encounter below a fundamentally different role for surfaces in the origin of life.

Fox (1965) demonstrated experimentally that mixtures of amino acids (rich in the dicarboxylic amino acids) polymerized under hot (less than 200°C) non-aqueous conditions. Upon hydration these condensates produced 'proteinoid microspheres', which loosely resembled cells (in size, shape, and in having a few general catalytic properties). Because of this Fox argued that the high temperature conditions associated with volcanic environments were those under which the organic compounds in the ocean repository became concentrated and reacted to give the prototypes of living systems.

Invoking additional theatres is a Ptolemaic solution to the standard scenario's problems — which to a large extent are due to the multi-theatre assumption. The true remedy may lie in single-theatre scenarios, in which the energy source can be in close proximity to or within the evolving system. These are conditions under which an energy flux can constantly generate a rich spectrum of organic biochemicals that are turned over rather than stored.

The organism—environment dichotomy; heterotrophy and self-assembly. For a sufficiently primitive system, the organism—environment distinction does not exist. The dichotomy arises only when the evolving system has become sufficiently complex and physically separated from its surroundings that it can be viewed as an entity in its own right. However, the standard scenario (shaped by the properties of extant life) tends to see an organism—environment dichotomy early in the evolutionary process — certainly too early. What occurs in the 'organism' is strongly distinguished from what occurs in its 'environment'. The dichotomy (together with the Garden of Eden image) then makes of the ocean repository a pre-existing store of 'food' for the aboriginal organisms. They, in turn, come into being as heterotrophs, and go on to deplete and ultimately exhaust their store of food. In other words, a prematurely forced distinction between organism and environment tends to place the replicative aspect of the primitive system in the former, its metabolic aspect in the latter.

In such a dichotomous world the environment does not naturally, automatically, give rise to the organism. The latter has to 'strive' to bring itself into existence; it is the product of accidental self-assembly from simpler components in the

environment — an improbable and, therefore, protracted process. (Subject to the vagaries of chance in this way the evolutionary process has to pass through a stage of instability, of uncertain outcome.) A more extensive quote from Haldane shows these features rather clearly: 'When the whole sea was a vast chemical laboratory the conditions for the formation of such films [membranes, that is] must have been relatively favourable; but for all that life may have remained in the virus ... half-living chemical ... stage for many millions of years before a suitable assemblage of elementary units was brought together in the first cell. There must have been many failures, but the first successful cell had plenty of food.'

Were life to have originated in an autotrophic rather than heterotrophic manner, the scenario would have been markedly different. Autotrophic evolution focuses on autocatalytic reaction networks, on metabolic pathways — whence all other evolutionary developments stem. It is a single theatre scenario, in which energy source, production of reactive compounds, and condensations to form complex organic structures, occupy the same locale. When life begins with autotrophic metabolic pathways, one avoids the kind of dichotomous separation that exists between a heterotrophic organism and its host environment. An autotrophic system is a *source* of biochemical energy and complexity, not a sink for these (as are heterotrophs). With autotrophy the protracted, chancy trial and error period no longer seems required; the self-replicating entity (its genetics) can arise simply as a more refined and complex extension of the primary autotrophic and autocatalytic process. While some self-assembly might have to occur even in this process, that requirement too can be reduced by eliminating the constancy of the chemical conditions. In other words, major changes in the evolving system could be driven by, or be responses to, local or global changes in the state of the planet.

The origin of genetics; templating and the genotype/phenotype dichotomy. Mendel's great discovery, that the cell has a phenotypic-functional aspect that is determined by a cryptic genotypic-reproductive aspect, has dominated our view of the origin of life. With the discovery in the nineteen-forties that each gene corresponds to a unique enzyme, the central question could then be phrased: 'Which came first, the gene or the enzyme?' Geneticists such as H. J. Muller felt that the gene had to have come first; only a few physiologists disagreed. (The gene at that

time was often thought of as proteinaceous and even as having its own primitive phenotype.) Watson and Crick's discovery of the double stranded structure of nucleic acid rendered the question meaningless. Since all genes appeared to have the same basic structure, they could not have unique phenotypes, could not be functional in their own right; and, proteins (i.e. enzymes) could not evolve without genes — a chicken and egg paradox.

At this point the central question should have become 'How did the genotype-phenotype relationship (i.e. translation) arise?' However, the attractive and specific mechanism for the origin of gene replication inherent in the double stranded structure for nucleic acid (plus our near total ignorance of the molecular mechanics of translation) took us in an opposite direction. The origin of the genotype (nucleic acid replication) separated completely from the origin of the phenotype (metabolism) — the former question totally eclipsing the latter (Eigen *et al.* 1981; Orgel 1973). Recently it has become popular to believe that (RNA based) 'nucleic acid life' must have preceded protein-based life; that initially nucleic acid was both the genotype *and* the phenotype. This point of view is supported by the facts: (1) that polypyrimidines can serve as templates that align complementary purine nucleotides, which (when properly activated) then go on to condense into polypurine chains; and (2) that some RNAs possess certain limited enzymatic or catalytic properties. Eigen has also reported that in the presence of a particular protein (the replicase of the virus Q β) a certain type of RNA will spontaneously arise (in the absence of a pre-existing template).

A fascinating variation on the templating theme is Cairns-Smith's (1985) proposal that life began with replicating patterns in *clay* layers (which could adsorb organic molecules and thereby influence the course of subsequent organic evolution). While daring in one way, this proposal is conventional in another; it takes for granted the need for templating as an initial step in the origin of life.

A totally dichotomous view of the origins of the genotype (replication) and the phenotype (metabolism) is an extrapolation in the wrong direction. It has even led Dyson (1985) to propose that life arose *twice*; initially somehow as protein-based life, within which nucleic acid then separately arose as a 'disease'. The earliest life forms were almost certainly not incarnations of our dichotomies, of our attempts to define extant life. Rather, primitive living systems were undoubtedly less well de-

finer, less compartmentalized, than their modern counterparts, and so in that unusual sense more 'integrated'. It is time to reassess the genotype–phenotype dichotomy as a paradigm for the origin of life.

A proper conceptualization of translation, the process that defines the genotype–phenotype relationship, should have an integrating, unifying effect on our concept of the origin of life. Unfortunately, the translation mechanism is large and complex, and, therefore, its molecular workings and evolution are not understood. The fact that some of the proteins involved in translation are also components of certain nucleic acid replication enzymes, however, suggests primitive connections between the two processes. The facts that cells today contain transfer RNA-like molecules as essential parts of non-translational ('non-programmed') polymerizations (e.g. polypeptide antibiotic and cell wall syntheses), and that nucleotides, other heterocyclic compounds, and even transfer RNAs play important roles in intermediary metabolism, hint at still deeper evolutionary connections.

The suggestions are strong that the programmed polymerizations (translation and nucleic acid replication) have arisen out of more primitive metabolic interactions. Therefore, what seems called for at this juncture is a general view of polymerization processes, one that attempts to relate polymer formation to the full spectrum of metabolic reactions in primitive systems — e.g. the types of polymers arising under primitive conditions; the range of monomer units and chemical linkages involved; whether polymers were formed by monomer or oligomer condensations; chirality constraints; whether the sequences of the aboriginal polymers were random or (simply) ordered (e.g. homopolymers, polymers of alternating sequence, etc.); the extent to which templating is or is not involved; and oligonucleotide–amino acid interactions.

Geological and phylogenetic constraints on the primitive ocean scenario

Knowing when the evolutionary process started is crucial to understanding how it occurred. Conditions during the first few hundred million years of Earth's existence were certainly very different from those occurring 2000 million years later.

The current understanding of the geological history of the Earth, Moon, and other planets, together with recent advances in the biologist's understanding of phylogeny, substantially restrict the

time interval during which the evolutionary process could have started.

The Earth's crust is now believed to have been initially quite hot, too hot to sustain liquid water. Any water present would have been partitioned between the primitive atmosphere and a semi-molten crust. There is also geological evidence to suggest that the Archaean oceans were warm. The oldest sedimentary rocks (3800 Ma), although somewhat metamorphosed, give evidence of life at that time; and the better preserved 3500 Ma sediments give clear evidence of bacterial life — showing both fossil stromatolite structures and microfossils (see also Section 1.2). In that stromatolites today are produced by photosynthetic bacteria, principally cyanobacteria (or thermophiles of the *Chloroflexus* type), photosynthetic bacteria (probably) already existed 3500 Ma.

The explosive developments in molecular phylogeny over the past decade have revealed a number of important facts: (1) the earliest phylogenetic branchings gave rise to three aboriginal lineages, the eubacteria, the archaebacteria and the eukaryotes; (2) photosynthesis appears to have arisen (early) within the eubacteria. If so (given the stromatolite evidence), eubacteria already existed at least 3500 Ma, so that the most recent ancestor common to *all* life lived at a still earlier time — probably far earlier, because of the enormous evolutionary distances that separate the three classes; (3) prokaryotic life (at least) arose in high temperature environments; (4) the ancestral environments were anaerobic; and (5) the ancestral forms of prokaryotic metabolism may have been autotrophic. Comparisons among the (sequences of the) genomes of diverse organisms will ultimately permit us to infer in some detail the nature of the most recent common ancestor of all extant life, and also certain things about still earlier evolutionary stages (see also Section 2.1). All the evidence to date, then, points to life having arisen quite early in the planet's history, and under thermophilic conditions.

Alternatives to the primitive ocean scenario

An important methodological rule of K. Popper is that a new theory should have a greater explanatory power than its predecessors, i.e. it should explain a multitude of facts with a minimum of assumptions. Clearly, today's consensus theory of the origin of life is little more than a highly amended version of the original Oparin/Haldane scenario it has replaced — which violates Popper's rule. Further

amendments to the standard scenario are not what is needed; true alternatives to it are.

Wächtershäuser (1988) has proposed one such alternative, which dispenses with the multi-theatre assumption, the ocean repository, heterotrophic origin, and modular self-assembly. This theory, moreover, is sufficiently detailed to make testable assertions regarding the nature and evolution of primitive biochemical pathways. The first organisms are assumed to be truly autotrophic (not heterotrophic) — the result of *de novo* biosynthesis of organic constituents by the uptake of inorganic material (e.g. CO₂), and subsequent rearrangement reactions. They are not the products of accidental modular assembly. The theory's central idea is that life began with autocatalytic, metabolic processes occurring in an essentially two-dimensional fashion, within organic monolayers anionically bonded to positively charged surfaces of minerals, such as pyrite, and in contact with water at high temperature. Adherence to the mineral surface is *not* the result of adsorption but of an *in situ* autotrophic growth of organic constituents that acquire their anionic surface bonding *in statu nascendi*. The concentration of dissolved organic constituents in the water phase is negligible. Hence the process by which a constituent loses its surface bonding is irreversible; detachment is tantamount to disappearance. (In this respect the theory is the opposite of Bernal's clay theory, which is based upon adsorption). On these pyrite surfaces large polyanionic constituents, with ever stronger surface bonding, are automatically selected — to begin with polyanionic coenzymes, eventually nucleic acids and polypeptides. The primitive system grows by spreading onto vacant surfaces, reproduces by producing its autocatalytic coenzymes, and its evolution is driven by environmentally induced ignitions of new autocatalytic cycles. The system evolves toward higher complexity, since the thermodynamic equilibrium in a surface metabolism would favour synthesis, not degradation (as would occur with solution reactions). High energy phospho-anhydride groups are not required for the formation of covalent bonds. Phosphate groups (whose source is taken to be the mineral substrate) have the sole function of surface bonding. The energy for carbon fixation is provided by the redox process of converting ferrous ions and hydrogen sulphide into pyrite, which is not only a waste product but provides the all-important binding surface for the organic constituents.

This initial laminar organism is succeeded by two

further stages. The second stage organisms are semicellular entities still supported by a pyrite surface but having an (autotrophically grown) lipid over-layer, with an internal broth of detached constituents. In this 'bleb' stage a membrane metabolism and a cytosol metabolism appear, first as a supplement to, and later as a substitute for, the aboriginal surface metabolism. Membrane-bound electron transport chains allow the tapping of other redox energy sources and ultimately of light energy. The cytosol metabolism allows the salvaging of detached constituents by catabolic processes and the development of modular modes of synthesis that rely upon energy coupling. Eventually heterotrophy appears, as a by-product of the catabolic salvage pathways. The cell's genetic machinery develops from surface-metabolic precursors. It produces self-folding enzymes which compete with the mineral surface for bonding the metabolic constituents. In this stage evolution becomes double tracked, an evolution of metabolic pathways and one of the bonding surfaces for their constituents. In the third stage the pyrite support is abandoned and true cellular organisms arise.

Since the ocean cannot reasonably function as a reaction pot in which life originated, and its role as a repository is suspect, the question is whether it played any significant role at all in the origin of life. Two types of scenarios exist that make minimal use of the ocean. One is the idea that hydrothermal vents served as the aboriginal environment. Since hydrothermal vents create chemical gradients, a single-theatre vent scenario can be developed that has no need for the ocean repository assumption. How the model would cope with the fact that vents, and so their products, are ephemeral (especially so on an evolutionary time-scale) is unspecified.

It was suggested by Woese (1979) that evolution began in the primitive atmosphere, at a time when the planet's surface was too hot to sustain liquid water. The early Earth can be pictured as surrounded by vast cloud banks, as Venus is today. The severe weather conditions that must then have existed would have caused large quantities of minerals (dust), from the dry surface, to be swept into the atmosphere. Atmospheric water vapour then condensed on the dust, dissolving it (in part). As a consequence, the primitive Earth was enshrouded in clouds of salt water. In addition to containing (possibly high concentrations of) minerals, the droplets in these clouds would accumulate organic compounds, produced by interactions among atmospheric gases and other constituents (or with

compounds produced by thermal reactions on the Earth's surface and swept into the atmosphere). These droplets are natural precursors of cells — their surfaces coated with mixtures of the larger organic compounds, their interiors solutions of reactive (organic and inorganic) compounds. The different layers of the atmosphere would each have characteristic chemistries, the whole being in effect a connected series of chemostats. Droplets (and hydrated dust) offer enormous amounts of surface, and so surface chemistry becomes all important in life's beginnings.

As the primitive Earth cooled, its surface would pass from a dry condition, through cycling damp/dry stages, to one where large bodies of (hot) water could accumulate. These major global transitions would bring about major changes in the evolutionary course (see above). The cloud setting suggests a single theatre scenario, requiring no repository assumption; it also suggests that major stages in evolution were driven by (were responses to) major changes in the state of the planet.

In one sense the origin of life problem today remains what it was in the time of Darwin — one of the great unsolved riddles of science. Yet we have made progress. Through theoretical scrutiny and experimental effort since the nineteen-twenties many of the early naive assumptions have fallen or are falling aside — and there now exist alternative theories. In short, while we do not have a solution, we now have an inkling of the magnitude of the problem.

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1.2 Precambrian Evolution of Prokaryotes and Protists

A. H. KNOLL

Introduction

The Phanerozoic Eon, the interval under discussion in most of this volume, encompasses the most recent 13% of our planet's history. A sedimentary record documenting more than 3000 Ma of Archaean and Proterozoic time extends below the base of the Cambrian System, and research conducted over the

past three decades has demonstrated that this entire sweep of history is the proper domain of palaeontology. Stromatolites, microfossils, and geochemical markers provide fragmentary, sometimes frustrating, but critically important evidence for early evolution. Like younger invertebrate fossils, fossil

prokaryotes and protists must be studied as populations characterized by a measurable range of morphological variation, reproductive pattern, behavioural orientation, taphonomic features, and distribution within and among sedimentary environments. Unlike invertebrate fossils, significant questions of metabolism may remain after populations have been otherwise characterized. The interpretation of early metabolic diversity requires that morphological investigations be supplemented by trace fossil studies (stromatolites and oncolites being the preserved traces of microbial communities) and geochemical analyses of ancient metabolic and environmental indicators. Geological data must be integrated with information from molecular phylogeny and the comparative physiology of living organisms, and interpreted with a clear appreciation of our incomplete understanding of both living micro-organisms and their geological record.

The Archaean Eon: the early diversification of micro-organisms

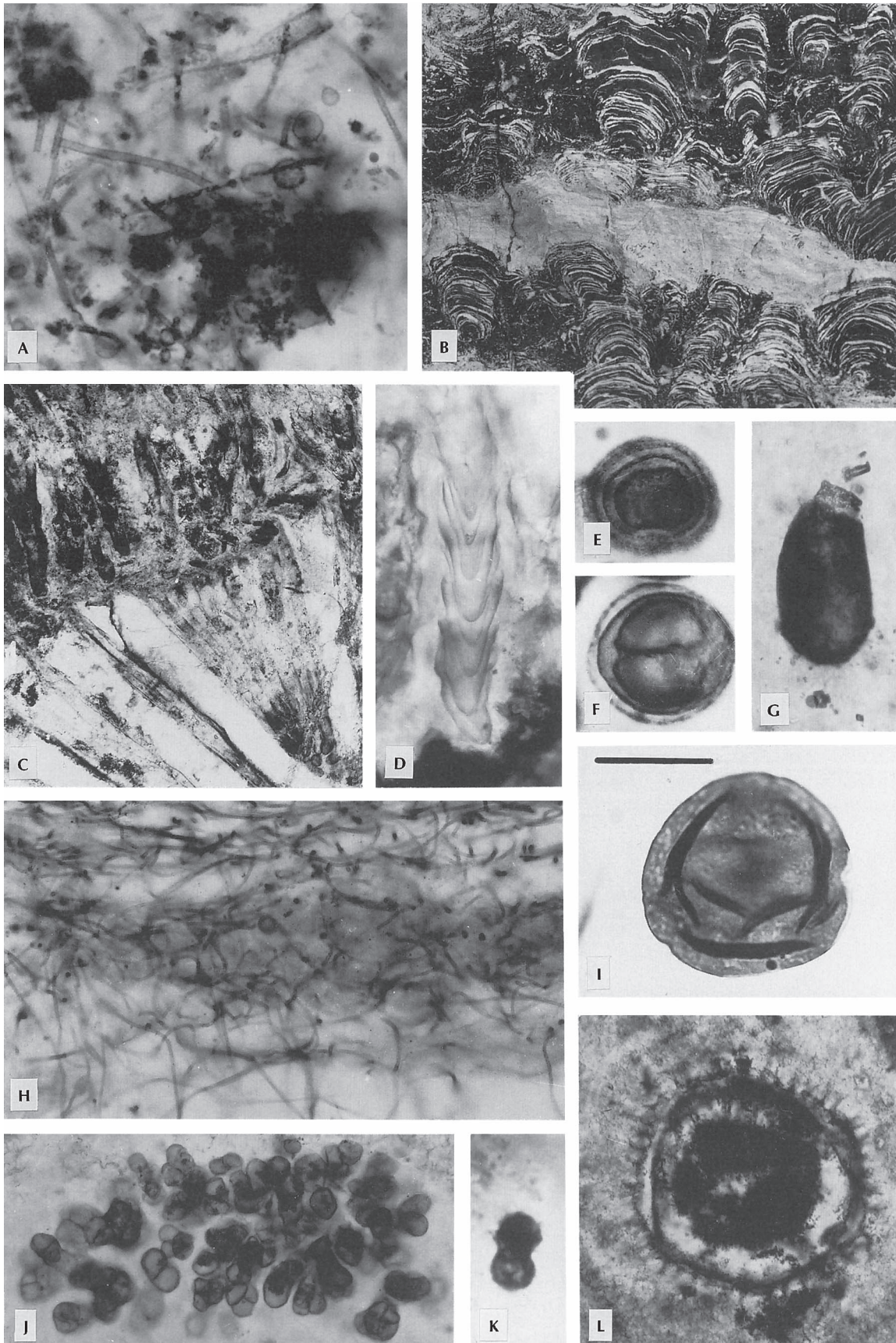
The age of the earliest palaeobiological record has not changed appreciably in more than 20 years, but the quality of interpretable evidence has improved significantly at decadal intervals. Palaeobiological investigations of Early Archaean rocks have concentrated on two successions, the Onverwacht Group of South Africa and the Warrawoona Group, Western Australia. Both sequences are dated at *c.* 3500 Ma. Both are little-metamorphosed greenstone belt successions characterized by thick mafic and ultramafic lavas, subordinate felsic volcanics, and intercalated sedimentary rocks. Sediments origi-

nated largely as volcanoclastics and chemical precipitates, including carbonates, but most have been extensively silicified. Stratiform, domal, and columnar to pseudocolumnar stromatolites occur locally in both areas (Byerly *et al.* 1986; Walter *in* Schopf 1983). These structures have generally been interpreted as the trace fossils of microbial communities. Although this interpretation is reasonable, no Early Archaean stromatolites are known to contain microfossils. Thus, abiological alternatives must be considered, and biogenicity defended on the basis of gross morphology and microstructure (Buick *et al.* 1981).

Microfossils have also been reported from both groups. Simple carbonaceous spheroids of varying size were reported from several horizons in the Onverwacht and overlying Fig Tree groups during the nineteen-sixties but the biogenicity of many of these structures is open to question. During the nineteen-seventies, several authors reported populations of spheroidal carbonaceous microstructures that show a number of features more consistent with a biological interpretation. These include a narrow, nearly normal size frequency distribution about a mean diameter of 2.5 μm , clear evidence for binary division, a sedimentary context comparable to that of younger, undisputed microfossils, and taphonomic features comparable to younger fossils such as flattened and wrinkled vesicles and the occasional preservation of internal carbonaceous contents (Fig. 1K). Rod-like and filamentous microstructures have also been reported from the Swaziland succession, but their antiquity and mode of origin remain subjects for debate.

Undoubted filamentous microfossils have recently been described from cherts of the Warra-

Fig 1 Representative Archaean and Proterozoic fossils. A, *Gunflintia* (filaments) and *Huroniospora* (spheroids) in stromatolitic chert from the Lower Proterozoic Gunflint Iron Formation, Ontario. B, Stromatolites from the Upper Proterozoic Backlundtoppen Formation, Spitsbergen. C, D, Low and high magnification views of a surface-encrusting cyanobacterial population from the Upper Proterozoic Limestone–Dolomite ‘Series’, central East Greenland — the nested cups are successive extracellular envelopes produced by coccoidal cyanobacteria that jetted upward from the sediment surface, much as morphologically similar populations in peritidal environments of the Bahama Banks do today. E, F, Chroococcalean cyanobacteria from silicified playa lake carbonates of the Upper Proterozoic Bitter Springs Formation, Australia. G, Vase-shaped protist from the Upper Proterozoic Elbobreen Formation, Spitsbergen. H, Low magnification view of oscillatorian cyanobacteria from the Upper Proterozoic Backlundtoppen Formation, Spitsbergen, showing the alternation of vertical and horizontal orientations characteristic of many mat-building populations. I, Acritarch isolated from shales of the Upper Proterozoic Chuar Group, Arizona. J, Endolithic hyellacean cyanobacterium in silicified ooids from the Upper Proterozoic Limestone–Dolomite ‘Series’, central East Greenland — ooid surface is toward the top of the photograph. K, Spheroidal microstructure from a population showing various stages of binary division, Early Archaean Onverwacht Group, South Africa. L, Large, process-bearing acritarch preserved in chert nodules within a moderately metamorphosed succession of latest Proterozoic age, Prins Karls Forland, Svalbard. Bar = 30 μm for A, 10 cm for B, 400 μm for C, 100 μm for D, 20 μm for E, F and I, 50 μm for G, H and J, and 75 μm for L.



woona Group (Schopf & Packer 1987), where they occur in association with clusters of spheroidal unicells encased in multiple extracellular envelopes. These microfossils are morphologically similar to extant cyanobacteria, and may be early representatives of this group; however, that interpretation is by no means assured. Even if the fossils do represent early cyanobacterial ancestors, there is no assurance that they were oxygenic photoautotrophs using two photosystems. In the presence of H_2S , many living blue-greens photosynthesize anoxygenically using only photosystem I, i.e. H_2S , H_2 , or organic molecules donate electrons, and no O_2 is produced. Comparative biochemistry indicates that this photosynthetic system evolved earlier than the cyanobacterial (and higher plant) pathway in which water donates electrons.

The apparent low morphological diversity of described Early Archaean microfossils cannot be taken too literally. Studies of Early Proterozoic assemblages from Western Australia have demonstrated that, as morphologically varied assemblages of fossils undergo increasing diagenetic and incipient metamorphic alteration, they become 'archaeonized' — i.e. they appear to converge morphologically on the simple microstructures found in weakly metamorphosed Early Archaean cherts (Knoll *et al.* 1988).

The biological fixation of CO_2 is accompanied by a marked fractionation of the stable isotopes of carbon, ^{12}C and ^{13}C . Carbon isotopic ratios in Onverwacht and Warrawoona carbonates and kerogens indicate significant fractionation between oxidized and reduced species, suggesting an Early Archaean carbon cycle fuelled by photosynthesis, possibly under conditions of elevated P_{CO_2} . Sulphur isotopes are likewise fractionated during dissimilatory sulphate reduction, but in contrast to carbon, Early Archaean sulphur-bearing samples show little fractionation between sulphides and sulphates. At the same time, sedimentological evidence indicates that sulphate was an important anion in the water bodies beneath which both the Onverwacht and Warrawoona beds accumulated. This apparent paradox has several possible explanations: (1) it is possible that Early Archaean oceans contained negligible sulphate concentrations, and that rocks containing evidence for sulphates in both the Onverwacht and the Warrawoona groups accumulated under non-marine conditions — an explanation that is unsatisfactory to many geologists familiar with the rocks; (2) it is possible that significant concentrations of sulphate existed in oceans

for several hundred million years before prokaryotes learned to use it — an explanation unsatisfactory to microbiologists, who note that bacteria evolve rapidly to exploit novel substrates; or (3) perhaps almost all sulphate in pore fluids was reduced biologically to sulphide in an essentially closed system with little fractionation because of high ambient temperatures (70°C or more) — a theory for which the geological record provides little supporting evidence. A generally acceptable solution to this problem has not yet been proposed.

Despite outstanding problems of palaeobiological interpretation, it seems clear that 3500 Ma the Earth supported complex prokaryotic ecosystems driven by photosynthesis. Oxygen may have been generated by Early Archaean cyanobacteria, but geochemical evidence indicates that any O_2 produced was largely consumed by the oxidation of organic matter, ferrous iron, and sulphides. Ambient P_{O_2} appears to have been low and physiological pathways, consequently, anaerobic. Oxide facies iron formation is found in Early Archaean basinal facies, but not in shallow volcanic platform sequences, prompting speculation that oxygenic photosynthesis may have originated in 'mid-gyre' environments far from sites of volcanic or sedimentary H_2S generation. Comparisons of informational macromolecules in extant micro-organisms independently suggest rapid metabolic diversification early in evolutionary history. Early branching groups in both the eubacteria and archaeobacteria are predominantly anaerobic, thermophilic, and sulphur-dependent; several are autotrophic (Woese 1984).

The search for older biological records is limited by the paucity of pre-3500 Ma sedimentary sequences. 3800 Ma rocks from Isua, southwestern Greenland, contain reduced carbon that is isotopically fractionated relative to carbonates in the same succession, but the metamorphism of these rocks to amphibolite grade has obliterated any unambiguous indications of biological activity. Later Archaean successions in Australia, Africa, and North America contain diverse stromatolites, rare microfossils of cyanobacterial aspect, and local evidence of unusually strong carbon isotope fractionation. Most of the isotopically light kerogens come from non-marine deposits, so their interpretation in terms of global conditions is not straightforward; however, it has been suggested that isotopically light kerogens fix a minimum age for the evolution of aerobic methylotrophy (the metabolic oxidation of methane or other one-carbon compounds; Hayes *in* Schopf 1983).

The Early Proterozoic Eon: the diversification of aerobes

The modern era of Precambrian palaeontology began in 1954 with the brief description by S. Tyler & E.S. Barghoorn of microfossils preserved in cherts from the 2000 Ma Gunflint Iron Formation, Canada. Subsequent research has demonstrated that several discrete microfossil assemblages occur in Gunflint rocks. Stromatolitic cherts near the base of the formation contain abundant microfossils preserved as organic, haematitic, or pyritic structures. Although more than a dozen valid species have been described from this facies, two taxa together comprise more than 99% of all individuals (Fig. 1A).

Gunflintia minuta is a thin (usually 1–2 µm) filamentous sheath that has been compared to both nostocalean cyanobacteria and iron bacteria. Its affinities remain uncertain; locally inflated areas along filaments interpreted as akinetes and heterocysts (distinct cell types produced by nostocalean blue-greens) are probably diagenetic in origin.

Small (2–15 µm) spheroidal fossils assigned to the genus *Huroniospora* occur in the same beds. The phylogenetic relationships of these populations are also unclear, but their recent interpretation as bacterial spores merits serious consideration. Other microfossils in the Gunflint stromatolitic assemblage are uncommon; they include probable iron-oxidizing bacteria, possible cyanobacteria, and problematica, but no strong candidates for eukaryotic assignment.

Although these fossils occur within laminated stromatolitic structures, *Gunflintia* and *Huroniospora* populations do not display the orientations characteristic of mat-building micro-organisms in younger rocks. Thus, like their phylogenetic relationships, their ecological interpretation as mat-builders is open to question.

Non-stromatolitic Gunflint assemblages include microbenthos preserved in silicified muds and probable planktic populations. The mud microbenthos is dominated by stellate microfossils interpreted as iron and manganese oxidizing bacteria, while the apparent planktic forms are 6–31 µm diameter spheroids of uncertain systematic position. Whatever the taxonomic affinities of Gunflint microfossils, it is clear that generally similar assemblages were widely distributed 2000 Ma. Assemblages comparable to Gunflint mud, mat, and plankton florules occur in Labrador, the Canadian Northwest Territories, and two areas in Western Australia (references in Knoll *et al.* 1988). Not all of

these occur in iron formations, and several contain microfossils not found in the Gunflint Formation itself. For example, silicified carbonate muds of the Duck Creek Dolomite, Western Australia, contain septate filaments as much as 63 µm in diameter — among the largest such fossils known from any Proterozoic formation. Although Gunflint-like assemblages are widely distributed in Lower Proterozoic formations, they are not the only fossils in rocks of this age. Assemblages from hypersaline peritidal rocks of the Belcher Supergroup, Hudson Bay, Canada, contain populations that are indistinguishable from cyanobacteria found today in comparable environments (Hofmann 1976).

Stromatolites are abundant and morphologically diverse in Lower Proterozoic platform carbonates (Walter 1976). It is not certain whether the observed increase in stromatolite diversity between the Late Archaean and Early Proterozoic eras reflects a radiation in mat-building prokaryotes, a preservational consequence of Late Archaean continental crustal growth and stabilization, or both.

What may have been the most profound evolutionary changes of the Early Proterozoic Era are events that must be inferred from sedimentological and geochemical data. During the Early Proterozoic, the degree of isotopic fractionation recorded in sulphur-bearing minerals increased substantially. Detrital uraninite ceased to be a significant constituent of fluvial and deltaic sediments, while red beds became widespread. Limited data suggest that iron retention in palaeosols developed on mafic parent materials decreased by the end of this interval.

Beginning with Preston Cloud, numerous commentators have suggested that these phenomena reflect a significant increase in the partial pressure of oxygen in the Earth's atmosphere. This has sometimes been interpreted as meaning that the Early Proterozoic atmosphere shifted from reducing to a composition comparable to the present; however, such a black-and-white view no longer seems tenable. The Archaean (especially the late Archaean) atmosphere undoubtedly contained some molecular oxygen, albeit in low concentrations. At the end of the Early Proterozoic Era, the atmosphere probably contained only one to a few per cent of present day O₂ levels. The difference, however, is metabolically significant; aerobic respiration is possible in the latter atmosphere, but not in the former. Some palaeontological evidence supports the idea of Early Proterozoic aerobic prokaryotes, but clearer insights come from molecular phylogeny and comparative

physiology. In many aerobic physiological pathways, oxygen-requiring steps are appended to an otherwise anaerobic series of reactions (Chapman & Schopf *in* Schopf 1983). Molecular data, specifically comparisons of nucleotide sequence in 16S ribosomal RNA molecules among different living microorganisms, suggest that aerobic respiration evolved independently in a number of groups, most of which are fundamentally photoautotrophic (Woese 1984). If one accepts that broad constraints on the timing of evolutionary events can be gleaned from molecular data, then it can be inferred further that the polyphyletic evolution of aerobic prokaryotes occurred during a relatively brief period following a long period of anaerobic evolution (Fig. 2).

The later Proterozoic Eon: the emergence of protists

Although treated last in this chronological account, the later Proterozoic Eon might have justifiably been discussed first, because its palaeobiological record, especially for the period 900–600 Ma, is far more extensive and better preserved than that of earlier epochs. Nearly 200 Late Proterozoic

microfossil biotas are known from seven continents (Knoll 1985). Environmental sampling is far better than for earlier eras. Thus, it is in later Proterozoic sequences — where the record is clearest — that principles of palaeoecological, palaeogeographical, taphonomic, systematic and, hence, evolutionary interpretation can best be established.

Late Proterozoic microfossil assemblages have been reported from silicified carbonates representing a variety of peritidal depositional environments. *In situ* microbenthic populations occur in stratiform stromatolites and, much less frequently, in conoidal, domal, or columnar forms (Fig. 1C–F, H). Microbenthos can also be found in silicified micrites, oncoids, and ooids, as well as in shales and, rarely, in unsilicified carbonates. There is a strong correlation between facies and assemblage composition. Many populations are convincingly interpreted as cyanobacteria, although under exceptional circumstances bacterial heterotrophs can be recognized. Less amenable to interpretation are populations of unornamented 10–20 μm spheroids that are distributed sporadically throughout most fossiliferous rocks. Although their simple morphology precludes confident systematic

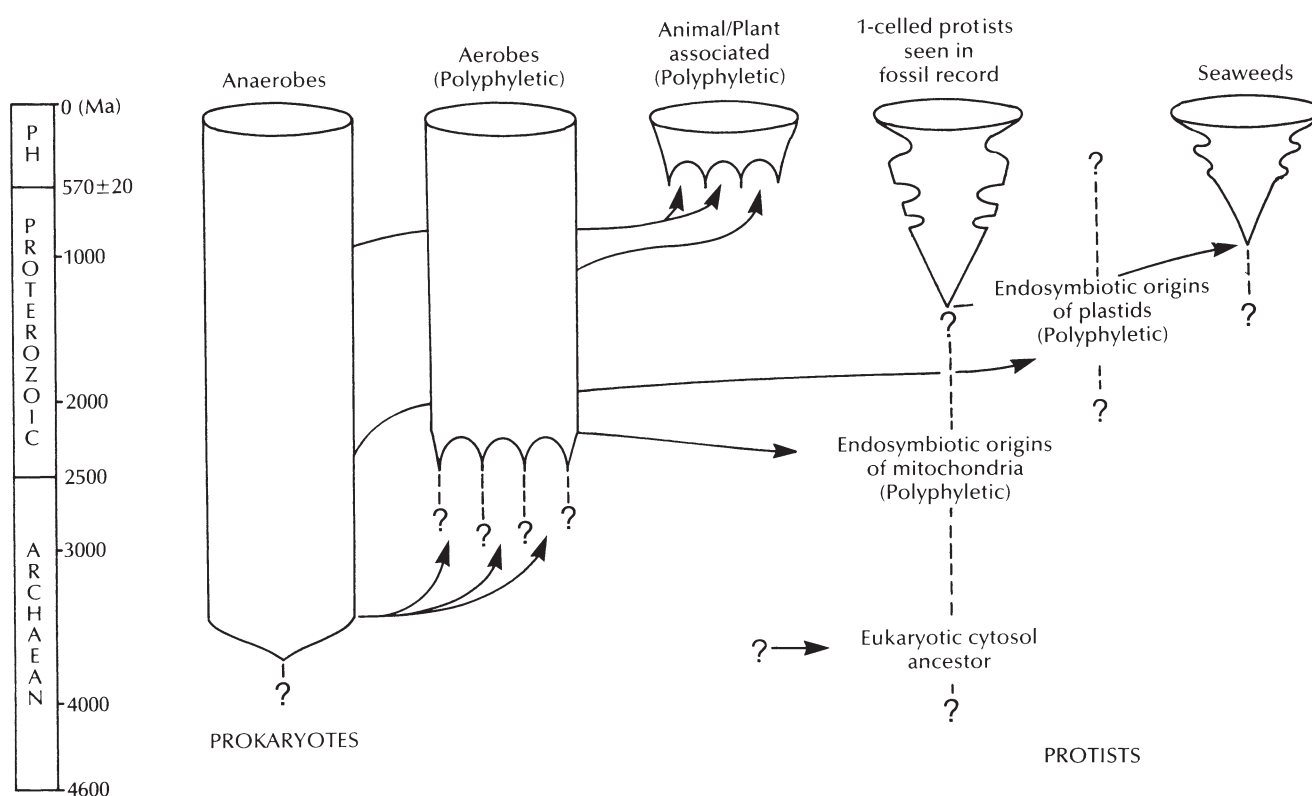


Fig. 2 Summary chart illustrating generalized patterns of prokaryotic and protistan evolution.

classification, some of these fossils resemble the cells and cysts of green algae and protozoans that occur in modern microbial communities of peritidal and hypersaline lake environments. Judging from their spatial distribution within and among facies, other spheroid populations appear to be allochthonous, probably planktic, elements.

Many Late Proterozoic prokaryotes differ little in morphology, development, or behaviour from living cyanobacterial populations found in physical environments like those inferred for the fossils. For example, endolithic microfossil assemblages found in silicified ooids from the 700–800 Ma Eleonore Bay Group, East Greenland, contain half a dozen discrete populations which have close modern counterparts in present day Bahamian ooid shoals (Fig. 1J). Late Proterozoic cyanobacteria appear to be essentially modern in their diversity and environmental distribution. One can hypothesize that the apparent increase in cyanobacterial diversity recorded in the Proterozoic as a whole is mainly a function of more complete sampling in younger successions; that is, the major features of cyanobacterial diversity were established during the Early Proterozoic Era or earlier. This hypothesis cannot be rejected on the basis of currently available data. The record of other prokaryotes is less clear, although the presence of Late Proterozoic sulphate reducers, methanogens, methylotrophs and other bacteria can be established or inferred on the basis of geochemical evidence.

Stromatolites provide sedimentary evidence for the continued wide distribution of microbial mat communities in later Proterozoic environments (Fig. 1B). It has been suggested that Proterozoic stromatolites changed systematically as a function of age, and that this provides indirect evidence for Proterozoic cyanobacterial evolution. Several objections can be raised against this view: (1) the debate over the stratigraphic distribution of stromatolite forms continues unresolved — hindered by the failure of many reports to place stromatolites in their proper sedimentological perspective and by the absence of a rational, internationally accepted system of nomenclature; and (2) it may well be true that certain stromatolites characterize particular time intervals, but this does not necessarily say anything about cyanobacterial evolution. Differences between Early and Late Proterozoic stromatolites may as easily reflect the addition of eukaryotic algae to mat-building communities, temporal changes in features of the physical environment (such as CaCO_3 supersaturation), the evolution of

uncalcified metaphytes that outcompeted microorganisms for space in certain environments, or the evolution of meiofaunal grade metazoans.

Undisputed protistan fossils are abundant in Upper Proterozoic rocks. Large (up to 2 mm) acritarchs occur in both silicified carbonates and shales (Fig. 1I); some of these may represent the phycmata of planktic prasinophyte algae, but the systematic relationships of most are uncertain. Latest Proterozoic cherts and finely laminated shales from China, Australia, and Svalbard contain particularly complex forms, including spiny and process-bearing populations (Fig. 1L). In their general level of morphological complexity, these resemble younger Palaeozoic acritarchs, but the Proterozoic forms are invariably much larger and are certainly distinct at the specific and, usually, the generic level. Recent discoveries in Spitsbergen and Arctic Canada demonstrate that the record of spinose and process-bearing acritarchs goes back at least to 800 Ma. Vase-shaped microfossils of uncertain systematic position also occur in Upper Proterozoic shales and carbonates (Fig. 1G); in some successions, they are among the most abundant fossils preserved.

Like fossil prokaryotes, protistan microfossils reflect palaeoenvironments in their distribution, but unlike prokaryotes, they change systematically through time. Therefore, acritarchs have proved useful in at least Late Proterozoic biostratigraphy (Vidal & Knoll 1983; Hofmann 1987).

The record of eukaryotes can be traced though time at least back to 1700 Ma, when both the morphological and molecular geochemical records of protists begin (Jackson *et al.* 1986). The record of metaphytes may be almost as long. Diverse multicellular algae occur in Upper Proterozoic rocks (Hofmann 1985); with somewhat less confidence, both carbonaceous and trace fossil remains in 1300–1400 Ma rocks can be interpreted as seaweeds. No unequivocal remains of metazoans have been described from pre-Ediacaran deposits. Thus, either seaweeds and animals originated at strikingly different times or, for the first half of their history, animals must have been tiny, meiofaunal grade organisms unlikely to survive as fossils or produce recognizable traces.

While the palaeobiological trail of early eukaryotes currently turns cold at about 1700 Ma, it must be admitted that nucleated cells that were incapable of fossilization or, at least, unlikely to be recognized as eukaryotic, almost certainly existed earlier. How much earlier is unclear. The ancestors of the eukaryotic cytosol (nucleus and cytoplasm) appear to

have arisen early in Earth history, either directly from the progenote or later from archaeobacterial ancestors. The Early Proterozoic PO_2 increase probably fostered endosymbiotic couplings between ancestral cytosols and purple nonsulphur bacteria, leading to the polyphyletic evolution of heterotrophic, mitochondria-bearing protists. The later acquisition of endosymbiotic cyanobacteria resulted in the origin of eukaryotic algae, again independently in several lineages. Indeed, it appears that the plastids of some algal groups are descended from endosymbiotic eukaryotic algae, giving such organisms a truly complicated phylogeny.

A postscript on continuing microbial evolution

It is obvious that protistan evolution did not grind to a halt at the end of the Proterozoic Eon. It may be less obvious that continuing diversification has also been a characteristic of Phanerozoic prokaryotes. On a broad scale, major features of anaerobic metabolic diversity were established during the Archaean, and aerobic pathways were in place by the Early Proterozoic; however, evolving metaphytes and metazoans have furnished bacteria with a continuing succession of novel substrates for metabolism and enteric environments for colonization. Throughout Earth's history, rates of prokaryotic evolution have probably been a function of environmental evolution. From the perspective of prokaryotes, then, the evolving multicellular biota can be viewed as a continually changing series of environments. Phanerozoic rates of bacterial evolution may have been low in groups little affected by metazoan evolution, but for the many bacteria that depend directly or indirectly on metazoans, evolutionary rates were probably comparable to those of the animals themselves.

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1.3 Precambrian Metazoans

M. A. FEDONKIN

Although palaeontology as a science began more than 200 years ago, the first descriptions of Precambrian animals appeared relatively late, only in the first half of this century. This is explained by the rarity of Precambrian animal fossils. This rarity is due to the absence of mineralized skeletons and possibly because of a low biomass of metazoans in late Precambrian ecosystems.

Distribution in time and space

Remains of the Precambrian fauna are now known from Australia, Africa, America, Europe, and Asia. The most representative localities are in the Nama Group, Namibia, the Pound Subgroup, South Australia, the Charnian Subgroup, U.K., the Conception Group, Southeastern Newfoundland, the Valdai Series of Podolia, Ukraine, on the Onega Peninsula, and in the Khorbusuonka Series in Northern Yakutia (Glaessner 1984; Fedonkin 1987).

Several thousand specimens assigned to more than 100 species have been found thus far in Precambrian deposits. Imprints and moulds of soft-bodied animals are mainly preserved in terrigenous strata accumulated in marine shallow water environments. Less typically, fossils come from deeper water deposits, in turbidite and carbonate sediments.

Unique taphonomic conditions in the Precambrian, due to a combination of special biotic and abiotic factors, resulted in excellent preservation of non-skeletal invertebrates revealing fine details of their anatomy, i.e. external morphology and, in some cases, internal organs.

The first unequivocal metazoan fossils appear stratigraphically above tillites of the Laplandian (Varangerian) glaciation, which took place approximately 650–620 Ma. The maximum geographical and stratigraphic distribution of Precambrian Metazoa occurs in the lower half of the interval between these tillites and the base of the Tommotian Stage of the Lower Cambrian above. This interval more or less corresponds to the terminal system of the Precambrian. Concepts of this stratigraphic system, known as the Sinian, Vendian, Ediacarian or Ediacaran according to different authors, are still

developing. The name most commonly used for the terminal Precambrian system is the Vendian. Its type area is the Russian Platform. In the upper half of this system most of the soft-bodied fauna disappears, though some trace fossils continue up to the top of the Vendian along with abundant Vendotaenian algae (Metaphyta) and acritarchs (Sokolov & Ivanovski 1985).

Origin of metazoans

The large number and morphological diversity of Metazoa in the first half of the Vendian indicate that their phylogenetic roots continue into older pre-Vendian periods. This situation is indirectly supported by a comparative analysis of amino acid sequences of globins of living invertebrates (Runnegar 1986) and by a decrease in the quantity and the diversity of stromatolites which began 1000 Ma and accelerated 700–800 Ma (Walter and Heys 1985).

The possibility cannot be excluded, however, that the decline of stromatolites was promoted not only by Metazoa, which influenced, grazed upon and disturbed bacterial mats and broke the stability of substrate, but by a series of glaciations which took place 850 ± 50 , 740 ± 20 and 650 ± 20 Ma. Little is known about this stage of Metazoan evolution, but it seems likely that the oldest animal communities, including Vendian ones, were characterized by relatively low diversity in comparison with Cambrian life. If diversity is considered to be a peculiar mechanism for maintaining the stability of the biosphere, then the low diversity Precambrian biota was rather vulnerable to external abiotic factors as well as biotic innovations. A low diversity Precambrian fauna could not match the stability of later Metazoan communities. The possibility cannot be excluded that as soon as multicellular animals appeared, their communities were subjected to radical change, including mass extinctions as they approached the Phanerozoic level of differentiation.

General characteristics

Late Precambrian animals have a wide geographical

distribution with many identical forms occurring at distant localities. This indicates cosmopolitanism, weak provincialism, and evidently low rates of evolution after a rapid adaptive radiation at the beginning of the Early Vendian transgression.

Although the systematics of Precambrian animals are still problematic, obvious features include a considerable diversity of life form and body plan, a pronounced domination by Coelenterata, a low ratio of the number of species to that of phyla, large size (even gigantism in many species, especially among the most primitive organisms), the presence of all major ecological groups, concentration in shallow marine environments, a low activity of vagile predators and scavengers, a relatively small biomass of infauna in benthic communities, an ecological organization into short trophic chains, an abundance of suspension feeders and detritivorous animals, and an absence of active filter feeders.

Systematics

The traditional approach to the systematic position of Precambrian invertebrates is based on comparison with younger Palaeozoic and even Recent animals (see also Section 5.2.5). For example, Glaessner (1984) placed Precambrian animals in the following taxa: phylum Coelenterata (classes Hydrozoa, Scyphozoa, Conulata, medusae of uncertain affinity and problematic Petalonamae); phylum Annelida (class Polychaeta); phylum Arthropoda (superclass Trilobitomorpha or Chelicerata of uncertain class, and superclass Crustacea: class Branchiopoda); phyla Pogonophora, Echiurida and some forms of uncertain systematic position. The classification of the Precambrian animals within the framework of living invertebrates produces many contradictions. Therefore other approaches and principles of classification have been developed. For example, an attempt of comparative morphological analysis of Vendian Radiata and Bilateria has led to different results and a new classification of the oldest Metazoa (Fedonkin 1987), which is outlined below.

Radial animals (Radiata). The coelenterate class Cyclozoa is characterized by a concentric body plan, a vast disc-shaped gastral cavity, and a wide distribution of methods of asexual reproduction. Some forms have simple marginal tentacles. The reproductive organs are not known. This class contains predominantly sedentary forms, and less commonly animals living at the water–air interface and in

the plankton. The following genera are included: *Nemiana* (Fig. 1A), *Cyclomedusa*, *Eoporpita* (Fig. 1E), *Kullingia*, *Ovatoscutum* (Fig. 1B), *Chondroplon*, *Medusinites*, *Ediacaria* (Fig. 1C), *Tirasiana*, *Nimbria* and *Paliella* (Fig. 2H).

The class Inordoza unites medusa-like organisms with a symmetry of uncertain order, which are characterized by a higher organization than the Cyclozoa. Various complicated systems of gastrovascular channels, the presence of reproductive organs (gonads), and the dominance of medusae in this group support this point of view. Asexual reproduction is not typical. The pattern of growth in these animals is unusual compared to that in Recent coelenterates: new radial elements (antimeres) are formed freely without any regularity throughout life. Thus, they increase in number and order of symmetry during ontogeny without restriction. The combination of concentric and radial symmetry indicates a phylogenetic relationship between the Inordoza and Cyclozoa. The Inordoza includes *Hallidaya*, *Lorenzinites*, *Rugoconites*, *Hiemalora* (Fig. 2G), *Elasenina*, *Evmiaksia*, and *Pomorina*.

The class Trilobozoa is characterized by an unusual three-rayed symmetry, which occurs only as a teratological phenomenon among recent Coelenterata; among other Metazoa it is known only as a secondary feature. Like the above mentioned classes of Precambrian Coelenterata, representatives of the Trilobozoa are characterized by a mode of growth unusual for recent Coelenterata. During ontogeny, instead of couples of opposite antimeres being formed, three antimeres or identical radial elements in multiples of three developed simultaneously. The domination of medusa life forms, complicated and regular systems of gastrovascular channels, and a stable quantity of reproductive organs, indicate a high level of organization comparable to that of the Scyphozoa. However, Trilobozoa are characterized by different growth and symmetry, and an absence of a circular channel and oral aperture. It includes *Skinnera*, *Tribraichidium*, *Albumares* (Fig. 1F), and *Anfesta* (Fig. 2D).

Conomedusites (Fig. 2F), the only sedentary organism having a rather dense conical theca and a four-rayed symmetry, is assigned to the class Conulata. Other medusoids with the same symmetry are doubtfully compared with scyphozoan medusoids; these include *Ichmusina*, *Persimedesites* and *Staurinidia*.

It is noteworthy that as the symmetry of the Precambrian Coelenterata is reduced, their organization becomes more complicated: from primitive,

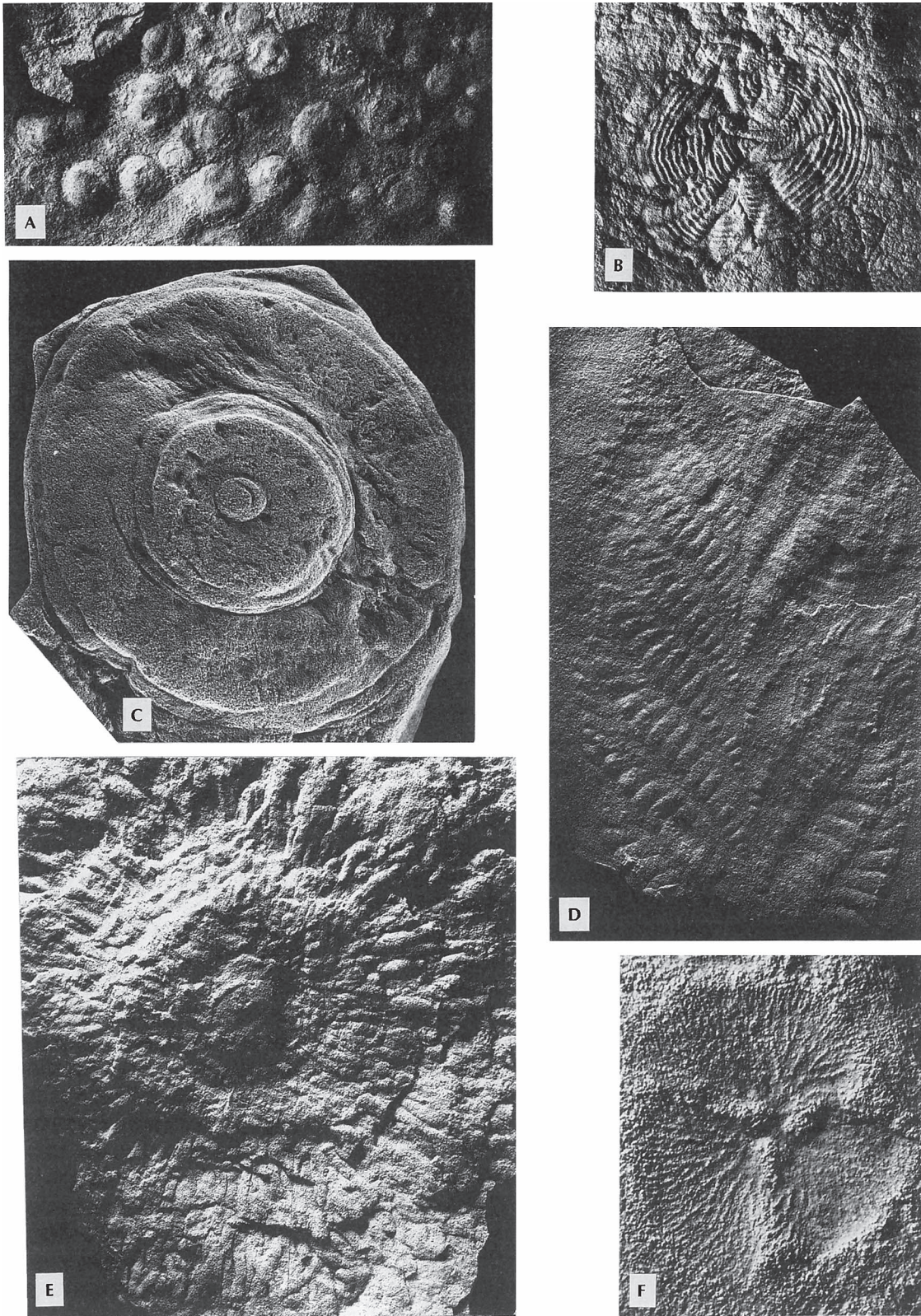


Fig. 1 Vendian metazoans. A, *Nemiana simplex*, $\times 0.5$. B, *Ovatoscutum concentricum*, $\times 1$. C, *Ediacaria flindersi*, $\times 1$. D, *Charnia masoni*, $\times 1$. E, *Eoporpita medusa*, $\times 1$. F, *Albumares brunsa*, $\times 4$. Specimens in A and D are from the Khatyspyt Formation, Northern Yakutia, U.S.S.R. Specimens in B, C, E and F are from the Ust-Pinega Formation, southeast of the White Sea region, U.S.S.R.

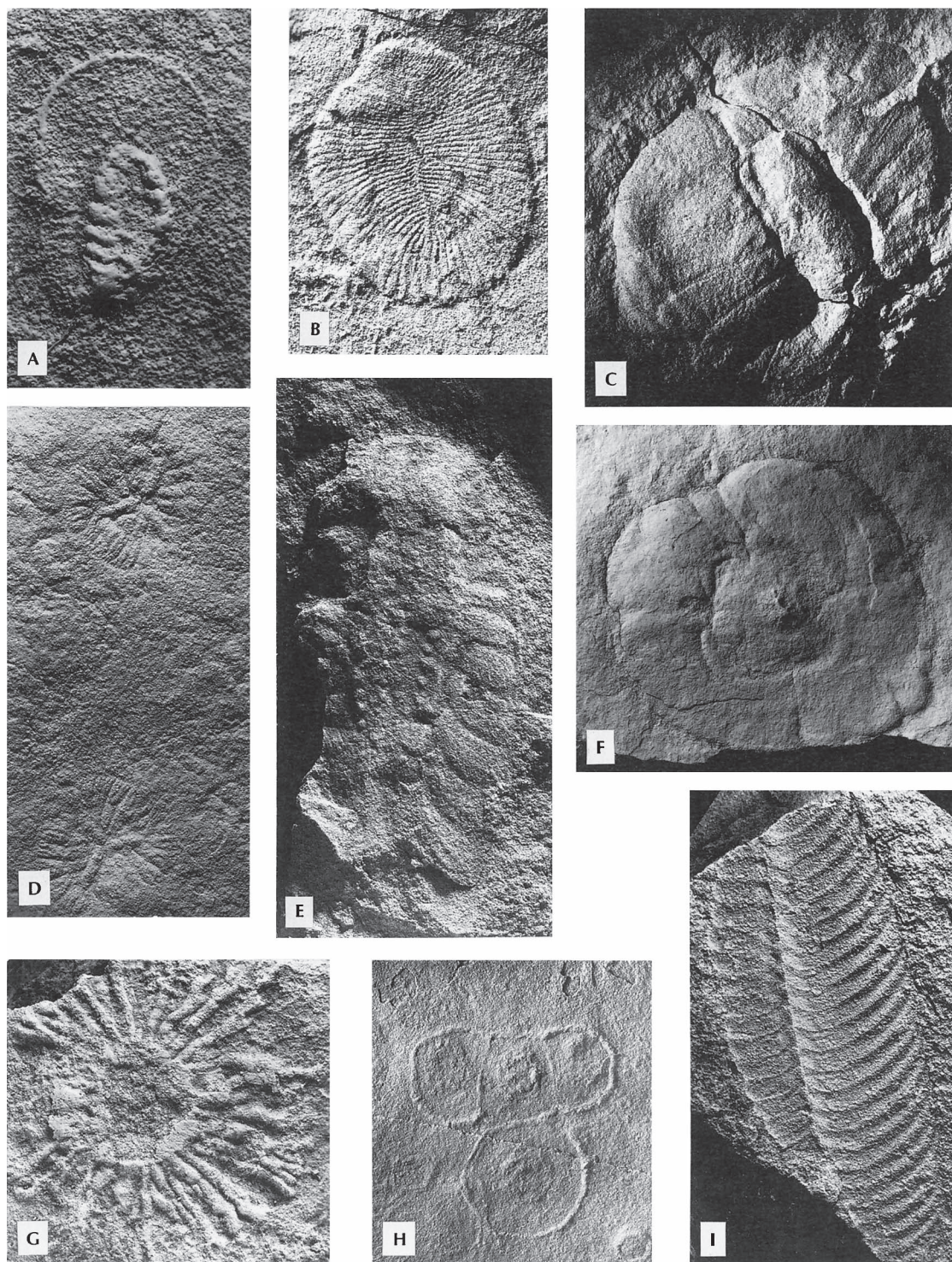


Fig. 2 Vendian metazoans. A, *Onega stepanovi*, $\times 5$. B, *Dickinsonia costata*, $\times 1$. C, *Mialsemia semichatovi*, $\times 1$. D, *Anfesta stankovskii*, $\times 1.1$. E, *Bomakellia kelleri*, $\times 0.7$. F, *Conomedusites lobatus*, $\times 1$. G, *Hiemalora stellaris*, $\times 1$. H, *Paliella patelliformis*, $\times 0.7$. I, *Pteridinium nenoxa*, $\times 0.7$. Specimens in A–E, G, I are from the Ust-Pinega Formation, southeast of the White Sea Region, U.S.S.R. The specimen in F is from the Mogilev–Podolsk Series, Ukraine, U.S.S.R., and the specimen in H is from the Khatyspyt Formation, Northern Yalutia, U.S.S.R.

dominantly sedentary Cyclozoa with a high order symmetry, through more advanced Inordozoa with a radial symmetry of variable (uncertain) order, to medusoid classes with a stable symmetry and the highest organization (Trilobozoa, Conulata, Scyphozoa). This sequence may reflect the early, pre-Vendian phylogeny of Precambrian Coelenterata.

Precambrian colonial organisms are shaped like feathers, combs, fans, and bushes (Ford 1958; Glaessner & Wade 1966; Jenkin & Gehling 1978; Anderson & Conway Morris 1982). Most forms were fixed to soft sediment by disc-shaped or sausage-like organs of attachment, but rare, pelagic, freely swimming colonies are also known. The degree of integration and habit of these colonies suggest assignment to the Coelenterata, but it is impossible to determine their exact systematic position without evidence of the structure of individual polyps and the nature of sclerites or spicules that may have been present in some colonies. Functional differentiation of polyps is not known. The possibility that the colonial organisms are representatives of the same coelenterate classes as the solitary forms cannot be excluded. Colonial forms include *Charnia* (Fig. 1D), *Charniodiscus*, *Paracharnia*, *Pteridinium* (Fig. 2I), *Rangea*, *Ramellina*, *Vaizitsinia*, and *Ausia*.

The Petalonamae is a special group of coelenterate grade described by Pflug (1970) as a group of high taxonomic rank that gave rise to many phyla of invertebrates. Most specialists now consider the Petalonamae to be a group of different, possibly unrelated Coelenterata of uncertain systematic position. Among them is the unusual class Erniettomorpha which includes 27 species and 13 genera. However, some authors consider this diversity to be a taphonomic artifact, and reduce Erniettomorpha to five genera or even to one species, *Ernietta plateauensis*. This sedentary organism had a multi-layered, sack-shaped body and lived with the base of its body partially buried in soft sediment.

Bilateral animals (Bilateria). Among bilaterally symmetrical Precambrian animals, very few forms have a smooth, nonsegmented body. These are usually represented by only a few or even single specimens, and their interpretation is doubtful. Two monotypic genera, *Vladimissa* and *Platypholinia*, can be compared with the turbellarians (Platyhelminthes). *Protechiurus* is considered to be the oldest echiurid.

The overwhelming majority of Precambrian Bilateria have features resembling segmentation or metamerism. This initially suggested comparison

with annelids, arthropods, and other articulates. However, some so-called 'segmented' forms have an unusual structure: semisegments of the right and left sides alternate. This symmetry of glide reflection is not typical of younger bilaterians, but is known in the Precambrian among polymeric (consisting of numerous anatomically identical body parts) forms in the Dickinsoniidae as well as among oligomeric (consisting of few similar parts) forms in the Vendomiidae.

The leaf-like *Dickinsonia* (Fig. 2B; up to 1 m body size) originally considered a coelenterate, or annelid worm or flatworm, represents an independent branch of metazoans derived from the Radiata long before other bilaterians. This is indicated by the absence of a definite mouth and anus, an imperfect position of numerous semisegments, and relics of radial symmetry in early ontogeny. Dickinsoniidae could represent a separate class Dipleurozoa in the primitive phylum Proarticulata. The family Vendomiidae also probably belongs to this phylum. These animals had a small, elongate discoidal body with a broadly arcuate anterior margin; a wide cephalic area is followed by a small number of segments or alternating semisegments. The distal ends of the (semi)segments do not always reach the lateral margins of the ovate flat body. This family tentatively embraces *Vendomia*, *Onega* (Fig. 2A), *Praecambridium*, and *Vendia*.

True segmented animals resembling annelids and arthropods did live in the Vendian oceans, and some of them can be compared to later Palaeozoic counterparts. For example, *Parvancorina* has a shield-like, rather soft carapace with a faint marginal rim and elevated anterolateral and median smooth dorsal ridges. Approximately five pairs of stout anterior appendages are followed by up to twenty pairs of posterior fine appendages. The similarity of *Parvancorina* to the Palaeozoic arthropods of the Marrellomorpha may indicate that it is close to the ancestors of Crustacea (Glaessner 1984).

A rather unusual body plan is characteristic of the family Sprigginidae, which includes *Spriggina* and *Marywadea*. These animals, generally interpreted as annelids, have a horseshoe-shaped or half-moon-shaped prostomium that resembles the head shield of primitive trilobites. The body segments, however, resemble those of rather primitive annelids. The same combination of a large head and a rather smooth body with long feather-like lateral appendages occurs in *Bomakellia* (Fig. 2E) and *Mialsemia* (Fig. 2C) – both united in the family Bomakellidae. These animals seem to have had a rigid carapace.

Their body plan does not correspond to that of any group of living invertebrates. Recently it was suggested that both the Sprigginidae and Bomakellidae should be assigned to the special class Paratrilobita, related to the phylum Arthropoda.

Vendian–Cambrian evolutionary transition

One of the anomalies in the Precambrian Vendian fauna is an absence of evident ancestors of the important Cambrian invertebrate groups, including Archaeocyatha, Mollusca, Brachiopoda, and Echinodermata, all of which appear early in the Lower Cambrian as discrete phyletic lines. The low species diversity and prevalence of monotypic genera may indicate a relatively short interval between the rise of these invertebrate groups and their acquisition of the ability to build a skeleton.

Skeletalization developed gradually during the Vendian (Section 1.4). The first half of the period saw the appearance of *Redkinia spinosa*, an annelid-like animal with chitinous, comb-like jaws. Chitinous tubes of sabelliditids appear at the same level, as well as the calcareous tubular fossils *Cloudina*. The end of the Vendian saw a wide distribution of tubular shells, sclerites and conodont-like forms. The small sizes and wide geographical distribution of the oldest shelly fossils could indicate that their Precambrian ancestors had small body sizes and a planktic mode of life.

Trace fossils show that the majority of the vagile benthos lived in shallow-water marine environments. Dominant among them were deposit feeders and forms of detritivore which collected small food particles. These animals moved by various peristaltic methods. Precambrian trace fossils are not as diverse or deep as later examples. The biomass of Vendian infaunal communities was much smaller even in shallow-water environments. Sedentary epifaunal forms of the Vendian period (i.e. mainly primitive groups of coelenterates) were dominantly passive suspension feeders and, more rarely, predators. Active suspension feeders (filter feeders) are unknown. The activity of vagile predators and scavengers was low, at least in the first half of the Vendian. Coelenterata were dominant in the plankton and nekton.

The end of the Vendian Period was a critical moment in the history of life when biological processing of sediments increased greatly and many new groups of invertebrates began to inhabit the sea floor. The body size of infauna, represented mainly by soft-bodied animals, also increased

at this time. All these phenomena, as well as the formation of a skeleton in other groups, may be adaptive and reflect increasing predation by vagile animals. Burrowing and the formation of skeletons had extremely important biological and evolutionary consequences that are not yet entirely understood by palaeontologists and zoologists.

Recently Seilacher (1984) offered a new morphological and functional interpretation of some Precambrian animals. Having noted that the Vendian fauna shows no close affinity with later invertebrates, he inferred that Precambrian organisms do not have Recent analogues and have a unique organization. They are characterized by an extensive body surface, which has developed mainly because of their very complicated relief, and a low body volume by virtue of being relatively flat. The high surface–volume ratio of the body allowed the absorption of oxygen and organic matter dissolved in water by diffusion through the body surface. Thus, neither a mouth and digestive organs nor respiratory organs were necessary.

No less attractive is an older point of view, that the body of many Precambrian animals was favourable for harbouring photosynthesizing endosymbionts. This is supported by the leaf-like form of the body of many Vendian organisms, their occurrence in shallow water marine environments within the photic zone, and the large size of many of the most primitive forms. A certain correlation between the presence of algae-endosymbionts and large body size is noted, for example, in recent Cnidaria.

The gigantism of many Precambrian invertebrates is especially striking when compared to the first very small shelly fossils which appear at the end of the Vendian and become numerous in the Tommotian Stage of the Lower Cambrian (Section 1.5). The larger body size of the Vendian Metazoa may reflect an adaptation of prey animals to increasing predation pressure. The first half of the Vendian was characterized by rapid speciation under the conditions of the vast postglacial transgression of the sea. The fauna rapidly reached its characteristic diversity, and rates of phyletic evolution decreased. This is reflected in the large sizes of populations and the absence of provincialism in many groups.

The middle of the Vendian saw a mass extinction of many groups (Section 2.13.1), especially those primitive animals which were characterized by a passive mode of feeding. One possible reason for extinction was the appearance of many small ancestors of Cambrian invertebrates, which had better

developed modes of feeding and could considerably impoverish food resources in the pelagic zone. The passive feeding of many Vendian sedentary forms was relatively inefficient and may have led to their extinction. The collection of detritus from the surface of the sediment also became less effective. These circumstances, as well as the increasing population densities and growing predation, could direct natural selection to favour forms that began active colonization of bottom sediment with its new trophic peculiarities. The ecological niche of Vendian sedentary Coelenterata in the shallow marine environment became occupied by active suspension feeders (sponges, archaeocyathids, brachiopods) in the Early Cambrian (see Section 1.6).

Possibly in parallel with the extinction of some groups, there was a decrease in body size in others in the second half of the Vendian. This could explain the sharp impoverishment, if not a gap in the fossil record, of invertebrates of the late Vendian. The decrease of body size may have led to the oligomerization of many primitive polymeric forms. This in its turn could have resulted in an increase in the level of organization and/or even in the specialization of some forms.

From the middle of the Vendian, the increasing activity of predators and scavengers and the destructive activity of burrowing organisms and perhaps the meiofauna inhibited the preservation of soft-bodied forms. Additionally, bioturbation led to more rapid biological oxidation of soft tissues of buried animals.

When comparing the world of the Vendian with that of the Cambrian we are comparing two different categories of fossils. This makes it difficult to analyse the early evolution of invertebrates but to some extent explains the apparent absence of phylogenetic connections between the faunas of these two periods.

The analysis of body plans of Vendian soft-bodied invertebrates reveals some previously unknown directions of morphological evolution in the Metazoa. The great abundance of Radiata in the Vendian reflects the predominance of radially-symmetrical animals of coelenterate grade in the early history of metazoans. The high diversity of symmetries reflects an early radiation of this phylum. The development of more complicated morphologies (i.e. the appearance of more complex systems of gastrovascular channels, reproductive organs, etc.) while symmetry was reduced suggests an evolution from forms with a symmetry of infinitely

high order, through forms with an uncertain multi-rayed symmetry, to forms with a stable order of symmetry. In the course of coelenterate evolution the archaic concentric body plan was replaced essentially by a radial one.

The dominance of segmented forms among Vendian Bilateria possibly reflects a relationship between processes leading to bilateral symmetry and to metamerism in the phylogeny of early Metazoa. But these processes did not always lead to coelomates. Unusual peculiarities of constructional morphology (from a neontological perspective), for example the plane of symmetry of glide reflection in some of the most primitive Vendian bilaterians, may indicate the early origin of bilateral quasi-segmented forms from rather archaic Radiata with an axis of symmetry of infinitely high or uncertain order.

The existence of a large quantity of short-lived phylogenetic branches in the Precambrian emphasizes the importance of comparative-morphological analysis at the Vendian chronological level in order to discover major directions in the early evolution of multicellular animals.

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1.4 Origin of Hard Parts — Early Skeletal Fossils

B. RUNNEGAR & S. BENGTSON

Introduction

Hard parts of organisms appeared almost instantaneously in the fossil record at the transition from the Proterozoic to the Phanerozoic. Biomineralization (Section 4.4) may have evolved close in time to that event. Earlier records of biogenic minerals are spurious and involve either very small, isolated crystals (magnetite of possible bacterial origin) or carbonate encrustation of cyanobacterial sheaths that may have been induced indirectly by the photosynthetic activities of the organism.

The earliest records of hard parts involve all major skeletal materials — calcite, magnesian calcite, aragonite, apatite, and opal. (About 40 minerals are known to be formed by modern organisms (Lowenstam & Weiner 1983), but many of them are unstable under normal diagenetic conditions and they seldom form structures large or distinct enough to be recognized in the fossil record.) All major types of skeletons are present — spicules, stiffened walls, shells, sclerites, and physiologically dynamic endoskeletons. The Early Phanerozoic skeleton-forming biotas (Fig. 1) represent practically all major taxa of multicellular organisms known to produce mineralized skeletons today, some groups of biomineralizing protists, and a number of extinct groups of organisms, mostly metazoans (see also Section 5.2.5).

The original mineralogy of the various groups of Late Precambrian and Cambrian fossils is not always well known. There are comparatively few studies on the diagenesis of early skeletal fossils. The composition of the skeleton in most groups is only known from their gross mineralogy in various types of rock, or inferentially through comparisons with known related taxa. More detailed information has been derived from petrographic and geochemical studies of fossils and surrounding rocks (e.g. James

& Klappa 1983), and from studies of replicated crystal morphologies (Runnegar 1985). This has been done in only a few cases, however, and further studies are needed.

Carbonate fossils

Calcium carbonates, mainly calcite, magnesian calcite, and aragonite, are the most common skeleton-forming minerals today, and appear to have been dominant already among the first skeletal fossils. Whereas aragonite is unstable in diagenesis and is rarely preserved in the fossil record, calcite and magnesian calcite may preserve their original crystallographic structure given favourable circumstances.

The tubular fossil *Cloudina* (see also Sections 1.3, 5.2.5) is often considered to be the earliest known example of a mineralized skeleton, but its stratigraphic position is somewhat uncertain, and it is not clear that it significantly predates the earliest more diverse assemblage of skeletal fossils. The tubular skeleton of *Cloudina* consists of stacked imbricating calcareous half-rings, suggesting that it was constructed by a secreting gland of an animal that was able to twist around in its tube. The wall was probably partly organic, stiffened by calcium carbonate impregnations.

Other early carbonate tube-building animals include the anabaritids, first occurring in the c. 550 Ma Nemakit–Daldyn assemblage (see Fig. 1). Anabaritids attained a wide distribution before their disappearance in the Atdabanian. They were triradially symmetrical — an unusual feature suggesting a possible phylogenetic relationship with triradial metazoans of the Ediacaran fauna — and appear to have been less mobile in their tubes than *Cloudina*. The original mineralogy of the tubes is

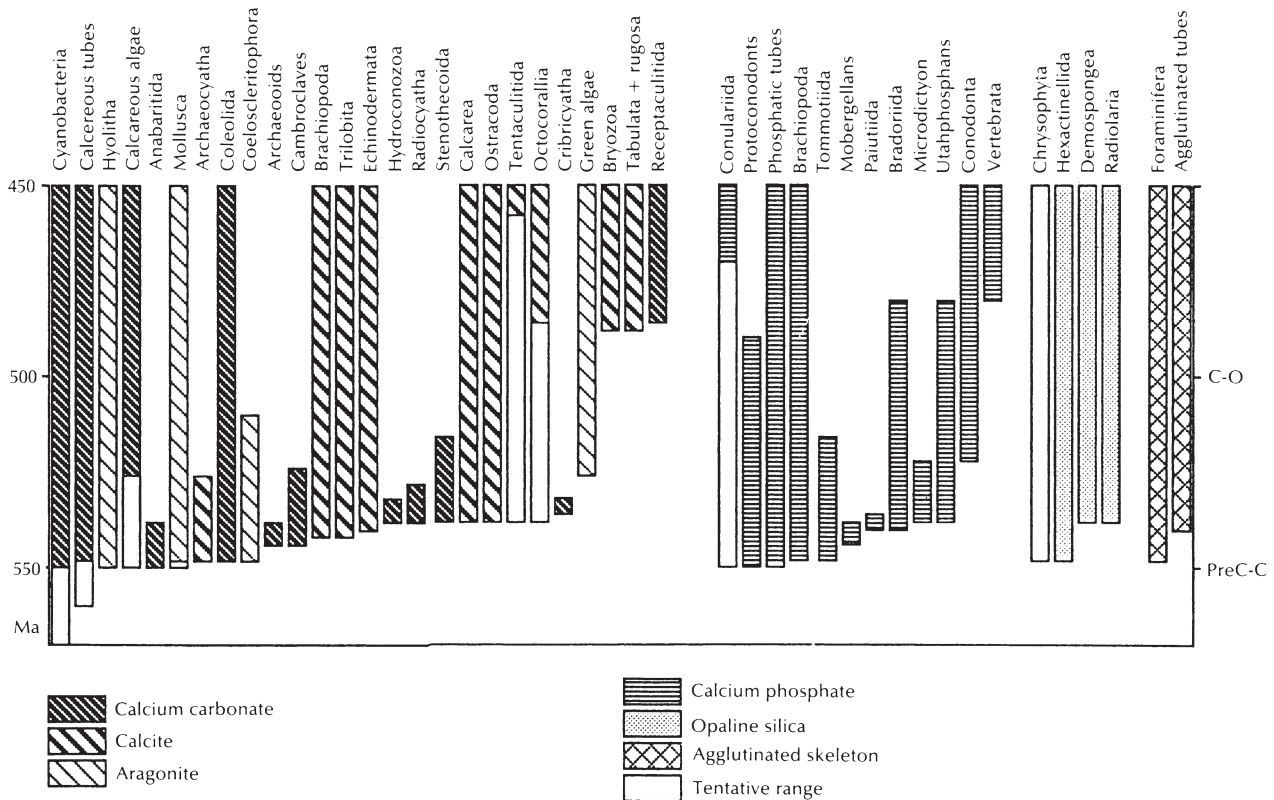


Fig. 1 Temporal distribution of clades of biomineralizing and agglutinating organisms in the Late Precambrian to Late Ordovician, compiled from various sources. Precambrian–Cambrian boundary (PreC–C) arbitrarily placed at the appearance of the *Protohertzina*–*Anabarites* assemblage and assigned an age of 550 Ma (see also Section 5.10.2). Clades defined as groups of taxa that appear to derive their biomineralizing habit from a common ancestor. (A few probably polyphyletic groups, such as ‘calcareous tubes’, have been retained due to their poorly known phylogeny.)

not known, but apparently ubiquitous recrystallization suggests that they may have been formed of aragonite.

The succeeding Cambrian faunas contain more diverse types of tubular fossils. Some were cylindrical, resembling, for example, protective structures built by certain modern annelids. Others, in particular the widespread and diverse hyoliths (see also Section 5.2.5), had more obtuse tubes and were closed by opercula. They were bilaterally symmetrical animals with a U-shaped gut. The shell mineral was most probably aragonite, and a structure resembling molluscan crossed-lamellar fabric has been observed in younger Palaeozoic members of this group.

Aragonitic shells are characteristic of early molluscs (Runnegar 1985). The most primitive shell structure in Cambrian molluscs seems to have consisted of a single layer of spherulitic aragonite prisms beneath an organic periostracum. This type of structure may grow in an inorganic manner, and

the shape of the spherulitic ‘prisms’ is moulded by surface forces rather than chemical bonds. These kinds of mineral deposits need not have been mediated by a protein substrate.

Nacreous linings in prismatic shells had appeared by at least the Middle Cambrian and may have been present in Early Cambrian time. The fundamental difference between the aragonitic fibres of spherulitic ‘prisms’ and the flat aragonitic tablets of nacre lies in the difference in the habit of crystals; in nacre, growth on the (001) face is very slow, whereas in the fibres it is very fast. The result is a layered microstructure (nacre) which is much stronger than fibrous aragonite.

Most of the common molluscan ultrastructures had evolved by the Middle Cambrian. In addition to spherulitic prismatic aragonite and nacre, these included tangentially arranged fibrous aragonite, crossed-lamellar aragonite, and foliated calcite.

Various solitary and colonial animals among the earliest skeletal biotas built basal skeletons of

calcium carbonate. Most of these are poorly known. The cup-shaped hydroconozoans and the probably colonial *Bija* and *Labyrinthus* may only questionably be referred to the cnidarians (Jell 1983). Others, such as *Tabulaconus* and *Cothonion*, have been studied in more detail and show certain similarities with corals, but their affinities nevertheless remain in doubt. Undoubted skeleton-forming cnidarians are not known until the Ordovician. The basic structural units in rugose and tabulate coral skeletons were spherulitic tufts (trabeculae) formed by fibrous calcite. Modern scleractinian corals form similar structures of aragonite fibres. As with the spherulitic 'prisms' of mollusc shells, the process of formation appears to involve little matrix-mediated control of crystal shape. However, nucleation of the fibrous trabeculae may be under more direct biochemical control.

The sponge-like archaeocyathans constructed a supporting skeleton typically shaped like a double-walled perforated cup. They are preserved as microgranular calcite, interpreted as representing original magnesian calcite (James & Klappa 1983). Calcium carbonate (aragonite or calcite) skeletons are also formed by several groups of sponges ('sclero-sponges' and 'sphinctozoans') from the Middle Cambrian until the Recent (Vacelet 1985). The more common type of sponge mineralization is, however, the spicular skeleton (see below).

All the skeleton types described above exhibit incremental growth, which occurs by addition of material to earlier formed growth stages. This type of growth puts strong geometrical constraints on morphology. Ways of avoiding this problem are: (1) periodical moulting of exoskeleton; or (2) continuous construction and destruction of the mineral phase by intimately associated living tissue.

Trilobites, common in Cambrian rocks from the Atdabanian (c. 540 Ma; Fig. 1), are an example of animals that periodically moulted their exoskeletons. These were of calcitic composition and often show well-preserved crystallographic fabrics in their mineralized cuticle. Other examples are the coeloscleritophorans, uniquely Cambrian organisms with a complex exoskeleton consisting of hollow carbonate sclerites with a basal opening. Their original mineralogy has not been definitely established, but the ubiquitous recrystallization and occasionally preserved fibrous structure suggest that they were aragonitic.

Echinoderms, first appearing in the Atdabanian and undergoing their first substantive radiation in the Middle Cambrian, developed a calcium

carbonate endoskeleton in which there was close interaction of mineral and living tissue. Modern echinoderms construct their skeletons of a mesh-work (stereom) of almost pure magnesian calcite, in which each individual skeletal component is part of a large single crystal. All fossil echinoderms, including the Cambrian ones, appear to have had an identical structure.

Spicules — mineralized elements formed within living tissues — are widely distributed among Recent organisms. Spicules of magnesian calcite are characteristic of calcareous sponges and octocorals. In both groups the spicules are formed by specialized sclerocytes, sometimes originating intracellularly and only later erupting from the cell membrane to be further enlarged by enveloping sclerocytes. Sponge spicules grow in crystallographic continuity, so that each spicule behaves optically as a single crystal of calcite. By contrast, octocoral spicules typically are composed of smaller acicular crystals. As the echinoderm plates, sponge and octocoral spicules are made of magnesian calcite, it has been suggested that magnesium is used to shape the crystals by selectively poisoning appropriate parts of the lattice (O'Neill 1981). Calcitic sponge spicules have been found in the late Atdabanian (c. 535 Ma, Fig. 1), and possible octocoral spicules also appear in beds of the same age. Undoubted spicules of octocorals are known from the Silurian. The fossil sponge and octocoral spicules have the same crystallographic properties as their modern counterparts.

Although fossil spicules of various origins are common, they are rarely dealt with in scientific literature because they tend to be disarticulated and therefore difficult to identify taxonomically. Some spicular skeletons may fuse to form frameworks, as in hexactinellids, 'lithistid' demosponges, and 'pharetronid' calcareous sponges, or the axial skeletons of pennatulacean and a few alcyonarian octocorals. Such structures are rare in the early history of these groups.

Fossils resembling calcified cyanobacteria became common in the Early Cambrian. One group of such organisms, the helically coiled filamentous *Obruchevella*, is present as uncalcified filaments in rocks of Vendian age, but is frequently calcified after the beginning of the Cambrian. Calcified cyanobacteria have their mucilagenous sheaths impregnated with crystals, perhaps as a by-product of the photosynthetic removal of CO₂ from the water in which they lived (Riding 1977). Fossils that may be true calcareous algae occur in the c. 550 Ma Nemakit–Daldyn

beds of the northern Siberian Platform. More convincing examples are first known from the Middle Cambrian.

Phosphatic fossils

As a skeleton-forming mineral, apatite occurs today only in inarticulate brachiopods and vertebrates. Some recent organisms are also known to produce amorphous calcium phosphate that may be crystallized later into apatite. Among the earliest skeletal organisms, however, calcium phosphate appears to have been more widespread.

Tubular fossils of phosphatic composition are a common constituent of Cambrian faunas. Most of them are referred to as hyolithelminths. The fine structure of hyolithelminth tubes has not been sufficiently studied, but they appear to have grown incrementally by addition of lamellae. At least in some forms a systematic change in the orientation of fibrous elements in adjacent lamellae occurs, producing a force-resistant structure similar to that of arthropod cuticles. The phosphatic tubes of the paicutiids had longitudinal septum-like structures on the inner surfaces. Conulariids had distinctly four-faceted cones built up of transverse phosphatic rods set in a flexible integument.

Phosphatic conchs or shells were also widespread. In addition to phosphatic inarticulate brachiopods, there are also a number of problematic phosphatic shells, such as *Mobergella* and related fossils, characterized by regularly placed paired muscle scars and a usually flattened shape. The brachiopods include a number of phosphate- and carbonate-shelled clades, many of which were short-lived.

One characteristic and diverse Cambrian group is the tomotiids — multisclerite-bearing animals presumably covered with more or less twisted conical sclerites built up of phosphatic growth lamellae. They vary in skeletal organization from the irregularly shaped and frequently fused sclerites of *Eccentrotheca* to the highly organized scleritomes of *Camenella* and *Tannuolina*, in which each of the two asymmetric sclerite types had its mirror-image counterpart.

Examples of periodically moulted exoskeletons of calcium phosphate are rare, but the valves of the ostracode-like bradoriids are commonly preserved as phosphate. Although some of them appear to have been flexible, they were most probably impregnated to varying degrees with apatite crystallites. Like most arthropod skeletons, they did not grow by accretion, but were periodically shed.

Whether or not the ecdysis involved resorption of mineral matter is not known, but resorption may explain the common occurrence of collapsed or buckled valves.

The problematic fossil *Microdictyon* formed plate-like structures with a more or less regularly hexagonal network of holes and intervening nodes. They were constructed of two or three distinct layers of apatite and show no evidence of incremental growth.

Vertebrates, similar to echinoderms, have a plastic mode of skeleton formation as a result of a constant physiological exchange between mineralized and cellular tissues. The phosphatic bone of vertebrates is intimately associated with fibrillar collagen, which does not seem to be the case in other phosphatic skeletons. Although undoubted vertebrate remains are not known until the Ordovician, certain Cambrian phosphatic fossils show a fine structure suggesting association with fibrous organic matter that may be homologous with vertebrate collagen.

The small button-shaped sclerites of the utah-phosphans consist of a thin dense apatite layer covering a porous core; the latter has fine tubules or fibrils perpendicular to the lower surface. The 'buttons' are more or less densely set in an integument that is impregnated with smaller apatitic crystallites. The tooth-shaped conodonts had a fibrous organic matrix in which the apatite crystallites were embedded (Szaniawski 1987). In both these cases, a chordate affinity has been proposed using partly independent lines of evidence. Other suggested biomineralizing chordates (*Palaeobotryllus*, *Anatolepis*) are even more problematic in their interpretation.

There are further examples of exclusively Cambrian fossils of phosphatic composition and unknown systematic affinity. Some of these are spine- or tooth-shaped objects, possibly reflecting the fact that apatite is a hard mineral suitable for the construction of wear-resistant structures.

Siliceous fossils

Because of its non-crystalline, isotropic nature and intracellular method of formation, opal (a mineral gel consisting of packed spheres of hydrated silica) has had limited potential as a skeletal material except in very small organisms. It is most widespread among protists. The only metazoans known to form it are hexactinellid sponges and demosponges, which use it for spicule formation. Most biogenic

opal formed today is either dissolved in the water column before it is incorporated in the sediment or dissolved during early diagenesis, but under certain circumstances opaline skeletons may be preserved, usually as microcrystalline quartz or replacements by other minerals.

The distribution of opal among the earliest skeletal fossils differs significantly from that of calcium carbonates and phosphates. Only four groups of silica-producing organisms are known from the time period under consideration (Fig. 1), hexactinellids, demosponges, radiolarians, and chrysophytes(?). All appeared during the Early Cambrian and all are still living. Whether this apparent immortality of opal-producing lineages is a chance effect due to the small number of clades involved, or whether it has a more profound meaning, the pattern differs considerably from that seen in the carbonate and phosphatic groups. In the latter two, the Cambrian radiation appears to have produced a large number of taxa of which only a few survived.

Early history of skeletal biomineralization

Present knowledge of the fossil record confirms that mineralized skeletons of many different kinds and composition appeared very rapidly in a number of clades at the beginning of the Phanerozoic. Analysis of the precise pattern is still difficult, because in many cases the original mineralogy is insufficiently known and the taxonomic understanding of the various enigmatic early skeletal fossils is incomplete (see also Section 5.2.5). It is therefore difficult to know how many clades developed the ability to form mineral skeletons at this time. It seems clear, however, that this ability evolved independently a number of times.

A current and widely held view is that those organisms that used phosphate rather than carbonate or silica were the first to diversify. Phosphate has been stated to be the dominant or even exclusive mineral of the earliest skeletal faunas. A phosphate-carbonate transition is said to have occurred within clades such as the Ostracoda, Brachio-poda, and Cnidaria, but also by the replacement through extinction of organisms with phosphatic skeletons by organisms with carbonate hard parts. Aragonitic materials are also postulated to have replaced calcitic ones throughout the remainder of the Phanerozoic.

Available data, including the pattern of distribution of clades of different biomineralizing habits through time (Figs 1, 2) and the phylogeny within

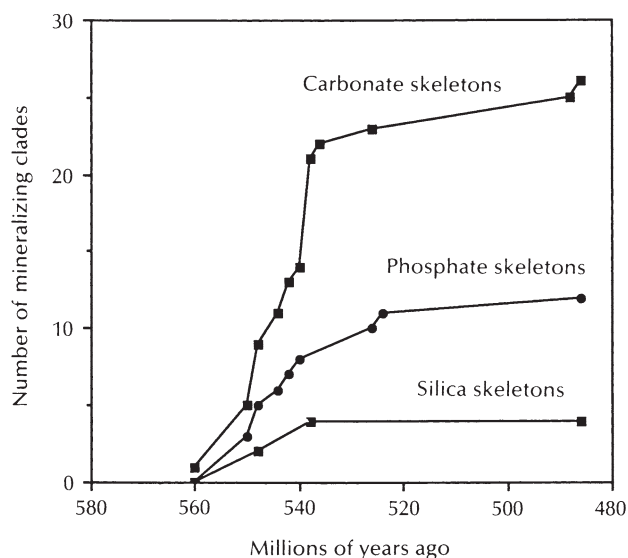


Fig. 2 Cumulative curves of appearance of clades presumed to have independently evolved a biomineralizing habit. Based on the same data as Fig. 1.

these clades, do not appear to support such views.

1 The relative amount of phosphate versus carbonate bound in biominerals in the Cambrian has been exaggerated by sampling biases (most early skeletal fossils are of millimetre size, and chemical extraction of microfossils is more likely to destroy carbonates than phosphates) and unrecognized cases of secondary phosphatization (the Cambrian was a time of extensive deposition of phosphatic sediments).

2 Whereas phosphate skeletons were certainly more widely distributed among different clades in the Early Cambrian than they are today, the same may be said about carbonate ones. Among the clades shown in Fig. 1, 42% of the carbonate skeletons survive until the present, as compared to 25% of the phosphatic ones (protoconodonts are regarded as chaetognaths with mineralized grasping spines). Both categories include clades that are today very successful and diverse. Thus the restriction of phosphate minerals to two major clades today may simply be the result of the different evolutionary success of various early lineages. Nothing in the history of vertebrates suggests that their skeletal mineralogy puts them at an evolutionary disadvantage, and there is no reason to assume that the shell mineral was the particular factor that decided the survival of each of the early lineages.

3 The quoted examples of phylogenetic transition from phosphate to carbonate, or from aragonite to

calcite, appear to be suspect. For example, a suggested evolutionary succession from phosphate to carbonate hard parts within the cnidarians depends upon the dubious taxonomic decision to place the extinct conulariids within the Cnidaria. The proposed secondary origin of carbonate brachiopods from phosphate ones and the derivation of carbonate ostracodes from pre-existing phosphate forms have the merit of linking groups that are clearly closely related, but the proposal of a mineralogical transition is nevertheless weakly founded. In neither case has a strict phylogenetic analysis been able to demonstrate that the carbonate forms are in fact derived from the phosphate ones.

The Early Phanerozoic radiation cannot be seen just as a radiation of biomineralizing taxa. The trace fossil record shows a similar rapid diversification of burrowing habits in non-biomineralizing organisms, and the appearance at the same time of resistant organic structures and agglutinating tubular fossils shows that the key event is not biomineralization as such (see also Section 1.5). To a certain extent, the appearance of mineralized skeletons may be seen as one of many aspects of the early radiation of multicellular organisms. Nevertheless, the apparent absence of biominerals in the Ediacaran fauna and the nearly simultaneous 'skeletalization' of cyanobacteria (notwithstanding reports of earlier sporadic cases of mineralized cyanobacterial sheaths), algae, heterotrophic protists (foraminiferans and radiolarians), and metazoans, seems to call for specific explanations.

Attempts to explain the appearance of skeletons have often foundered on lack of universality. For example, models involving calcium availability or regulation do not explain the simultaneous appearance of opaline skeletons, and the proposal that biomineralization began as a phosphate-excreting process at a time of high phosphate availability is not consistent with the pattern of appearance of various biominerals as discussed above. Models based on increasing PO_2 may have more explanatory power, as an increasing availability of oxygen would have made it easier for organisms to form skeletal minerals and proteins, and made outer mineralized skeletons less of a respiratory disadvantage.

(There is a general but not perfect correlation between distribution of mineralized skeletons and oxygen levels in modern marine faunas.)

A synecologically based explanation is that biomineralization in animals and plants primarily arose in response to selection pressures induced by grazers and predators. No evidence of grazers or predators is known from the Ediacaran fauna, whereas the first probable macrophagous predators (protoconodonts) appear with the first diverse skeletal biotas. Although the various types of skeletons in the early Phanerozoic biota often had complex functions, most of them would have had the advantage of at least passively deterring predators or grazers. Such an explanation stresses the view of the early evolution of skeletons as a complex event, integrated with other aspects of the rapid biotic diversification at this period. It is not in conflict with physiologically and geochemically based models explaining how biomineralization became possible in the first place.

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1.5 Late Precambrian—Early Cambrian Metazoan Diversification

S. CONWAY MORRIS

Introduction

Life on this planet is customarily divided into six kingdoms, the prokaryotic archaeobacteria and eubacteria, and the four eukaryotic kingdoms of prototists, fungi, plants, and metazoans. Because the multicellular metazoans had their origins in unicellular eukaryotic ancestors, in principle the identification of such an organism in the fossil record would constrain the time of appearance of the metazoans. However, even the recognition of the first eukaryotes has proved problematic. It has been customary to regard eukaryotes as being derived from prokaryotes, and given the profound differences between the two cell types such a distinction might seem to be readily identifiable in the fossil record. However, even these critical characters (e.g. presence of nucleus, cell wall composition) fail to survive fossilization, and the only guide is relative cell size.

Thus, the search for the earliest eukaryotes has concentrated on evidence for either relatively large unicells (see also Section 1.2) or, better, a more complex multicellular organism, perhaps even with differentiated tissues. In terms of the former criterion, the appearance of large cells in sediments dated at approximately 1300–1400 Ma is generally taken as the first reliable indication of eukaryotes. In similar aged strata, fossils composed of large carbonaceous films probably represent multicellular prototists, perhaps brown algae. Nevertheless, given the overlap in cell diameters between eukaryotes and prokaryotes, it is not impossible that some cellular remains from yet older sediments are eukaryotes masquerading as prokaryotes.

Given these problems, it is necessary to review first the generally agreed bench-marks leading to the appearance of metazoans. The earliest definitive metazoans are taken as the Ediacaran faunas (Glaessner 1984) that span the interval c. 550–620 Ma. Allowing for considerable uncertainties the earliest eukaryotes may be as old as 1600 Ma, allowing a possible 1000 Ma for the development of metazoans. This article, therefore, is divided into two sections. The first reviews such slender evidence as is available

on pre-Ediacaran metazoans, much of it questionable. The second section then addresses the outlines of the adaptive radiation that is marked by the Ediacaran faunas and the succeeding Cambrian biotas.

Pre-Ediacaran metazoans

The most compelling pre-Ediacaran evidence would be soft-bodied remains. Recently, structures interpreted as worms (Sun *et al.* 1986) have been reported from Northern China (Anhui and Liaoning provinces). In overall form some of these carbonaceous structures, known as *Sinosabellidites* and *Protoarenicola* are very similar to a sausage-like megascopic Precambrian alga known as *Tawuia*, but they differ in possessing fine annulations. Another supposed worm, referred to as *Pararenicola*, also possesses annulations, but is somewhat smaller and stouter than *Sinosabellidites*. Nevertheless, their identification as metazoans is otherwise equivocal, not least because neither internal structures, such as a gut trace, nor cephalization are recognizable. In particular, claims for a so-called proboscis in *Pararenicola* and *Protoarenicola* are dubious. Moreover, the quoted dates of between 850 and 740 Ma are based on questionable radiometric determinations and correlations with other regions in China, and the pre-Ediacaran status of these fossils is still open to doubt.

With regard to trace fossils from pre-Ediacaran strata, there are numerous claims, but few have won acceptance. Supposed metazoan traces from the Medicine Peak Quartzite of Wyoming (Kauffman & Steidtmann 1981), dated at c. 2000–2400 Ma are remarkable in view of the current consensus that the seas were colonized by nothing higher than cyanobacterial mats. Another widely quoted example is a possible feeding trace (*Brooksella canyonensis*) from the Grand Canyon. This is ostensibly from the 1100–1300 Ma old Grand Canyon Series, but renewed searches appear to have been unsuccessful. While other specimens from a wide variety of localities provide a seemingly

from a wide variety of localities provide a seemingly impressive roster of evidence for trace fossils, in nearly every case unresolved doubts remain. Even if some pre-Ediacaran traces prove genuine, their general scarcity is difficult to explain unless extrinsic factors (e.g. oxygen levels) prohibited the wide-scale expansion of macroscopic metazoans into an effectively empty ecospace.

While these relatively large trace fossils continue, therefore, to excite scepticism, it may be that more convincing evidence could be found at a microscopic level. For example, possible faecal pellets have been reported from the c. 900 Ma Zilmerdak 'Series' of the Urals (Glaessner 1984), which, if confirmed, which, would indicate a grade of organization above that of the turbellarians. Clearly, a more extensive survey in suitable lithologies is required. In particular, ultrastructural studies of sediments may show features diagnostic of bioturbation. For example, documentation of grain orientation and cation concentrations (e.g. iron, aluminium) around undoubted Phanerozoic trace fossils suggests a possible approach to establishing the biogenicity of some Proterozoic examples (Harding & Risk 1986). Moreover, cherts that evidently formed at a very early stage of diagenesis, from the c. 700 Ma Doushantuo Formation in the Yangtze Gorges of Hubei Province, China, preserve narrow burrowlike structures that may represent the activities of a meiofauna.

While the Precambrian fossil record is dominated by stromatolites, it has long been realized that they undergo a decline in diversity during the late Precambrian (see Fig. 2). A recent reanalysis of the data (Walter & Heys 1985) indicates that, in terms of both relative abundance and diversity, stromatolites began to decline in quiet, subtidal environments (where coniform varieties were especially abundant) from about 1000 Ma. This trend was established also in intertidal environments from c. 800 Ma, so that stromatolites were relatively unimportant by the beginning of the Cambrian. The traditional explanation links this pattern to the rise of grazing metazoans whose activities were detrimental to the formation of the microbial mats. Thus, the initial dip in stromatolite diversity at 1000 Ma may herald the rise of primitive grazers, while the accelerating process of decline after c. 800 Ma could represent the widespread distribution of metazoans. However, the development of disrupted stromatolitic fabrics (a thrombolitic texture) that may be a result of extensive burrowing by metazoans, only appears in the Cambrian.

Further indirect evidence for the evolution of

metazoans at least one billion years ago comes from molecular studies. If it is demonstrated that the substitution of either nucleotides in nucleic acid chains or amino acids in polypeptides is stochastically constant and occurs at a known rate, then the differences between the sequences in any species pair should indicate their time of divergence. Using this assumption of the so-called molecular clock, existing data on haemoglobins (a group with a substitution rate that is appropriate for the time-scales involved) have been used to suggest that the metazoans evolved between c. 800 and 1000 Ma. A related approach utilizes 5S ribosomal RNA sequences, and such comparisons (Hori & Osawa 1987) suggest that Mesozoa might be the most primitive metazoans (if they are not derived independently from protoctists). Moreover, although the Mesozoa may have arisen before 1000 Ma, other metazoans such as the turbellarians and nematodes have divergence points at only c. 700 Ma.

Ediacaran faunas

The evidence for pre-Ediacaran metazoans is mounting, but the view that the fossil record indicates no metazoan older than c. 600 Ma is still respectable and it is the Ediacaran faunas that provide our first useful glimpse of metazoan evolution (Glaessner 1984; Conway Morris 1985; see also Section 1.3). Such faunas were described from Namibia, at that time Deutsch Sud-West Afrika, before the Second World War, and shortly afterwards in Australia. At first regarded as Cambrian, their persistent occurrence beneath abundant shelly fossils soon led them to be consigned to the Precambrian, and continuing reports from numerous localities around the world have confirmed this observation. Until recently these faunas have been dated at c. 620–680 Ma, with some claims of even 800 Ma. However, recent radiometric dating has cast major doubt on these estimates. High resolution uranium–lead dating of zircons from an ash fall that entombed an Ediacaran assemblage in South-east Newfoundland (Fig. 1) yields a date of c. 565 Ma. Even so, the age range of the Ediacaran faunas may be considerable, and a span of c. 550–620 Ma may not be unrealistic.

The Ediacaran faunas are reviewed elsewhere (Section 1.3), and only a general survey in the present context is required. At present, there seem to be two broad assemblages. There are those of a shallow-water type that are superbly represented in the Flinders Ranges of South Australia, including the

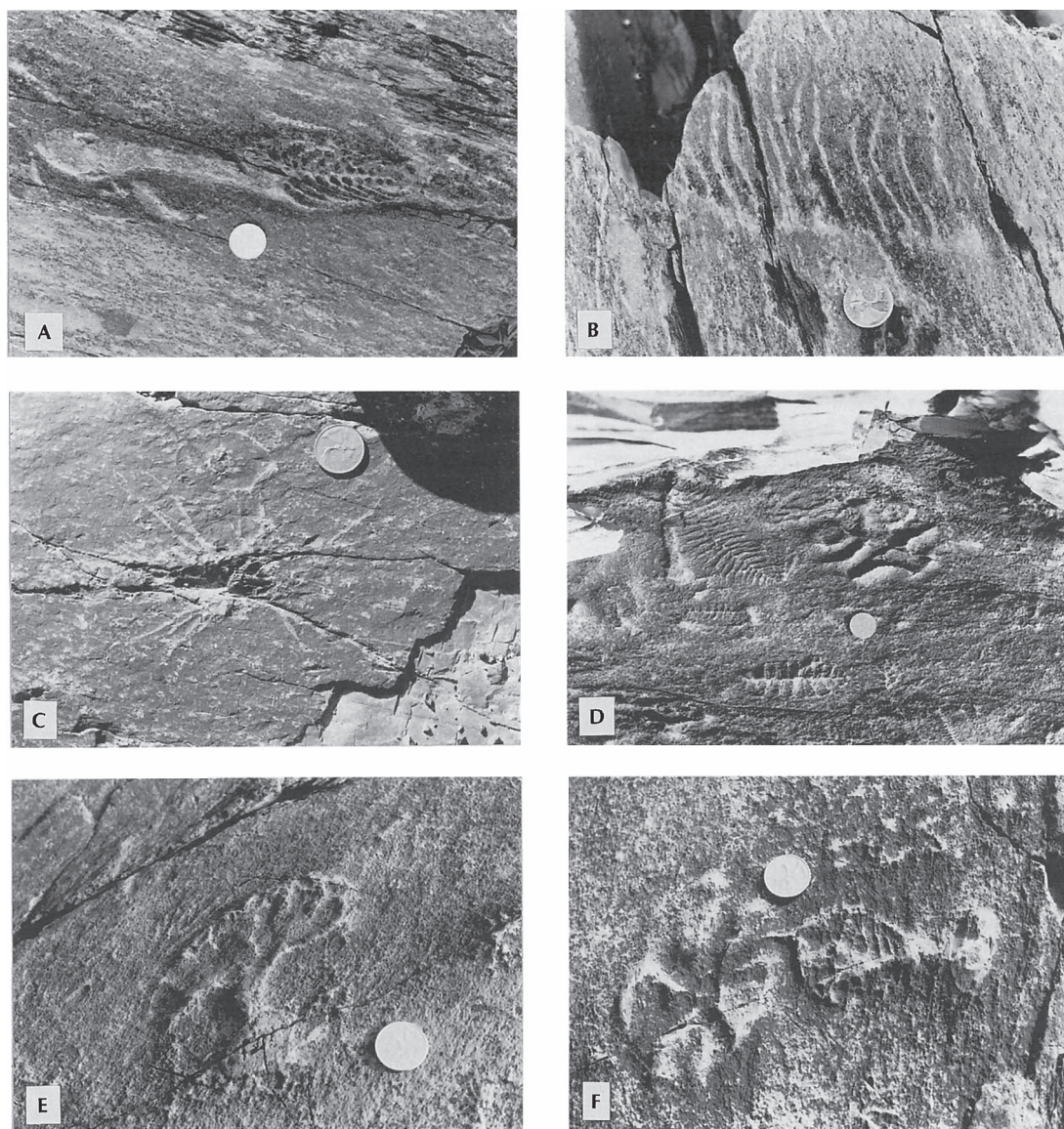


Fig. 1 Ediacaran fossils from the Mistaken Point Formation (Conception Group) of Southeast Newfoundland, Avalon Peninsula. A, Pennatuloid with hold-fast. B, Pectinate organism. C, Stellate organism. D, Bedding plane with spindle organisms and medusoids. E, Branching organism with hold-fast. F, Pennatuloid with hold-fast and medusoid. Diameter of coin 23 mm.

Ediacaran Hills, and the closely similar fauna from the White Sea of northern U.S.S.R. In contrast, the faunas of the Avalon Peninsula of southeast Newfoundland, which may be referred to as the Mistaken Point assemblage (Fig. 1), in reference to the spectacular locality near Cape Race, appear to represent a deeper-water facies. Similar occurrences in Charnwood Forest, U.K. are one of the many lines of evidence that in the early Phanerozoic this area was joined to the Avalon area on one side of the Iapetus ocean. Possibly deeper-water faunas may

also occur in the Flinders Range, but as yet only preliminary reports are available.

Despite the range of environments inhabited by these Ediacaran assemblages, they show several characters in common. Most typical are forms that the majority of workers would ascribe to the cnidarians. These include medusoids (Fig. 1D, F), some of which may be placed with reasonable confidence in cubomedusoids, chondrophores, and perhaps scyphozoans. However, other jellyfish have a highly characteristic three-fold symmetry

that finds no parallel amongst living cnidarians. Yet others lack sufficient characters to be assigned with confidence to any group. In addition, stalked forms with an expanded leaf-like body arising from a central rachis (Fig. 1A, F) invite comparisons with the pennatulaceans (the sea-pens). However, these similarities become increasingly tenuous amongst a variety of other foliate to bag-shaped organisms, and their cnidarian affinity is more questionable. Other organisms include a possible worm, the sheet-like *Dickinsonia*, a medley of arthropod-like forms, and a possible echinoderm with penta-radial symmetry (Gehling 1987).

Although the Mistaken Point assemblages evidently owe their preservation in most instances to being overwhelmed by volcanic ash, in many other cases the occurrences of these soft-bodied metazoans as sandstone impressions above siltstone intervals are difficult to explain, given the absence of such preservation in younger clastics. The problem is compounded by abundant trace fossils in some Ediacaran assemblages, most typically simple sinuous trails, that cannot be linked to the activities of any of the known body fossils. It seems necessary to invoke a contrast between entirely soft-bodied organisms, such as the trace-producing worms that were possibly largely infaunal, and those with a tougher integument, many either epifaunal or pelagic and coming to rest on the sea-floor prior to burial. It was only this latter group that was sufficiently tough to take impressions when immured by sediment. However, the explanation has not won universal approval. In a sweeping reappraisal Seilacher (1989) proposed that the Ediacaran organisms represent an entirely separate group, possibly a distinct kingdom, that owe their preservation to a unique composition consisting of a sac-like body with a tough integument. While Seilacher has highlighted the taphonomic problems posed by this preservation, his ingenious proposal seems to be oversimplified and, while perhaps applicable to some of the sac-like ernietids (see also Section 1.3) and *Pteridinium*, is difficult to reconcile with the bulk of the biota.

Whatever disagreements surround the biological affinities of the Ediacaran fauna, it is clear that they lacked hard skeletal material, the widespread appearance of which was to usher in the Cambrian some 20 Ma later. However, one notable exception demands comment. In Namibia carbonate units, intercalated with clastics containing Ediacaran fossils, yield calcareous tubes referred to as *Cloudina* (Grant 1990) (see also Section 1.4). The tubes are

double walled with connecting partitions that give a cone-in-cone appearance, although the exact mode of secretion is not clear. There is evidence that originally the walls contained substantial amounts of organic matter, and this helps to fuel the speculation that the origin of skeletal hard parts was as separate spicules or granules embedded in an organic matrix. The facies contrast in Namibia between the clastics bearing the Ediacaran fauna and the carbonates with *Cloudina* emphasizes the need for taphonomic judgements concerning original faunal distribution. However, occurrence of Ediacaran faunas in dolomites in northern Siberia demonstrates that preservation is not governed simply by lithology.

The role of the Ediacaran faunas in determining the origins of the Cambrian fauna at present is enigmatic. With the possible exception of the arthropod- and echinoderm-like forms, existing reports would indicate little continuity with either the shelly faunas or soft-bodied Burgess Shale-type assemblages. Descriptions of new finds from Siberia and Australia may go some way towards alleviating the problem, and it is likely that many of the putative ancestors are represented either by the unknown trace makers or animals too small to be preserved.

The evident demise of the Ediacaran fauna has resulted in two alternative hypotheses that are not entirely exclusive. One appeals to a change in taphonomic conditions, in particular the rise of Cambrian predators and scavengers that militated against soft part preservation. It is, however, of considerable significance that a distinct gap separates the disappearance of the Ediacaran fauna from the debut of Cambrian assemblages, an interval that contains facies that otherwise would appear suitable for preservation (Narbonne & Hofmann 1987). If indeed a substantial fraction of the Ediacaran fauna became extinct over a geologically brief period, then it may be that the subsequent Cambrian diversification was largely a response to the ecological opportunities presented. The evidence for such an end-Ediacaran mass extinction (Section 2.13.1) at present is very tenuous. It is necessary to emphasize, however, that as yet no data point to any extra-terrestrial mechanism. If comparisons were to be drawn with other mass extinctions, then there are possible similarities with the end-Permian event (Section 2.13.4) in which the formation of a super-continent and possibly development of brackish oceans because of massive evaporite deposition are invoked as significant factors.

Cambrian biotas

Whether or not there was an end-Ediacaran mass extinction, the ensuing diversifications of the Cambrian were a spectacular evolutionary event (Brasier 1979; Conway Morris 1987). Most obvious is the appearance of abundant skeletal parts (Section 1.4) composed of calcium carbonate, calcium phosphate or silica, which together provide for the first time in the history of Earth an adequate fossil record.

Given that the bulk of the fossil record consists of shelly fossils, it is not surprising that the many explanations offered for the Cambrian diversifications have focused on the origin of hard parts. While special explanations may be called for, soft-bodied organisms may have outnumbered greatly those with skeletons in the original Cambrian communities and the history of diversification of trace fossils during this interval is also an important component in documenting these adaptive radiations. Although the rise of the skeletal faunas is clear in outline, detailed resolution is hampered by uncertainties regarding inter-continental correlations, such that the exact sequence of events is still uncertain. Present evidence, however, suggests that (apart from *Cloudina*) the earliest skeletal fossils included anabaritids (elongated tubes with a highly characteristic trifoliate cross-section) and the teeth of protoconodonts, a group probably related to the modern chaetognaths (arrow-worms). Shortly afterwards they are joined by more shelly fossils, including a distinctive monoplacophoran known as *Purella*, the gastropod *Aldanella*, and primitive hyoliths. The succeeding horizons record an abundance of additional shelly fossils (Bengtson 1977), many of enigmatic affinities (see also Section 5.2.5) but also including additional monoplacophorans, the first gastropods, hyoliths, brachiopods, sponges, and, somewhat later, echinoderms. The majority of these fossils are relatively small (c. 1–2 mm), and are either composed of phosphate or are replaced secondarily by this compound. These small shelly fossils (see also Section 1.4) are the subject of active study, with special interest in the more enigmatic taxa (Bengtson 1977).

Although for many species biological relationships are entirely speculative, in others a natural classification is beginning to emerge. Three important groups include the tomotiids, which possessed a primary phosphatic skeleton, the coeloscleritophorans which comprise halkieriids, siphonochitids, and cancelloriids, and the cambroclaves,

the last two having calcareous skeletons. In each group the skeleton is composite, being composed of a series of sclerites that disarticulated on death. This extraordinary array of small shelly fossils persists during the early stages of the Cambrian, especially the Tommotian and Atdabanian, with some lingering into the Middle and even Upper Cambrian. It is noteworthy that the trilobites, which dominate the majority of Cambrian shelly faunas, are absent from the earliest assemblages. However, their appearance in different sections was probably not synchronous, and their debut was probably due to mineralization on pre-existing forms with only a chitinous skeleton, rather than an evolutionary event *per se*.

The rise of these skeletal faunas has been interpreted in both ecological terms, especially the rise of predators conferring the need for protective structure, and in terms of changes in the physico-chemical environment (Conway Morris 1987; see also Section 1.4). The evidence that many groups possessed either tightly interlocking sclerites that probably formed a coat over the exterior, or valves that enclosed or allowed the retraction of the soft parts, certainly supports a response to predation. In some specimens, especially tubicolous taxa, small boreholes occur. They probably represent predatory activity, but the nature of the attacker is speculative. It is also likely that the protoconodonts formed part of a predatory feeding apparatus, but in general it is necessary to infer that many of the early Cambrian predators were more or less entirely soft-bodied.

Examples of Lagerstätten that might reveal the nature of such soft-bodied organisms are not known until the Atdabanian, and of these the Burgess Shale-like Cheng-jiang fauna in Yunnan Province, South China is by far the most important. This fauna has not yet received detailed analysis, and much of our information on the role of soft-bodied organisms in the initial Cambrian diversifications must continue to rely on evidence from trace fossils (Crimes 1987). A general diversification that parallels the skeletal record is now well known. In particular, Vendian traces typically are rather small and two-dimensional. Some ichnotaxa survive into the Cambrian, but a number (e.g. *Harlaniella*) are restricted to this interval and therefore have a biostratigraphic utility. The striking increase in trace fossil diversity near the Precambrian–Cambrian boundary (Section 5.10.2) includes vertical burrows, scratch marks that generally are attributed to arthropods, and other traces that often indicate increasing behavioural complexity. It is also striking that

ichnotaxa regarded as diagnostic of either shallow- or deeper-water where they occur later in the Phanerozoic, are found together in shallow-water environments (Crimes & Anderson 1985). Indeed, it has been proposed that the deep oceans were not colonized until later in the Palaeozoic, and that the displacement of some trace makers into deeper water was a result of competitive pressure in the shallows.

While the role of ecological changes has dominated discussion on the evolution of early metazoans, it now appears that substantial alterations in the extrinsic physico-chemical environment were also taking place during this time (Conway Morris 1987). The extent to which such changes influenced or even controlled evolutionary events is far from clear, although the near synchronous nature of them is certainly suggestive.

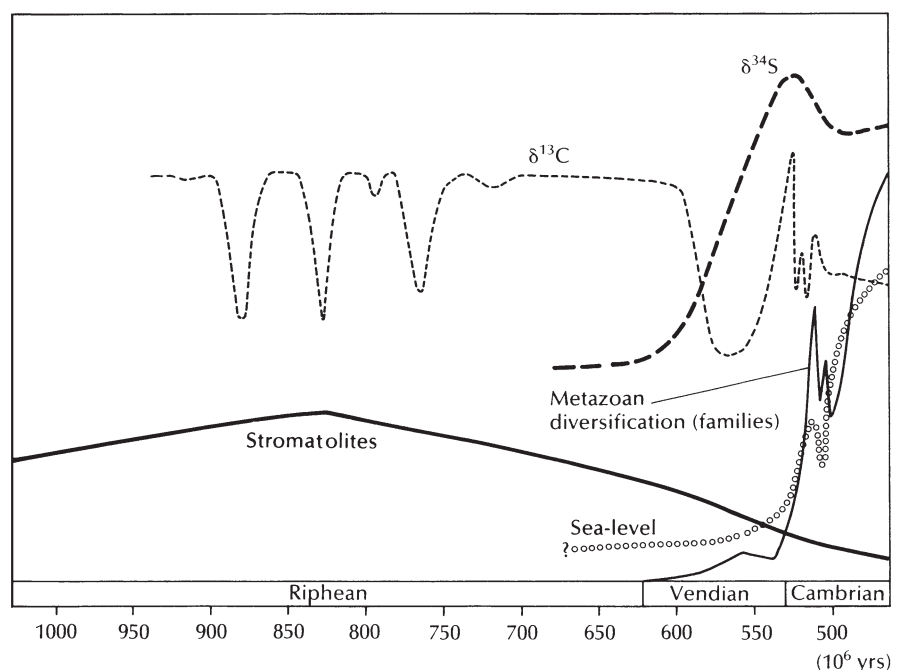
Changes in the physico-chemical environment

Extrinsic changes are registered in several ways, including: palaeocontinental distributions, sea-level curves, stable isotope variations (especially of carbon and sulphur), preference for either aragonite or calcite precipitation, and phosphate deposition. While the extent and nature of the late Precambrian super-continent is still under debate, there is clear evidence for major rifting episodes close to the Precambrian–Cambrian boundary that heralded its break-up. While the separation of continental

blocks would have encouraged the development of endemic faunas, the formation of hot, spreading ridges would have led to displacement of seawater and hence a major transgression. While the history of this Cambrian transgression is not well known in detail, it had the dual effect of increasing the habitable area for shallow-water marine life and providing an increasingly complete rock record as the facies belts migrated cratonward (Brasier 1979).

There is also evidence for substantial changes in ocean chemistry close to the Precambrian–Cambrian boundary (Fig. 2). For example, measurements of sulphur isotopes ($\delta^{34}\text{S}$) from very late Precambrian evaporites record a massive positive shift (the Yudomski event) that reflects the introduction of substantial amounts of isotopically heavy seawater into areas of evaporite formation by some sort of upwelling. The shift is so significant that it probably represents long-term storage of deep-water brines, where bacterial fractionation of sulphur led to accumulation of increasingly 'heavy' water. The sites of such storage may have been narrow 'Mediterranean-like' basins formed at an early stage of continental breakup, and the upwelling episode may also be linked to continuing evolution of the basins. It is probably no coincidence that the Yudomski event overlaps with a major episode of phosphogenesis, that is now reflected in huge economic reserves of phosphate in China and elsewhere. It has been speculated that the influx of phosphorous raised levels of productivity and

Fig. 2 Changes in ocean chemistry as registered in $\delta^{13}\text{C}$ and $\delta^{34}\text{S}$, inferred sea-level, and diversity of metazoans and stromatolites during intervals of the Riphean, Vendian and Cambrian. (Data for stromatolites from Walter & Heys 1985; other data sources listed in Conway Morris 1987.)



helped to fuel the evolutionary radiations. Inferences on ocean productivity have also been drawn on the basis of changes in carbon isotopic ratios ($\delta^{13}\text{C}$), which show a series of substantial shifts. However, in some instances storage of organic matter (rich in photosynthetically sequestered ^{12}C), such as in anoxic basins, may be invoked as an explanation and could be linked to the formation and destruction of narrow marine basins alluded to above. Although somewhat less constrained in terms of timing, there is also evidence for a shift in inorganic precipitation (e.g. ooids) of calcium carbonate polymorphs, from aragonite in the late Precambrian to calcite in the Cambrian. The reasons for this shift are complex, but stem from processes of plate tectonics. These include hydrothermal metamorphism at spreading ridges that lower the Mg:Ca ratio of seawater, rise of partial pressure of CO_2 by volcanic exhalations, and deposition of carbonates in shallow seas versus their weathering on exposed continents. Taken together, the shift towards calcite precipitation appears to be controlled in part by continental breakup, growth of spreading ridges and subduction zones, and transgression of continental margins.

Just how important extrinsic factors, most of which seem to stem ultimately from the processes of plate tectonics, were in controlling evolutionary events is still uncertain. Metazoan diversification may have had its roots far back in the Riphean but, as yet, the possible influence of extrinsic factors on biological evolution in this interval is largely speculative. Nevertheless, the rise of skeletons near the Precambrian–Cambrian boundary can be linked with slightly more confidence to changes in ocean chemistry, and it is interesting that similar suggestions have also been made in connection with skeletal evolution during the great Permo-Trias faunal turnover. Some workers have even suggested that environmental factors may have led to sequential mineralization, from aragonite to high magnesium calcite to phosphate to low magnesium calcite (Brasier 1986). The complexity of the processes and the paucity of evidence in several critical areas, however, make this a challenging area for future palaeobiological research.

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1.6 Evolutionary Faunas

J. J. SEPKOSKI, Jr

Evolutionary faunas are sets of higher taxa (especially classes) that have similar histories of diversification and together dominate the biota for an extended interval of geological time. The expansion and decline of evolutionary faunas can be used to describe large-scale variations in faunal dominance and to interpret temporal changes in global taxonomic diversity in the fossil record. The concept was introduced by Sepkoski (1981), who identified three 'great evolutionary faunas' in the Phanerozoic marine record. These faunas were defined statistically in a factor analysis of familial diversity within taxonomic classes, which grouped together classes that attained their maximum diversities around the same time. The analysis permitted the histories of the aggregate faunas to be traced from initial diversification through dominance and into decline. This treatment of the faunas as units throughout their histories distinguishes the concept of evolutionary faunas from that of 'dynasties', used by some authors for assemblages of dominant taxa during specified intervals of geological time.

Marine evolutionary faunas

Characteristics. The three evolutionary faunas identified in the marine fossil record are the Cambrian Fauna, important during the Cambrian Period, the Palaeozoic Fauna, dominant from Ordovician to Permian, and the Modern, or Mesozoic–Cenozoic Fauna, dominant in the post-Palaeozoic (Fig. 1A). The classes in each fauna share a number of characteristics, or central tendencies, suggesting that they are not randomly assembled groups of taxa. The most striking characteristic is that the classes tend to diversify together, each successive fauna displaying a slower rate of diversification but higher level of maximum diversity than those preceding it. These properties lead to a sequential expansion of evolutionary faunas and a resultant step-like pattern of increase in global marine diversity (with the step between the Palaeozoic and Modern faunas disrupted by the massive Late Permian extinction event — Section 2.13.4). This pattern is present even though most marine classes originated early in the

Phanerozoic and the total number of classes has remained virtually constant since.

The expansion of each evolutionary fauna is associated with the decline of the previously dominant fauna. The declines are much slower than the initial diversifications, giving the faunas very asymmetrical histories. Such a pattern is difficult to simulate in 'random' models of diversification (Sepkoski 1981) but can be described with coupled logistic equations of the form

$$dD_i/dt = r_i D_i (1 - \Sigma D_j / \hat{D}_i),$$

where D_i is the diversity of the i th evolutionary fauna at time t , r_i is its initial diversification rate, \hat{D}_i is its maximum or 'equilibrium' diversity, and ΣD_j is the summed diversity of all faunas at time t (Sepkoski 1984; Kitchell & Carr *in* Valentine 1985). This equation states that an evolutionary fauna will diversify and replace the preceding fauna only if its initial diversification rate is lower and equilibrium diversity is higher. If r_i is higher, the evolutionary fauna will expand so rapidly that the preceding fauna will never appear to diversify; if \hat{D}_i is lower, the evolutionary fauna will never be able to expand and replace the preceding one. Thus, the coupled logistic equation suggests a certain inevitability in the sequential diversification of evolutionary faunas, although it does not specify their timing or relative differences in maximum diversity.

Classes within evolutionary faunas tend to have similar mean rates of taxonomic turnover. Classes in the Cambrian Fauna tended to have high turnover rates, those in the Palaeozoic Fauna intermediate rates, and those in the Modern Fauna comparatively low rates (with some exceptions in all cases). These differences are reflected in the responses of the faunas to mass extinctions (Sepkoski 1984): the Cambrian Fauna suffered large proportional reductions in diversity relative to the Palaeozoic fauna during mass extinctions in the Ashgillian and Frasnian, and the Palaeozoic Fauna suffered more than the Modern at all major mass extinctions of the Phanerozoic. This differential reaction seems to have led to the great change in faunal dominance associated with the Late Permian mass extinction (Section 2.13.4).

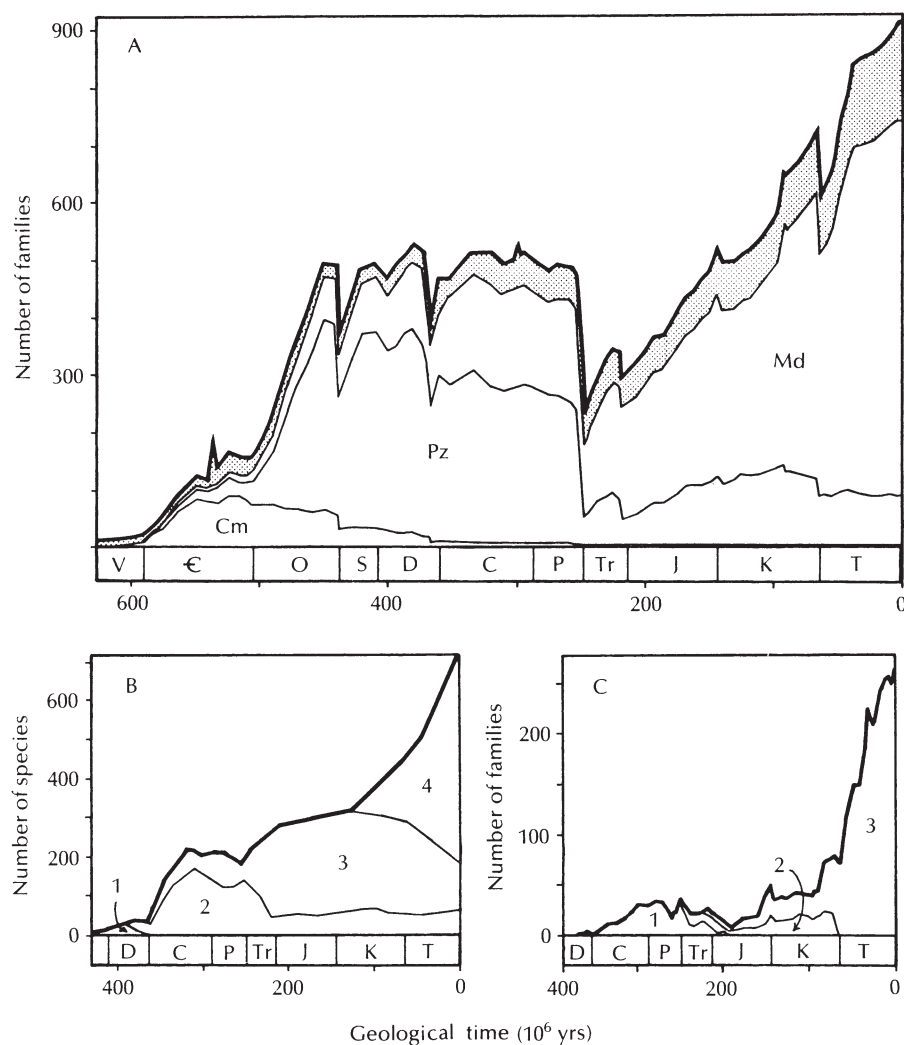


Fig 1 Diversity curves. A, Marine animal families. B, Terrestrial vascular plant species. C, Terrestrial tetrapod families. Each curve is divided into fields that illustrate the diversities of the constituent evolutionary faunas and floras. A, After Sepkoski (1984); Cm = Cambrian evolutionary fauna, Pz = Palaeozoic fauna, Md = Modern fauna; stippled field represents known diversity of families with rarely preserved members that lack heavily mineralized skeletons. B, After Niklas *et al.* (1983); numbered fields as in text. C, After Benton (1985); numbered fields as in text.

Evolutionary faunas also seem to have differing ecological characteristics. The Cambrian Fauna tended to be assembled into broadly intergrading communities that were dominated by generalized deposit feeders and grazers and had low epifaunal and infaunal tiering (Bottjer & Ausich 1986; see also Section 1.7.1). Communities of the Palaeozoic Fauna were dominated by epifaunal suspension feeders with complex tiering; many other ecological guilds were also represented so that the fauna as a whole seems to have occupied more 'ecospace' than the Cambrian Fauna (Bambach *in* Tevesz & McCall 1983). Finally, the Modern Fauna is represented by yet more guilds and is characterized by large numbers of durophagous predators (Vermeij 1987) and mobile deep infauna (Thayer *in* Tevesz & McCall 1983); epifaunal tiering is reduced in most communities.

Sepkoski and Miller *in* Valentine (1985) demon-

strated that evolutionary faunas tended to form coherent assemblages within shelf environments throughout the Palaeozoic Era. Members of the Cambrian Fauna were spread across the entire shelf early in the Palaeozoic Era but became progressively restricted to deeper-water environments during the Ordovician as members of the Palaeozoic Fauna expanded across the middle and finally outer shelf. At the same time, early members of the Modern Fauna came to dominate inner shelf environments and later, deeper, low-oxygen environments. The Late Permian mass extinction eliminated dominance of the Palaeozoic Fauna from middle and outer shelf environments and led to expansion of the Modern Fauna across the entire shelf.

It must be emphasized that none of these evolutionary and ecological differences between the faunas is absolute. In a sense, the faunas are 'fuzzy

bounded sets' with their characteristics overlapping and some members of each fauna mimicking members of others. The characteristics thus represent nodes on a continuum. Major unsolved problems are why such nodes should exist and why they seem to change so little through the Phanerozoic.

Composition and history. The individual histories of the marine evolutionary faunas are illustrated in Fig.

2. The Cambrian Fauna was dominated by trilobites along with inarticulate brachiopods, monoplacophorans, hyoliths, and eocrinoids; most of the problematical taxa of the so-called 'small shelly faunas' of the Tommotian are also included. Various of these classes are paraphyletic, with descendent monophyletic taxa belonging to other evolutionary faunas; however, in most cases the paraphyletic classes either declined long before their descendent

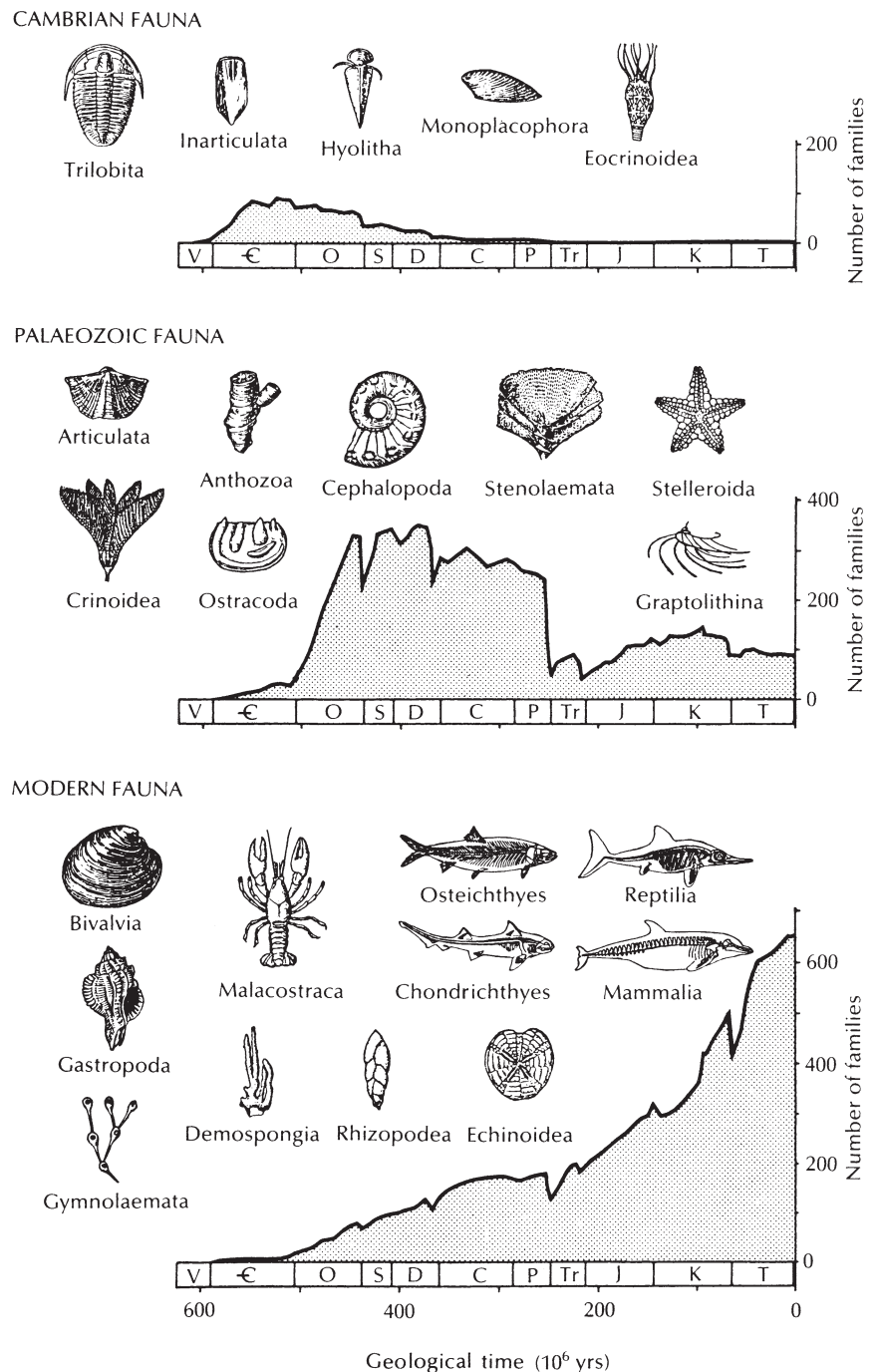


Fig 2 Histories of the three great evolutionary faunas of the marine fossil record as represented by their familial diversities through the Phanerozoic. Representatives of the important classes in each fauna are illustrated above the diversity curves. (After Sepkoski 1984.)

taxa diversified (e.g. the Monoplacophora) or contained monophyletic subtaxa that diversified in parallel with the rest of the evolutionary fauna (e.g. the Inarticulata). The Cambrian Fauna diversified very rapidly from the latest Vendian into the Early Cambrian and was the principal constituent of the 'evolutionary explosion' across the Precambrian–Cambrian Boundary (see also Section 1.5). Its maximum diversity was attained in the late Middle and early Late Cambrian. Beginning in the latest Cambrian, the fauna began a long, gradual decline, accentuated by the Ashgillian and Frasnian mass extinctions (Sections 2.13.2, 2.13.3).

The Palaeozoic Fauna initiated its expansion as the Cambrian Fauna began to decline; this combination resulted in nearly stable global diversity throughout the Late Cambrian. The Palaeozoic Fauna was dominated by articulate brachiopods with important contributions from crinoids, corals, ostracodes, cephalopods, and stenolaemate bryozoans. These groups were major components of the Ordovician radiations, which tripled global taxonomic diversity over a 50 million year interval. The Palaeozoic Fauna attained its maximum diversity from the Late Ordovician to Devonian and then began a long decline. During the Carboniferous and Permian, this decline was matched by a slow expansion of the Modern Fauna so that again global diversity remained nearly constant. The Palaeozoic Fauna was severely reduced by the Late Permian mass extinction (Section 2.13.4) but in the Mesozoic underwent two radiations: one in the Triassic, terminated by the Norian mass extinction (2.13.5), and a second, slower expansion in the Jurassic. The Jurassic expansion was reversed in the Cretaceous when global diversity exceeded Palaeozoic levels, and the remnants of the Palaeozoic fauna again went into decline.

The Modern Fauna is dominated by gastropod and bivalve molluscs, osteichthyan and chondrichthyan fishes, gymnolaemate bryozoans, malacostracans, and echinoids. Most of these classes appeared during the Cambrian and Ordovician Periods but diversified only slowly through the Palaeozoic Era. They suffered minor extinction relative to the Palaeozoic fauna during the Late Permian and became the dominant fauna in the Triassic. Through the Mesozoic and Cenozoic, the Modern Fauna continued the rather slow and steady diversification initiated earlier, producing the long post-Palaeozoic increase in global taxonomic diversity.

Throughout their histories, the three 'great' evolutionary faunas experienced considerable internal

turnover, with continuous change in ordinal and lower-level taxonomic composition. This was particularly true of the Cambrian Fauna, which underwent very rapid changes during its initial radiation. It may prove useful to subdivide this fauna and define two more evolutionary faunas: an Ediacaran Fauna, encompassing the distinctive soft-bodied animal fossils of the Vendian (Sections 1.3, 1.5), and a Tommotian Fauna, comprising the mostly problematical skeletal taxa of the earliest Cambrian (Sections 1.4, 1.5, 5.2.5). These possible faunas seem to fit into the general progression of evolutionary rates and diversity levels observed for the three great evolutionary faunas. The Ediacaran and especially Tommotian taxa appear to have had higher diversification rates and more rapid evolutionary turnover than the remainder of the Cambrian Fauna, and seem to show successive increases in diversity leading into the Cambrian Period. Further analysis of diversity patterns and faunal change in the Vendian and Early Cambrian are needed to assess whether such additional evolutionary faunas are useful for describing the early metazoan radiation.

Terrestrial biotas

The concept of evolutionary faunas has proved useful for organizing faunal turnover and diversity change in the marine record and has been extended with varying success to other evolutionary systems, specifically terrestrial vascular plants and tetrapod vertebrates. Niklas *et al.* (1983) identified four major plant groups, which can be termed evolutionary *floras*, in species-level data on tracheophyte diversity (Fig. 1B). These are: (1) an initial Silurian–Devonian flora of early vascular plants that radiated and then disappeared during the Devonian; (2) a pteridophyte-dominated flora, including ferns, lycopods, sphenopsids, and progymnosperms, that diversified in the Late Devonian and Early Carboniferous and dominated plant communities to the end of the Palaeozoic Era; (3) a gymnosperm-dominated flora of seed plants that appeared in the Late Devonian and rose to dominance in the Mesozoic; and (4) an angiosperm flora that originated in the Early Cretaceous and rapidly radiated to dominance thereafter, replacing the preceding gymnosperm flora. As in the marine system, each of these floras (excepting the angiosperms) originated early in the history of vascular plants and radiated sequentially to produce step-like increases in global tracheophyte diversity.

Three 'assemblages' of terrestrial tetrapod families

have been identified by Benton (1985) in the vertebrate fossil record (Fig. 1C). These comprise: (1) the labyrinthodonts, anaspids, and synapsids, which appeared during the Middle Palaeozoic and completely dominated the terrestrial vertebrate record to the end of the Palaeozoic; (2) the early diapsids, dinosaurs, and pterosaurs, which arose in the Triassic, attained maximum diversity in the Late Jurassic and Cretaceous, and disappeared at the terminal Cretaceous mass extinction (Section 2.13.7); and (3) the lissamphibians, turtles, crocodiles, lizards, birds, and mammals, which originated in the Triassic and Jurassic, expanded through the Cretaceous, and then diversified to very high levels in the Cenozoic. Although these assemblages have some similarities to marine evolutionary faunas, there are some important differences: the assemblages do not all appear early in the history of tetrapods and their sequential diversifications are not all associated with step-like increases in global diversity. It remains to be seen whether such patterns could be identified if more terrestrial taxa (e.g. the arthropods) were included and analyses performed at lower taxonomic levels. If so, evolutionary

faunas and floras would appear to be a general property of the development of Phanerozoic biotas.

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1.7 Early Diversification of Major Marine Habitats

1.7.1 Infauna and Epifauna

W. I. AUSICH & D. J. BOTTJER

Introduction

Benthic marine habitats and the organisms that populate them represent an intricate and diverse ensemble. Much of the initial development and diversification of metazoans was for life in this realm. Marine benthos have invaded most types of substratum at depths ranging from the supertidal to abyssal. This array of habitats, with concomitant physical and chemical limiting factors, has probably been relatively constant through most of the Phan-

erozoic. Similarly the general trophic strategies for exploitation of marine benthic habitats has been constant. Both infaunal and epifaunal organisms developed, including suspension feeders, deposit feeders, predators, scavengers, grazers, and others. However, through eustatic changes in sea-level and plate motion in the lithosphere, the habitat location has been constantly changing.

The great diversity in this benthic system is contributed by organisms. At any one time organisms

differentially adapt to a plethora of physical, chemical and biological limiting factors. The development of simple to complex ecological structuring within habitats is variable; and, of course, through evolution and extinction, the organisms populating benthic habitats have been continually in flux.

The benthic habitat

The infauna. In modern environments particulate organic material is abundant immediately above and below the sediment–water interface and decreases in quantity both up into the water column and down into the sediment (Fig. 1). Both suspension feeders and deposit feeders exploit this resource. Infaunal deposit feeders mine particulate organics within the sediment, whereas infaunal suspension feeders typically feed from the water that is immediately above. The primary physical constraints on depth of burrowing are the position of the redox boundary, and sediment stiffness, which increase with depth. Phylogenetic constraints on the development of specialized structures (e.g. fused siphons) have also been important in the history of the infauna.

Infaunal suspension feeders are largely stationary. They all feed as active suspension feeders from water immediately above the sediment surface, and particulate food in that water moves past them horizontally. In contrast, infaunal deposit feeders are mobile, and they feed on a stationary food

resource scattered through the upper part of the sediment column (Bottjer & Ausich 1986).

Durophagous predation, space competition, and adaptation to conditions in the intertidal zone are considered to have been important influences in the development of infauna and in changes in infaunal tiering structure. Increased durophagous predation pressure led to greater infaunalization of the benthos and may have also promoted the development of more complex infaunally tiered communities. Different authors have argued either that densities of infaunal bivalves are generally too low for space competition to be important, or that space competition can be important to avoid interference competition among suspension feeders which all feed from the same basic resource (Bottjer & Ausich 1986). For infaunal deposit feeders, space competition may be much more important.

The initiation of deep burrowing may have resulted from adaptations to life in the intertidal zone, where regular fluctuations in the water table are driven by the tidal cycle. Organisms in the intertidal zone track these water table changes. The ability of infauna to cope with such conditions may have preadapted them to medium- and deep-burrowing habits in the subtidal zone (Bottjer & Ausich 1986).

The epifauna. Epifaunal suspension feeders live within the benthic hydrodynamic boundary layer, i.e. the zone of diminished current velocity caused by drag across the bottom. Current velocities are

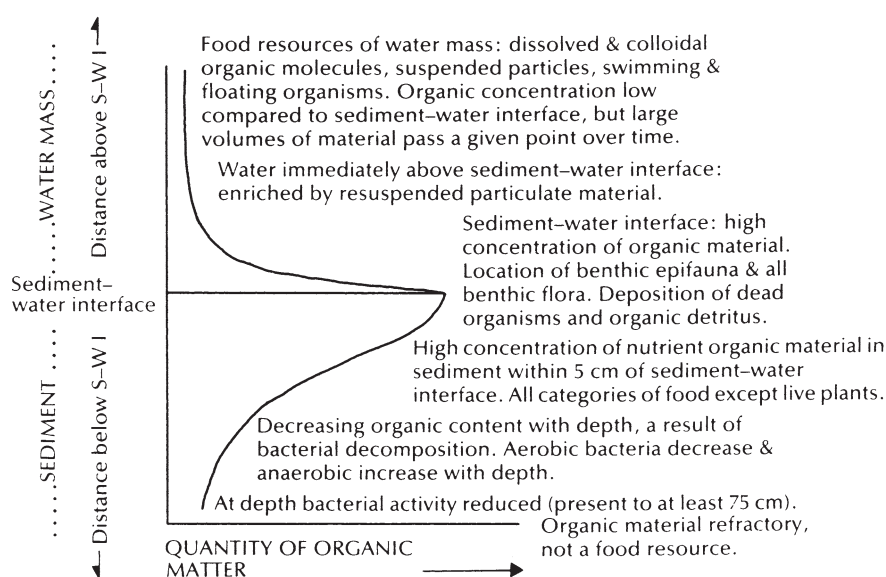


Fig. 1 Location of food resources with respect to the sediment–water interface. (From Walker & Bambach 1974.)

lowest immediately above the sea floor and increase upward into the water column (Fig. 2). The thickness of the boundary layer is a function of factors such as current velocity and substratum roughness; however, velocity always decreases toward the ocean floor. Given equal concentrations of particulate organics, more food would be available to a suspension feeder where current velocities were greater, i.e. higher within the boundary layer; however, particulate organics generally increase toward the ocean floor. In this physical setting epifaunal suspension feeders, which are largely stationary, must exploit a food resource that is moving past them horizontally at specific distances above the sediment–water interface.

Many constraints and processes are likely to have been important for the development and maintenance of epifaunal tiering (Bottjer & Ausich 1986). Phylogenetic constraints on structural materials and modes of growth, as well as the biomechanical properties of structural materials, strongly influence the height to which organisms can reach above the sea floor. The mode of growth and whether organisms are clonal or aclonal are important constraints controlling an organism's exploitation of food resources within the benthic boundary layer. Only clonal organisms (e.g. bryozoans, corals), and aclonal organisms that grow by addition of new parts (e.g. stalked echinoderms) have been able to develop medium- to high-tiered forms (Bottjer & Ausich 1986; see also Sections 4.5, 4.16).

The mode of suspension feeding also appears to be correlated with utilization of epifaunal resources. Three basic suspension feeding modes have been defined: passive, facultatively active, and active. Passive suspension feeders rely completely on ambient currents for food supply, whereas facultatively active suspension feeders rely to a large extent on ambient currents but also pump a weak current of water into the filtration apparatus. Active suspension feeders rely on pumping water. Ecological studies and documentation of the historical record (Bottjer & Ausich 1986) show that passive and facultatively active suspension feeders alone develop morphologies to become high level primary tier feeders in the epifauna. In contrast, active suspension feeders are dominant low in the boundary layer.

Competition, in conjunction with other processes and constraints, has surely played a key role in the development of ecological structure in epifaunal benthos. Space, a place from which to feed, and food competition have been important for suspen-

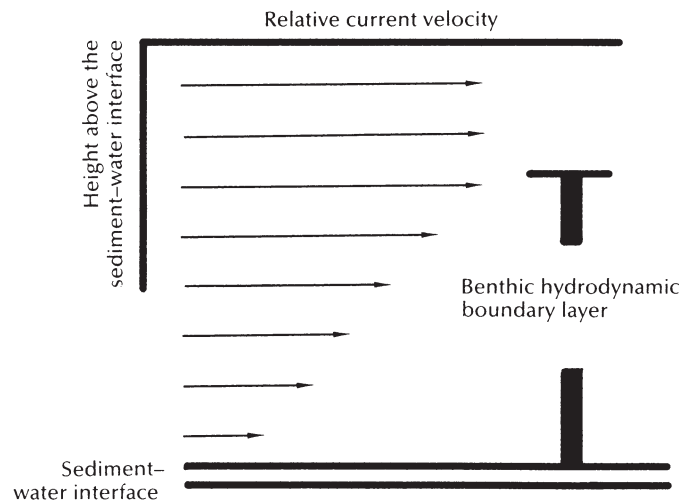


Fig. 2 Velocity profile of the benthic hydrodynamic boundary layer.

sion feeding benthos on soft substrata (Bottjer & Ausich 1986).

Tiering. Spatial separation and structuring is a common biological method of resource partitioning within communities. Vertical community structure has been documented for epifaunal and infaunal suspension feeding communities (Bottjer & Ausich 1986) and infaunal deposit feeding communities (Levinton & Bambach 1975). Bottjer & Ausich (1986) called this spatial arrangement of organisms tiering. They developed a history of tiering complexity through the Phanerozoic for suspension feeding palaeocommunities in soft substrata, deposited in subtidal shelf and epicontinental sea settings at depths greater than several metres below fair-weather wave base (Fig. 3). A comprehensive Phanerozoic history of tiering for deposit feeding palaeocommunities in these environments has yet to be compiled. Evidence for such a history, which must come primarily from studies on various features of bioturbation (cross-cutting relationships of trace fossils, burrow depths, extent of reworking) is currently being developed (e.g. Crimes & Anderson 1985; Wetzel & Aigner 1986; Droser & Bottjer 1988).

The suspension feeder tiering history (Fig. 3) displays the maximum heights and complexity of tiering in a characteristic benthic palaeocommunity at various times. Physically dominated settings are unlikely to support a biota with this maximum development of tiering complexity. The tiering history is of primary tier feeders (Bottjer & Ausich 1987), which are organisms whose body or burrow intersects the sea floor. Although detailed tiering

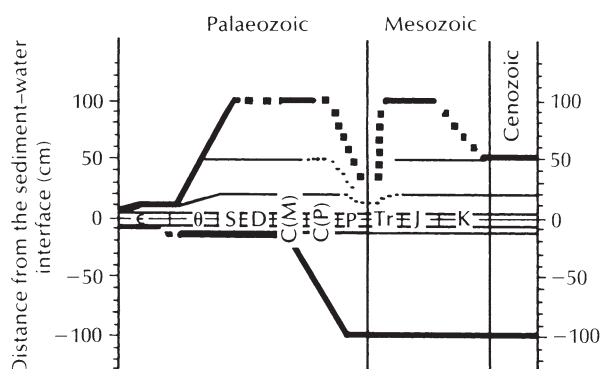


Fig. 3 Tiering in soft-substrata suspension-feeding communities through the Phanerozoic. The heaviest lines represent the maximum level of tiering above or below the substratum at any time. Other lines represent levels of tier subdivision. Solid lines represent data, and dotted lines are inferred levels. (From Bottjer & Ausich 1986.)

histories have not been compiled for other major environmental settings, such as reefs or hard-grounds, they should reflect the relative changes in suspension feeder tiering.

Faunal histories and ecological structure

Faunal diversifications and the history of benthic faunal ecological structure can be understood best in the context of temporally distinct faunas, which include the following: Vendian Fauna, Tommotian Fauna, Cambrian Fauna, Palaeozoic Fauna, and Modern Fauna. Sepkoski (1984; Section 1.6) defined the Cambrian Fauna, Palaeozoic Fauna, and Modern Fauna based on familial diversities.

Vendian Fauna. Fossils of the first benthic 'metazoans' are known from the Vendian (c. 620–570 Ma). This fauna (Sections 1.3, 1.5) was initially best described from the Ediacaran Hills in South Australia, but is now recognized world-wide (Glaessner 1984). Glaessner (1984, page 52) recognized 31 named species from the vicinity of Ediacara and assigned these fossils principally to modern metazoan groups, including Hydrozoa, Scyphozoa, Conulata, colonial Cnidaria, Polychaeta, and Arthropoda. Seilacher (1984) offered a sharply contrasting interpretation for the Vendian Fauna. He argued that many fossils interpreted as medusoids are actually trace fossils and that the non-medusoid fossils represent a clade distinct from all extant metazoans.

Clearly the zoological affinities and autecology

of Vendian taxa must be understood before community ecological structure can be reconstructed. However, whatever the trophic habit of members of the Vendian Fauna, it is apparent that Vendian communities displayed some ecological structure. *Charniodiscus* and *Glaessnerina* species apparently attained variable heights above the sea floor. Maximum preserved heights of individuals include the following: *G. grandis*, 16 cm; *C. longus*, 25 cm; *C. arboreous*, 60 cm. Other organisms lived directly on the bottom. It is possible that this height distinction among members of the Vendian Fauna may represent an ecological structuring analogous to epifaunal tiering.

The widely distributed Vendian Fauna apparently suffered major extinction (if not total extinction; Seilacher 1984) at the end of the Proterozoic (Section 2.13.1). The Phanerozoic record of benthic faunas has always been significantly different from that present during the Vendian.

Trace fossils from the Vendian are Palaeozoic in affinity and indicate that a worm-like fauna of shallow-burrowing deposit feeders existed during this time (Glaessner 1984). Vertical dwelling burrows are generally lacking, indicating that infaunal suspension feeders were rare or had not yet developed. Thus, at most a shallow infaunal tier of deposit feeders existed, up to several centimetres below the sediment–water interface, in soft substrata Vendian environments.

Tommotian Fauna. The first major occurrence of fossilized metazoan hard parts was during the Tommotian at the base of the Cambrian (c. 570 Ma). The Tommotian Fauna preceded the first occurrence of trilobites, which was approximately at the base of the Atdabanian (c. 560 Ma) (Conway Morris 1987). This fauna (Sections 1.4, 1.5) is recorded by a variety of very small, principally phosphatic skeletons. Characteristic taxa include small conical shells such as *Protohertzina* and *Anabarites*, inarticulate brachiopods, the sclerites of *Lapworthella*, archaeocyathids, and trace fossils (e.g. McMenamin 1987). Like the Vendian Fauna, the Tommotian Fauna has recently been documented to occur worldwide.

More autecological study on elements of the Tommotian Fauna is necessary before the palaeoecological structure of these early Phanerozoic communities can be fully understood. Problems include (1) which of the component taxa are skeletal remains of single organisms and which are sclerites of some larger creature (for example *Halkieria*; Conway Morris 1987); and (2) the autecology and

functional morphology of Tommotian organisms that have no clear living counterpart.

Regardless of shortcomings in the detailed understanding of the Tommotian Fauna, it is clear that it represents the initial establishment of the basic benthic ecological structure, albeit simple and composed of small organisms, that would characterize the remainder of the Phanerozoic. The Tommotian Fauna includes sessile and mobile forms, simple suspension feeders such as *Sinotubulites*, more complex suspension feeders such as archaeocyathids and inarticulate brachiopods, and predators such as *Protohertzina* (McMenamin 1987).

Tommotian skeletons and skeletal elements are typically smaller than one centimetre. Epifaunal suspension feeders were confined to the lowest levels within the benthic boundary layer and were probably characteristically within the 0 to +5 cm tier of Bottjer & Ausich (1986). Trace fossils associated with Tommotian faunas indicate that the initial appearance of vertical burrows 4–5 cm deep occurred during this time (McMenamin 1987) in near-shore settings above fairweather wave base. In general, though, trace fossils formed in soft substrata settings below normal wave base appear to penetrate depths no greater than several centimetres in the substrate (e.g. Crimes & Anderson 1985); thus the 0 to –6 cm tier of Bottjer & Ausich (1986) was present for both suspension and deposit feeders.

Cambrian Fauna. Whether driven by ecological processes, general laws of size increase, or intrinsic diversification after approximately 10 million years, the Tommotian Fauna was replaced by the Cambrian Fauna. The Cambrian Fauna represents a diversification of metazoans and an increase in body size of benthos, both of which resulted in more complex benthic communities. From analysis of familial diversities, dominant faunal elements in the Cambrian Fauna include trilobites, inarticulate brachiopods, hyolithids, monoplacophoran molluscs, eocrinoid echinoderms, and archaeocyathids. The Cambrian Fauna dominated the benthic habitat for approximately 55 million years.

Typical preservation of a Cambrian benthic community reveals a simple tiering structure; a relatively simple structure is also evident in the Burgess Shale fauna despite preservation of the soft-bodied faunal component (Section 3.11.2). Tiering levels for both epifaunal and infaunal suspension feeders remained quite low (Bottjer & Ausich 1986). Two tier levels are defined for epifaunal suspension feeders: 0 to

+5 cm, and +5 to +10 cm (see Fig. 4). The +5 to +10 cm Cambrian tier included eocrinoids, edrioasteroids, crinoids, archaeocyathids, and sponges (Figs 4, 5). The 0 to +5 cm suspension feeders included, among others, a variety of echinoderms, sponges, archaeocyathids, and inarticulate brachiopods.

Infaunal suspension feeders were also close to the sediment–water interface during the Cambrian. Only the –6 cm tier was occupied in environments below fairweather wave base (Bottjer & Ausich 1986). Droser & Bottjer (1988) reported that in Cambrian inner and middle shelf carbonate deposits of western U.S.A. bioturbation occurs at depths no greater than 6 cm. If these results are typical for such Cambrian environments, they indicate the continued presence of the 0 to –6 cm tier for both deposit and suspension feeders through the Cambrian. In contrast, deeper *Skolithos*, possibly made by deposit feeders, is abundant in Cambrian strata deposited in nearshore settings above fairweather wave base, forming the typical pipe-rock.

Palaeozoic Fauna. The Palaeozoic Fauna (Sepkoski 1984; Section 1.6) characterized benthic habitats from the Ordovician to the Permian and was dominated by articulate brachiopods, crinoids, anthozoans, ostracodes, cephalopods, stenolaemate

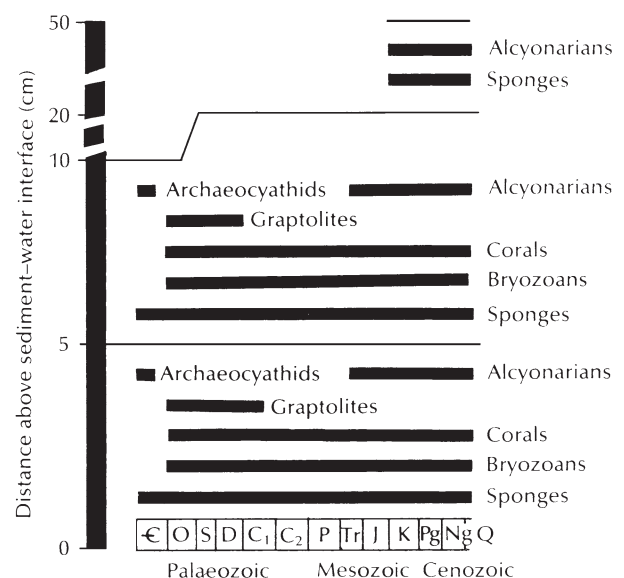


Fig. 4 Tiering history of Phanerozoic colonial suspension feeders on soft substrata from non-reef, shallow subtidal shelf, and epicontinental sea settings. Vertical distribution within each tier is arbitrary and only implies occupation in a tier for the duration indicated. (From Bottjer & Ausich 1986.)

Whereas mass extinction at the close of the Palaeozoic (Section 2.13.4) greatly affected epifaunal

organisms and the tiering structure of epifaunal suspension feeders, infaunal suspension feeders were relatively unaffected. No change in tiering structure is apparent in the record of infaunal suspension feeders between the Permian and Triassic.

Modern Fauna. The Modern Fauna, characteristic of the Mesozoic and Cenozoic, has been dominated by the following benthos: bivalves, gastropods, gymnolaemates, malacostracans, demosponges, rhizopods, and echinoids (Sepkoski 1984; Section 1.6). Immediately following the terminal Palaeozoic extinction, epifaunal suspension feeder tier levels were significantly reduced, but infaunal suspension feeder tiers were not. However, by the Middle Triassic, tier heights and complexity were restored to Middle Palaeozoic levels (see Fig. 3). Again, crinoids with 100 cm stems were present in shallow-water settings. Probably the same suite of processes and constraints that was responsible for the development of epifaunal tiering in the Palaeozoic was involved in its re-establishment during the early Mesozoic. A typical Jurassic suspension feeding community may have been composed of the following epifaunal organisms: 0 to +5 cm tier — brachiopods, bryozoans, bivalves, sponges, corals and crinoids; +5 to +20 cm tier — sponges, bryozoans, alcyonarians, and crinoids; +20 to +50 cm tier — crinoids, sponges, and alcyonarians; +50 to +100 cm tier — crinoids. Infaunal suspension feeding organisms included a variety of bivalves (Fig. 6), gastropods, and worms and crustaceans as indicated by trace fossils (Bottjer & Ausich 1986). Deposit feeders at this time apparently existed in a tiered structure (e.g. Wetzel & Aigner 1986), but in general the tiering structure for this trophic group has not been documented for the Mesozoic.

This well developed infaunal and epifaunal suspension feeder tiering complexity only lasted for approximately 100 million years. By the Cretaceous, stalked crinoids were absent from shallow-water benthic habitats, and the maximum characteristic tier height was reduced from +100 to approximately +50 cm. Displacement of stalked crinoids to deeper-water settings was a gradual process that may have been the result of increased levels of predation in the later Mesozoic (Bottjer & Ausich 1986). Since the beginning of the Cretaceous, epifaunal suspension feeders typically have not been important in soft substrata settings. Both infaunal and epifaunal suspension feeder tiering structure were relatively unaffected by the terminal Mesozoic extinction.

Post-Jurassic benthic communities in shallow-water soft substrata settings have been dominated by infauna. This basic organization has remained relatively constant for c. 140 million years. A characteristic Neogene community with maximum development of suspension feeder epifaunal tiering would include the following: 0 to +5 cm tier — bryozoans, bivalves, sponges and corals; +5 to +20 cm tier — bryozoans, sponges, alcyonarians; and +20 to +50 cm tier — sponges, alcyonarians. Characteristic infaunal suspension feeding organisms would include, as for the Mesozoic, a variety of bivalves (Fig. 6), gastropods, and worms and crustaceans as indicated by trace fossils (Bottjer & Ausich 1986). Deposit feeders had a tiered structure during this time in related environments (e.g. Savrda & Bottjer 1986), but, as for the Mesozoic, tiering structure for this trophic group has not been documented for the Cenozoic.

Conclusion

Examination of the fossil record for trends in tiering provides a means of tracing patterns of ecological structure independently of enumerations of taxa. Only the Phanerozoic history of suspension feeding palaeocommunities from below fairweather wave base continental shelf and epicontinental sea environments is relatively well known. However, some general contrasts between infaunal and epifaunal tiering in Vendian–Recent settings can be noted. Infaunal tiering, from the beginning, has had a history of slow but steady increase in complexity through attainment of greater burrowing depths and development of additional tiers. In contrast, if the height distinction among members of the Vendian Fauna reflects epifaunal tiering, it records the first of three periods of development of epifaunal tiering which were followed by reduction. These differences in tiering history may indicate a relatively greater resistance of the infaunal habitat to perturbations in ecological as well as evolutionary time.

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1.7.2 Plankton

R. B. RICKARDS

Introduction

The origin and early diversification of the Earth's plankton is largely shrouded in mystery, hypotheses leaning heavily upon a rather meagre fossil record and what seems like reasonable supposition. Consider briefly the two main periods to be discussed: the Vendian and the Lower Palaeozoic. Research workers dealing with Vendian fossils have been concerned, to a large extent, with establishing that they *are* fossils, and much less concerned with major ecological niches. Those organisms that give least trouble with respect to identity, such as stromatolites or trace fossils, are also the most obvious as regards mode of life. The more problematic creatures may yet have greater scope for the current objective, namely indicating the origin and defining the nature of early plankton. By contrast, the real problem in the Lower Palaeozoic lies in deducing the composition of the plankton and the relative importance

and functions of those components. Bulman (1964) gave a broad-based review of Lower Palaeozoic plankton: the improvements in our knowledge since then are considered below.

The Vendian

The general aspect of Precambrian fossil life is not today in much dispute (Sections 1.2, 1.3). Blue-green 'algae' (cyanobacteria or cyanophytes), the earliest proven life form, occurred at 3500 Ma and continue today. Grouped with early, reducing bacteria they comprise the Monera. The fossil record of the bacteria is less satisfactory, but stalked representatives may have been involved in the creation of the banded iron formations, and it seems possible that purple and green bacteria were involved with the earliest stromatolites. The question is, which prokaryotes, which Monera, could have comprised an early plankton? It is not sufficient to note that carbon isotope ratios of Precambrian black shales and dark limestones indicate an organic origin for the carbon: that merely begs the question, as well as hiding the implication that such organic carbon must be of planktic ('algal') origin. Berry & Wilde (1983) suggested that an Archaean anoxic ocean would have had similar conditions to present day deep ocean vents, and that early carbon-fixing could have been by chemautotrophic bacteria using geothermal H₂S as their primary energy source (*Anoxium*). Peripheral isolates in *Anoxium* populations probably would have evolved to take photic energy from sunlight, because they would have been disadvantaged in the competition for reduced sulphur. Berry & Wilde (1983) also support the contention that the carbon cycle was effectively stabilized by 3700 Ma (i.e. in pre-Isua time). Their first plankton would be *Anoxium* isolates at the ocean surface, developing the ability to use light as an energy source, and occupying similar ecological niches to modern purple and green bacteria.

Blue-green algae share the ability with bacteria to fix their own nitrogen. They are resistant to high and low temperatures, and to dessication, and operate best in neutral to alkaline systems. Further, phycocyanin can work in very low light (it is sensitive to blue light) and in consequence confers visibility to depths of 1000 m and more. The modern blue-green *Trichodesmium* exhibits gas vacuolation, the considerable vesicular strength of which causes it to sacrifice some control of vertical mobility. In general modern blue-greens lack buoyancy control and the open ocean is considered too turbulent for

their survival. The possibility that part of the development of *Trichodesmium* occurs in a benthic environment may also be of adaptive significance. It is clear from this that *Trichodesmium*-like blue-greens in Archaean oceans would have found conditions to their liking if deductions concerning the nature of those oceans are correct; and it may partly explain the converse, that in today's oceans, despite such seeming flexibility, blue-greens are not common. (There are, however, difficulties in identifying them in plankton samples, unless epifluorescence techniques are used, when blue-greens fluoresce a distinctive orange.)

Schopf (1976) has disputed the true fossil nature of many of the claimed Archaean microfossils, but it is widely accepted that the 3200–3100 Ma *Archaeosphaeroides* (from the Onverwacht and Fig Tree Cherts) is a coccoid cyanophyte (e.g. Brasier 1979), as is *Huroniospora*. However, if these are truly chroococcales, then it should be noted that extant species do not fix nitrogen. By 2000 Ma (early Proterozoic; Aphebian) oscillatoriacids and notocacids may well be represented. Possible Riphean microfossils, which might be planktic, are almost equally contentious, but the chlorophycid *Eosphaera* from the Gunflint Chert was a *Volvox*-like green algal colony, and the prasinophycid *Tasmanites* a 100–700 µm globular form with uninucleate cells. Thus the eukaryotes were probably represented in Riphean plankton. It is generally assumed that bacteria in general preceded cyanophytes, and that some of these could have been planktic and bacillus-like.

Glaessner (1984), in his wide-ranging review of the Ediacarian fossils (Sections 1.3, 1.5), concluded that the coelomate radiation must have been pre-Ediacarian (Varangerian), and that a change from zooplankton to benthos preceded the coelomate radiation itself. This implies the existence of zooplankton in the Varangerian or earlier. Protists certainly could have been present: the Pyrrophytes begin with *Arpylorus* in the Silurian, but non-tabulate forms could have occurred in profusion in the late Precambrian. Other records of Precambrian plankton include the acritarches, some of which may have been spores of multicellular algae.

Acritarch occurrences in the upper Riphean to latest Precambrian have been widely documented (e.g. Vidal & Knoll 1983). The evidence suggests that there was a gradual rise in the number of taxa from about 1400–900 Ma, followed by a peak and decline in the late Varangerian and Valdaian: this late Precambrian extinction event was a prelude to a

spectacular Cambrian diversity increase, to at least twice that of the lowest Vendian. In terms of Vendian palaeoecology there was a recognizable division into lower diversity planktic assemblages in inshore environments, and higher diversity communities in offshore shelf regions or open shelf regions.

With the onset of Ediacarian time, in addition to the many benthic forms, there were undoubted medusoids. These included the chondrophorans, stiff-walled medusoids, floating at the surface and exploiting a phototrophic plankton. According to Glaessner (1984), their presence indicates that an ozone layer was then developed and that the ocean was of normal salinity and warmth. A lack of macrophagous predators may account for size increases in the zooplankton, with some medusae reaching 1 m. This model is apparently compatible with a progressive ventilation of the oceans (Berry and Wilde 1983), because Glaessner refers only to the surface layers, or to shallow shelf water bodies, which could be almost normal, tropical, oxygenated marine bodies.

The sequence of events in the evolution of plankton in the Precambrian was probably as follows (Fig. 1):

- 1 Chemautotrophic *Anoxium* at outgassing submarine geothermal vents before 3700 Ma. Such 'plankton' would have been local in distribution, above the vents?
- 2 *Anoxium* isolates began to use light energy, 3700–3500 Ma (and later?).
- 3 Late Archaean: *Archaeosphaeroides* and *Huroniospora* together with bacillus-like and other bacteria, to about 2500 Ma.
- 4 Early Proterozoic (Aphebian): oscillatoriacids and notocarids around 2000 Ma, with presumably more varied changes to eukaryotic microplankton.
- 5 Riphean: green algae well developed.
- 6 Varangerian: presumably development of zooplankton.
- 7 Ediacarian: planktic medusae, often of large size; still no macrophagous predators.

The Lower Palaeozoic

The Cambrian is typified by a dramatic diversity increase, mirroring that in the coeval benthos (Sections 1.5, 1.6). The very earliest chrysophytes may have occurred at this time, an additional phytoplankton component, though these are typically post-Palaeozoic. Radiolarians were present in the Cambrian and equatorial in their distribution.

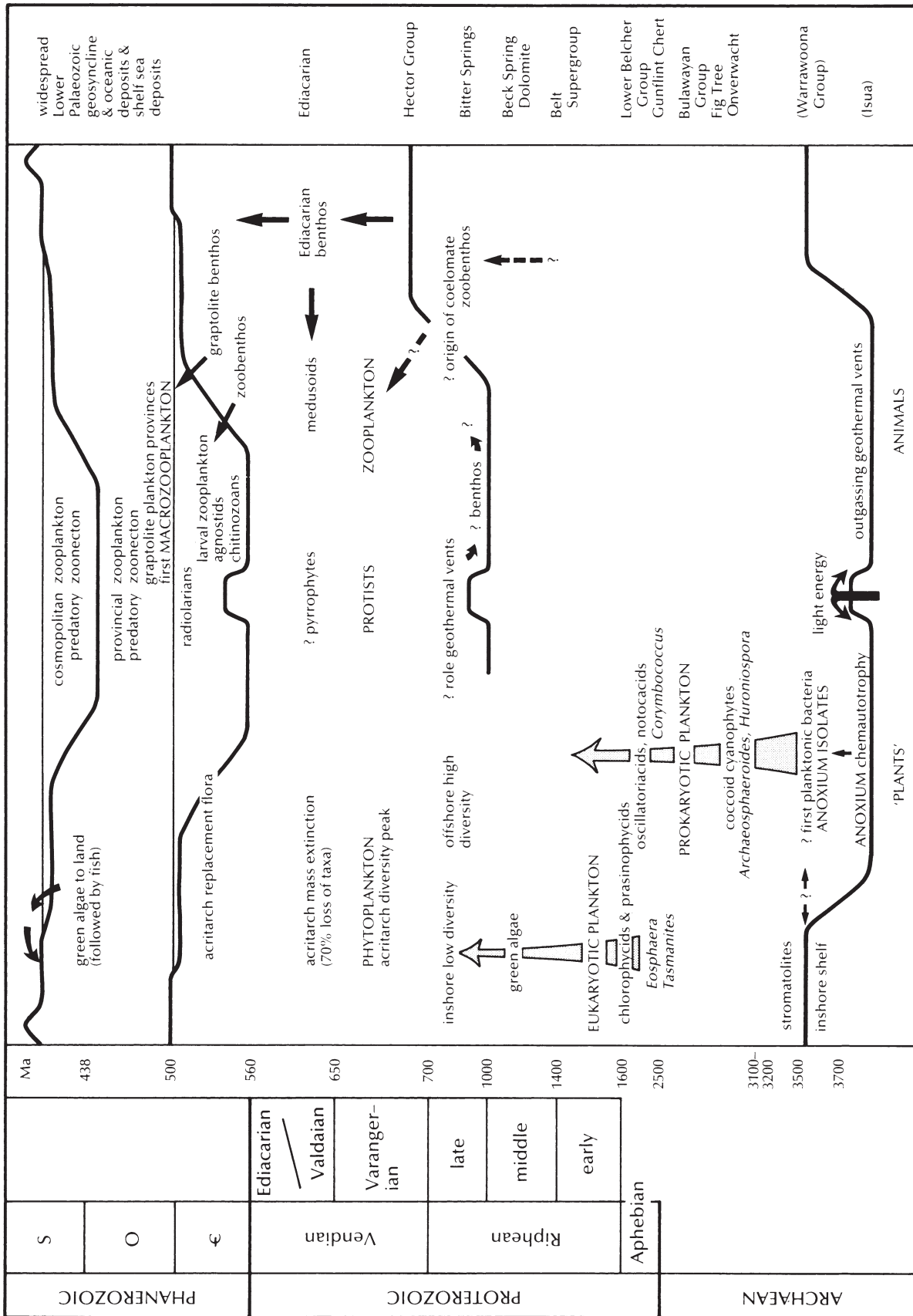


Fig. 1 Time and place in the origin and broad evolution of plankton. Inshore, shelf and slope environments are indicated diagrammatically to the left and right of the main part of the figure; narrowing oceans are suggested from the Cambrian to the Silurian; main depositional units of the plankton record are shown in the right hand column and approximate time correlations to the left of the figure. The position of the Warrawoona and Isua rocks are shown in parentheses.

Foraminifera, by contrast, were almost wholly benthic throughout the Lower Palaeozoic. Larval stages (including giant larvae) of most benthic organisms were of increasing importance in the plankton, though of immeasurable proportions. One of the major components was the pelagic agnostid trilobites whose entire life cycle would have been enacted in the upper layers of the ocean. Further, there have been convincing arguments for a pelagic component in such faunas as the Burgess Shale (Section 3.11.2) indicating the presence of a soft-bodied pelagic element. In the Cambrian there is still no direct evidence of planktic macrophagous predators, and the mix must have been composed essentially of most of the above phytoplankton groups with an increasingly diverse zooplankton.

Several very major changes took place at the beginning of the Ordovician. It is clear that acritarchs became an important constituent, with a major diversity peak spanning the Ordovician–Devonian periods: in some Silurian series over 2000 species have been identified in relatively small geographical regions. Radiolarians are extremely abundant in some offshore shelf graptolitic deposits (in modern tropical planktic environments they may number in excess of 80 000 individuals per m³). The Chitinozoa, although occurring in the Cambrian, have dramatic peaks of abundance and diversity in the Ordovician and Silurian. Their occurrence in both species diversity and facies type matches that of the graptoloids, which were undoubtedly planktic. Chitinozoans are presumed egg capsules of metazoans, which may not necessarily have been plankton themselves.

The planktic graptoloids arose from benthic forms in the earliest Ordovician, showed considerable evolutionary development, and achieved large rhabdosomal size (approaching or exceeding 1 m in several species). It is probable that they were the first abundant macrozooplankton, and their food was almost certainly minute phyto- and zooplankton. Huge numbers are preserved in black shale formations where they are often associated with sponge spicules and what may be epiplanktic bivalves and brachiopods. There is, in addition, an increasing number of nekctic elements, such as cephalopods and trilobites, yet still few large predators in the *planktic* environment: orthocone cephalopods probably constituted the most important groups of (nekctic) large predators. The graptoloids, associated closely with a vastly abundant algal phytoplankton (represented by the high carbon component of the black graptolitic shale), appear

to have dominated the Ordovician and Silurian planktic environment, but their large size may give a misleading impression of relative abundances and proportions within the plankton at the time. An understanding of the ecological diversity of graptoloids is still at an early stage (Rickards 1975). They may have used gas vacuoles to control their depth within the photic zone. Other specialized features such as nemata, 'floats', vanes, webs, thecal spinosity, rhabdosomal stabilizers, and overall rhabdosomal shapes may have been designed for particular hydrodynamic roles in the plankton.

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1.7.3 Reefs

C. T. SCRUTTON

Introduction

Fully diversified, large scale, shelf to shelf-edge, wave-resistant organic structures like the Great Barrier Reef represent the end member of an evolutionary continuum of ecosystems from small, simple, and local communities of benthic organisms. They are well developed when suitable constructors are available and poorly developed otherwise. Following important extinction events, re-establishment of major reef tracts lags behind the restructuring of level bottom communities, presumably

reflecting not only the availability of suitable constructors but the evolution of the more complex community structure associated with successful reef-building associations. Biostromes and bioherms are respectively sheet-like and mound-like structures dominated by skeletal organisms and either may occur in isolation or as component parts of fully differentiated reef complexes. Build-ups are any accumulations of carbonate sediment with topographic relief on the sea floor (see discussion in Heckel 1974).

The Precambrian

Reefs extend well back into the Precambrian (Copper 1974; Heckel 1974; James 1983). The earliest unquestioned stromatolites (see also Section 1.2) are from the Fig Tree Group of the Barberton Mountain Land, South Africa, 3300–3500 Ma. They are regarded as the product of a photoresponsive microbial community in a shallow, evaporitic environment, and associated microfossils include filamentous forms. There is no certainty that the microbes are true cyanobacteria but already a range of stromatolitic forms from linked domes to pseudocolumns is present. The stromatolitic carbonate ecosystem became widespread some 2500–2300 Ma (Fig. 1). Our knowledge of the evolution of the microbial communities responsible is vague but increasing. Most were probably eubacteria, but true cyanobacteria may not be very old. Eighteen morphotypes are known from the 1600–2000 Ma Gunflint Chert in Canada; most are of blue-green appearance but many are of unknown affinity. In Australia, the 1600 Ma Paradise Creek microbiota is morphologically comparable, and the 800–1000 Ma Bitter Springs community is extremely similar to that of modern stromatolite communities (Walter 1976).

Early Proterozoic stromatolites ranged from non-marine to deeper-water environments. Extensive shelf biostromes, mainly of linked domes, grade into shelf-break bioherms with several metres relief of branching columnar morphs in the Slave Province of Canada. Individual build-ups reach 100 m diameter and 20 m thickness. They are cut by channels draining the shelf and die out rapidly down slope into the basin. Although extremely simple ecosystems, these are regarded as positionally and functionally comparable to modern reef ecosystems. Elsewhere stromatolitic masses on Proterozoic shelves < 60 m thick and 1–2 km long are reported. Precambrian stromatolites tend to be larger than

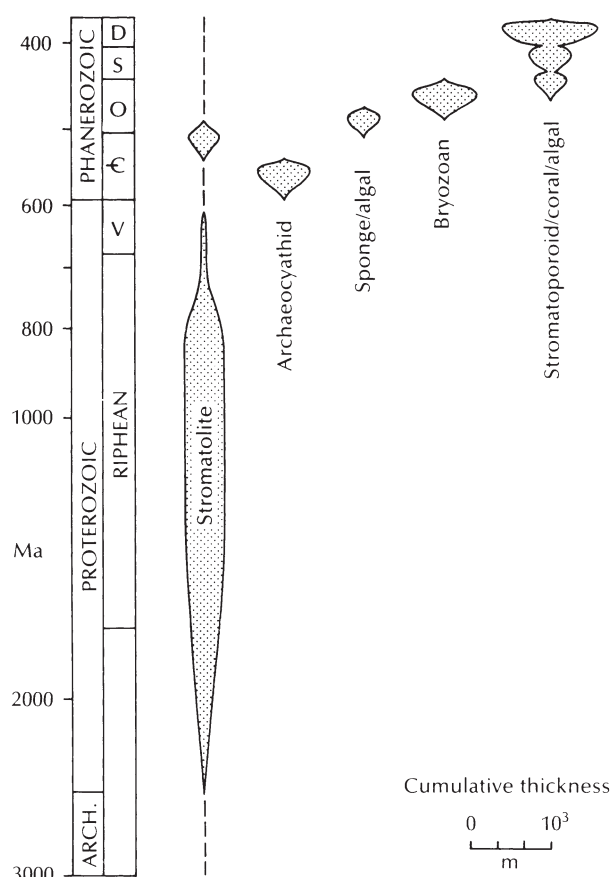


Fig. 1 Distribution in time of the major reef building biotas of the Precambrian and Early Phanerozoic.

Phanerozoic examples, and up to the early Palaeozoic, tall, narrow, erect, branched columnar morphologies dominated. This is in contrast to the broader unbranched forms which subsequently dominated. Columnar stromatolite diversity increased up to the Middle–Late Riphean but a sharp decline in abundance and diversity set in about 800 Ma.

With the earliest claimed eukaryote being from the 1200–1400 Ma Beck Springs Dolomite of California, and traces of metazoans, although poorly documented and often doubtful, known from about 1000 Ma, the decline in stromatolite build-ups seems likely to reflect the rise of grazing heterotrophs. However, Copper (1974) pointed out that the first well preserved metazoans of the Ediacara fauna (Sections 1.3, 1.5) appeared not to include algal grazers, although this fauna was not recovered from carbonate facies. He timed the decline of stromatolites as slightly later and implicated the widespread 675–570 Ma Late Precambrian glaciation.

The Cambrian

The first metazoan reefs date from the earliest Cambrian. In clastic facies, skolithid reefs are common world-wide. They form extensive masses of agglutinated sand grains, an early equivalent of modern sabellid buildups, < 80 cm thick and hundreds of kilometres long as fringing reefs in the breaker zone cut by surge channels. Accumulated thicknesses of skolithid sands often precede the first development of archaeocyathid reefs in the Lower Cambrian, the earliest of all skeletal framework reefs. Archaeocyathids, with small, usually cup-shaped, mainly solitary, porous carbonate skeletons, have been considered a distinct phylum but modern opinion tends to favour their classification as a subgroup of the Porifera. They form mainly small patch reefs, mostly < 3 m thick and 10–30 m in diameter, although larger fringing or barrier reefs are claimed in the later Lower Cambrian with accumulated thicknesses < 100 m.

Bioherms are dominated by three to four structurally different genera, some rooted and functioning principally as bafflers. *Renalcis*, *Epiphyton* and *Girvanella* are frequently associated as overgrowths and may form the bulk of the skeletal material. About 30–50% of the build-up is fine carbonate mud with some bioclastic debris, little pore space, and few cavities. There may be pockets or lenses of shelly material but generally fauna of the adjacent facies is rare. There is no evidence of biological destruction by borers or grazers.

No obvious reef zonation is reported for archaeocyathid build-ups. They are the first of a range of skeletal organisms to form patch colonizations of the sea floor with minor relief, which persist in time to form biohermal masses in the rock record. They declined at the end of the Lower Cambrian and became extinct in the early Middle Cambrian, initiating a period which, in the absence of suitable skeletal organisms, lacked significant reef growth. Algal stromatolite build-ups made a brief comeback, possibly with a decline in grazers, as gastropods are scarce in the later Cambrian (Copper 1974). Lithistid sponges occur in some of these stromatolite masses and skeletal algae are not uncommon. Stromatolite build-ups with or without a sponge contribution persist into the early Ordovician but an explosion in diversity of grazing gastropods correlates with the effective disappearance of stromatolites as major components of build-ups on open shelves.

The Ordovician

The early Ordovician sees a rise in small bioherms constructed of lithistid sponges, particularly *Archaeoscyphia* (somewhat archaeocyathid in appearance), and skeletal algae. Locally, the receptaculitid alga *Calathium*, or *Pulchrilamina* of dubious affinities but possibly a stromatoporoid, may be important biohermal components. Again, these mounds show no zonation and little relief, no borers but common burrowers, and increasingly diverse associated biotas including echinoderms, trilobites, brachiopods, crinoids, early bryozoans, and rich pockets of gastropods and cephalopods. Build-ups reach cumulative thicknesses of 20 m and lengths of 87 m. Larger examples may show simple succession (James 1983), climaxing in encrustations of *Pulchrilamina*. In addition, the early Ordovician has the earliest examples of mud mounds dominated by the cavity structure stromatactis (variously considered as of organic or purely physical origin) and lacking any (other) sign of organic framework, < 76 m thick and 300 m across. Similar structures are recorded sporadically through the rest of the Palaeozoic, whilst stromatactis is frequently a component of build-ups dominated by (other) metazoans.

There was a great expansion in benthic marine life in the early Middle Ordovician. The stromatoporoids, with doubtful Cambrian representatives, the bryozoans, and the tabulate corals had all evolved and the rugose corals appeared for the first time. These groups, including the major components of the most successful Palaeozoic reef communities, diversified rapidly and non-stromatoporoid sponges declined as reef builders. However, it was almost another 100 million years before these new components realized their full potential.

Initially, bryozoan reefs dominated, constructed of small encrusting, domed, massive, plus erect bifolial and cylindrical colonial morphologies trapping and binding lime mud. A few small sponge reefs were bound by bryozoans and stromatoporoids, with blankets of shell coquinas and pelmatozoan debris. These mainly small, unzoned build-ups may have had as much as 1 m relief and formed accumulations up to 4 m thick, but in the later Middle Ordovician, large shelf-break carbonate masses, < 250 m cumulative thickness and 60 km long, are dominated or largely constructed by bryozoans (Webby 1984). Associated faunas included crinoids, brachiopods, together with blue-green (*Girvanella*, *Sphaerocodium*) and red (*Solenopora*)

algae, some sponges and, in some of the larger build-ups, stromatactis. Tabulate coral and bryozoan build-ups coexisted briefly, with later Middle Ordovician *Labyrinthos* patch reefs, but by this time the stromatoporoids were beginning to diversify. From the later Ordovician until the end of the Devonian, major build-ups were dominated by stromatoporoids, with corals and skeletal algae as major contributors, whilst bryozoans and other sponges were reduced to minor roles. However, corals alone and less commonly bryozoans continued to contribute patch reefs, forming bioherms and sometimes extensive biostromes, whilst sponges sometimes dominated build-ups in deeper water.

Upper Ordovician build-ups range from small patches dominated by *Tetradium*, fasciculate Rugosa, *Receptaculita* and other skeletal algae, through small algal and stromatolitic pinnacle reefs < 30 m high and 0.8 km in diameter, to zoned and unzoned coral–stromatoporoid build-ups and large stromatactis mounds < 100–140 m high and 1 km in diameter. A shelf-break complex of patch reefs, individually < 15 m high and 50 m in diameter, grades from talus flanked domical stromatoporoid mounds at the margin, through communities of laminar and domical stromatoporoids, to patches of diverse corals, algae, and ramose bryozoans in the

shelf interior. By the late Ordovician, there is increasing evidence of borers and skeleton-breaking organisms at work.

The development of reef communities suffered another set-back with the late Ordovician extinctions (Section 2.13.2). Build-ups are few and small until mid Llandovery times. Thereafter, patch reef development becomes widespread, particularly in the later Llandovery and Wenlock, with individual examples developing < 5 m relief on the sea floor, < 60 m cumulative thickness, and 100 m or more in diameter. Succession may be well developed with pioneering faunas of syringoporids, favositids, spheroidal stromatoporoids, halysitids, or crinoid groves. In the diversification stage, stromatoporoids of various morphologies, colonial rugose corals, and tabulate corals (particularly heliolitids) may be prominent, with a rich associated fauna of brachiopods (often in nests), bryozoans (some cryptic), crinoids, microfauna, and stromatactis. Algae are not so prominent. Stromatoporoids, with or without tabulate corals, form the domination stage. Most build-ups show little lateral differentiation internally. However, among the hundred or more patch reefs of Middle Silurian age in the Great Lakes area, the largest structures show greater complexity. The 15 km² Marine Reef of Illinois has a core largely constructed of stromatactis, with a cen-

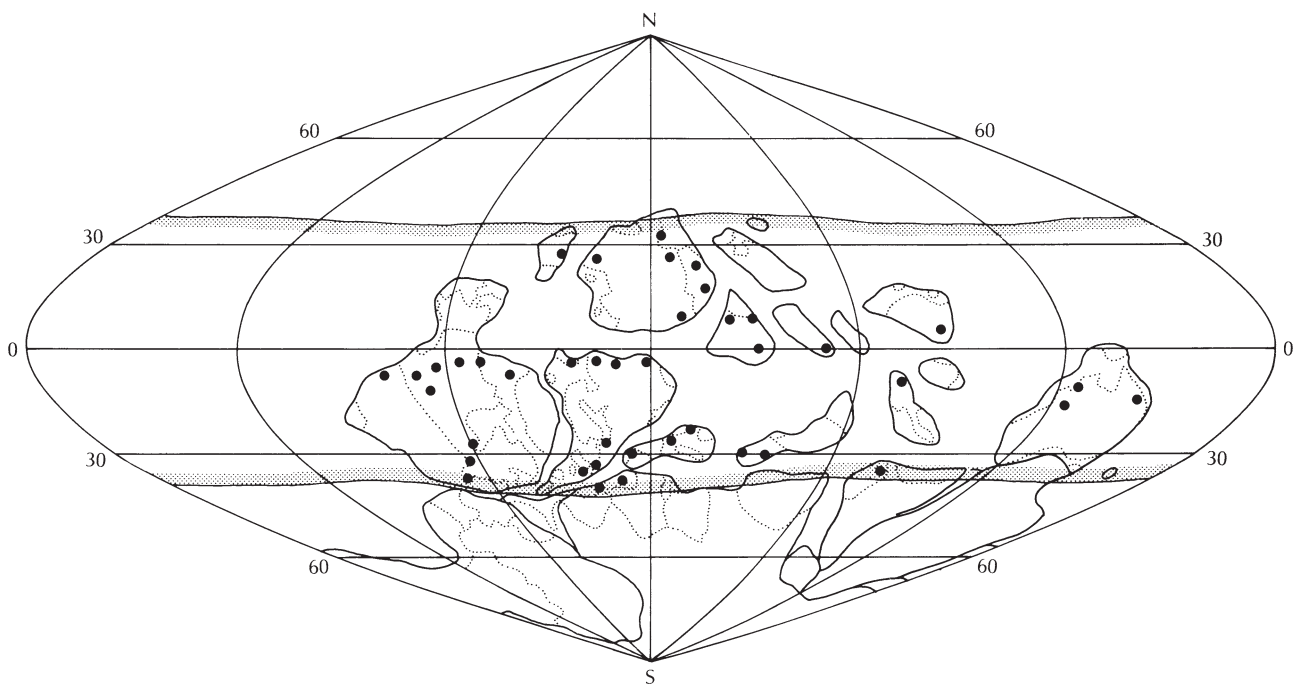


Fig. 2 Devonian continental reconstruction showing the distribution of organic build-ups (reefs and bioherms) and their latitudinal limits. (After Heckel & Witzke 1979.)

tral lagoonal facies, an externally fringing community of corals and stromatoporoids and a flanking apron composed largely of skeletal debris.

The Siluro–Devonian

These Silurian build-ups were the forerunners of the spectacular development of reef growth in the Devonian, representing the first major peak in reef diversification and possibly the all time acme for reef ecosystems (Fig. 2). Major reef complexes, persisting over tens of millions of years, resulted in cumulative thicknesses of reef and perireefal carbonates < 2 km thick and stretching for hundreds of kilometres along shelves. Fringing, barrier, and shelf based atolls (faros) are represented. Reef edge, fore reef, and back reef zones are clearly differentiated with detailed palaeoecological zonation comparable in complexity and in variation of constituent faunas and floras to modern major reef complexes. Principal constructors of the reef margin were stromatoporoids and the blue-green algae *Renalcis*. Stromatactis is often present, and corals play a subsidiary role although they were more important on the reef flat and in areas where a reef rim was poorly developed or missing. Back reef facies are characterized by distinctive lithologies and assemblages, in particular by the stromatopore *Amphipora*.

In some places, for example the Canning Basin of Western Australia, talus aprons and pinnacle reefs can be demonstrated on fore reef slopes descending to basinal facies < 180 m below contemporary sea level. Compared with Recent reefs, those of the Devonian show much less evidence of the activity of borers, grazers and scrapers; much of the breakdown of the rapidly cemented reef rock appears to have been physical.

This episode of reef building was terminated by the collapse of shallow-water ecosystems and the extinction or near extinction of the principal frame-building organisms near the end of the Frasnian (Section 2.13.3). In the Canning Basin, reef growth locally continued into the Famennian almost totally dominated by skeletal and non-skeletal algae. In the succeeding Carboniferous major build-ups are rare, although mud mounds are common, reflecting the relative paucity of suitable constructors among the skeletal organisms in the re-established level bottom communities. It was almost another 100 million years before large scale reef complexes were again developed, and then not on the scale of those of the Devonian.

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1.8 Terrestrialization

1.8.1 Soils

V. P. WRIGHT

Introduction

The soil is probably the most studied and best understood ecosystem on Earth, yet very little is known of its origins or the timings of each developmental stage in its evolution. This situation arises both because of the low preservation potential of soils and through a lack of study.

A variety of soils have been recognized in Precambrian sequences ranging back to over 3000 Ma. During the latter half of the Precambrian and through the Phanerozoic a gradual diversification of soil types occurred (Retallack 1986), reflecting both atmospheric evolution and biological diversification, especially since Middle Palaeozoic times.

Although many, if not most, details of the evolution of soil communities and their interactions remain conjectural, several major stages can be defined. The evidence, circumstantial at best, suggests that biologically active soils have existed since at least Middle Cambrian times (Fig. 1).

Abiotic soils

No direct evidence has been found for biologically active soils during the Precambrian, although a variety of weathering profiles and structural palaeosols have been discovered (Retallack 1986). Organic-rich palaeosols apparently occur in the 2400 Ma Blind River Formation of Ontario (Campbell 1979). High levels of radiation, adverse temperatures and atmospheric conditions must have prevented colonization of the land surface, even though microbial life existed in the contemporaneous seas. The soils which developed during the Precambrian were the products of purely physical and physico-chemical processes.

Microbial soils

Cyanobacteria were abundant in the Precambrian, including intertidal forms which were adapted to

daily wetting and drying and to salinity variations. As such they were preadapted to life on land. Some silicified Precambrian forms can be compared directly to extant cyanobacteria found in subaerial settings (Campbell 1979). In present day environments, too hostile for higher plants (such as deserts or at high altitude), primitive microbial communities are dominated by cyanobacteria, both filamentous and coccoid, and chlorophytes. If such forms are capable of widely colonizing modern deserts, it would be naive to doubt their ability to colonize the ancient land surfaces. Golubic and Campbell (1979) have compared the mid-Precambrian microfossil *Eosynechococcus moorei* with the extant cyanobacterium *Gloeotheca coerulea*, which is a subaerial form, providing a suggestion of the earliest terrestrial microbiota.

Biogenically influenced terrestrial to supratidal phosphates have been recorded from the Middle Cambrian of the Georgina Basin of Northern Australia (Southgate 1986). In these examples very well preserved phosphatized microbial tubes, identical to calcified fungal tubes in present day calcrete soils, occur in phosphate horizons associated with shallowing-upwards peritidal deposits. The exact setting for their formation (supratidal or fully terrestrial) is uncertain but the remarkable similarities between these phosphatic fabrics and those of present day microbial soil carbonates must place this discovery as the strongest candidate for the earliest biologically active soil.

The 'greening' of the land surface, albeit by a microbial sludge, would have begun a series of wide reaching changes in weathering and sedimentary processes. Land surfaces, lacking any biological cover, are prone to erosion by wind and runoff. Even simple microbial mats on the surface would have provided some binding of weathered materials (Campbell 1979), although roots provide a much more effective binding agent. As a result of binding, rates of erosion may have decreased and weathered materials would have had a longer residence time in the soil, allowing greater decomposition. The biological cover might also have increased levels of carbon dioxide in the soil, and would have added organic acids; both factors would have promoted chemical weathering in the soil. All these effects

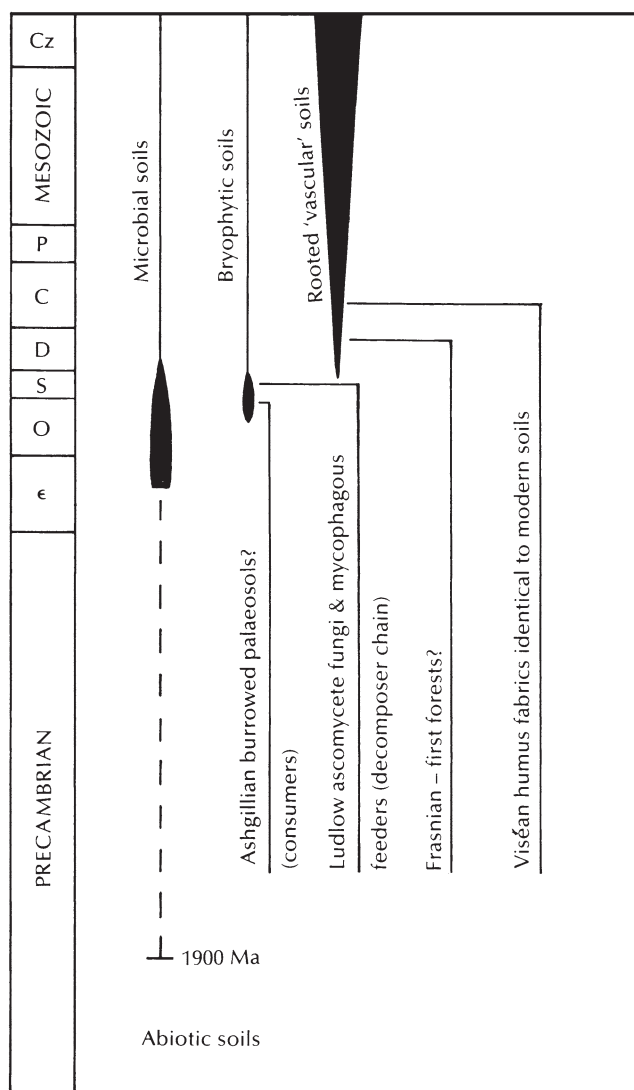


Fig. 1 Geological ranges of major soil categories and first known appearances of important soil ecosystem components.

must have increased many-fold with the advent of rooted vegetation.

On newly exposed surfaces cyanobacteria are usually the first colonizers, followed by lichens. Fungally produced oxalic acid in lichens is a major factor in rock decomposition, but the timing of the appearance of the fungal–cyanobacterial association is unclear. The vast majority of lichen-forming fungi belong to the ascomycetes, but the earliest record of these is from the Ludlow of Gotland (Sherwood-Pike & Gray 1985).

Present day microbial soils are best developed in restricted settings which do not provide guides to

the sorts of soils possible in the past. Under suitable conditions relatively thick microbial mats may have developed, especially in humid climatic regimes. Such soils must have provided suitable microclimates for the first terrestrial invertebrates (Rolfe 1985; Section 1.8.3), even if the bare landscapes were still too hostile. However, no records of such microbial soil faunas are known with confidence. Highly bioturbated palaeosols have been recorded from the Late Ordovician (Ashgillian) Juniata Formation of Pennsylvania, U.S.A. (Retallack 1986). These consist of burrows 3–16 mm in diameter, extending to depths of 50 cm in the now compacted argillaceous palaeosol. The burrows occur in fluvial overbank deposits, and it is often very difficult to determine if such burrows are truly those of soil dwellers or the result of burrowing during temporary subaqueous phases caused by flooding. As yet no attempt has been made to detect organic carbon isotope signatures in pedogenic carbonates in Lower Palaeozoic palaeosols, but this might prove a fruitful avenue of investigation.

Bryophyte soils

By the Late Ordovician bryophytic-like terrestrial vegetation had appeared (Section 1.8.2). Such a vegetation cover, although relatively thin, would again have provided opportunities for faunal colonization. The nearest possible present day analogues for such biotas are to be found associated with lichens or moss cushions. They are characterized by a community of microarthropods, such as mites and springtails, but these only have a geological record back to the Early Devonian (Siegenian) Rhynie Chert. Could it really have taken over 40 million years for invertebrates to have colonized the bryophyte 'felt' covering the land surface, a land surface which probably already had a long history of microbial cover? The earliest known terrestrial faunas of the Early Devonian (Section 1.8.3) were already diversified and contain representatives of the major soil ecosystem components.

The earliest evidence of a terrestrial biota, although tentative, consists of faecal pellet-like ovoid and cylindrical bodies of hyphal fragments from the Ludlow of Gotland (Sherwood-Pike & Gray 1985). These may provide evidence of mycophagous feeders, and the presence of associated ascomycete fungal remains indicates that the decomposer subsystem of the soil ecosystem had already evolved.

Rooted soils

The next major step was the development of a rooted plant cover. This happened progressively with the diversification of the vascular plants from Early Silurian times, with a further major step in late Devonian times when true forests first appeared. The final stage in this series of events, at least to date, was the rise of the grasses in the Tertiary (Section 1.11). The consequences of a rooted plant cover were far greater than those of a simple microbial or bryophytic one. The increased stability of the soil, and increased biomass, would have resulted in thicker soils and thicker humus. The degree of biochemical and biophysical weathering would have increased dramatically, and from Devonian times on soil-types diversified in response to these changes (Retallack 1986).

The advent of a prominent rooted zone would have been associated with the development of the rhizosphere, with its own complex biotic interactions. A critical event would have been the initiation of symbiotic fungal–root relationships (mycorrhizal associations), in which the fungal component acts as a nutrient supplier to the roots. These fungal associations occur either internally within the root (endomycorrhizae) or as sheaths around the roots (ectomycorrhizae). Occurrences of actual fungal remains with roots have been recorded from the Rhynie Chert and also abundantly from early Carboniferous soils, as calcification products of basidiomycete fungi around root tubes. In such cases, however, it is difficult to categorically establish that the fungi were not simply saprophytic forms.

Ecology

The soil is an essential component of the terrestrial ecosystem, and one of its most critical functions is to decompose organic matter, making plant nutrients available for recycling. The primary producer subsystem must, by all reasonable considerations, have been present from Cambrian times or earlier. The possible occurrence of fungal tubes in middle Cambrian terrestrial phosphorites of Australia, and the presence of ascomycete remains from the Ludlow of Gotland suggest that by the Middle Silurian, if not much earlier, the decomposer subsystem had also developed. Thus recycling became possible. Possible microarthropod faecal pellets in the Silurian suggest the presence of consumers (mycophagous forms). Some 20 million years later,

as revealed in the Siegenian Rhynie Chert, a fauna of spring-tails, mites, spiders, and trigonotarbid arachnids had appeared, representing many of the important components of the ecosystem (Section 1.8.3).

By early Carboniferous times the soil ecosystem had evolved to a point where it produced a variety of humus fabrics identical to those found in present day soils (Wright 1987), which must reflect the action of the same types of complex biogenic processes.

The evidence is frustratingly incomplete, and further work is required especially to integrate the occurrences of the early soil faunas with their associated soils. The effort needs to be made to search for evidence of biofunction in early Palaeozoic terrestrial deposits, since such soils were probably organically active. What can be said, with growing confidence, is that the first vascular plants must have colonized a land surface which already had a long history of biological activity. Studies of microbial or bryophytic soils today will provide us with some clues as to the possible forms taken by these earliest soils.

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1.8.2 Plants

D. EDWARDS & N. D. BURGESS

Introduction

Land plants encounter problems relating to water stress, uptake, and transport, and to aerial dispersal of propagules. Survival in such habitats is associated with three major strategies:

1 Drought avoidance via opportunism and ephemeral life cycles completed under favourable conditions.

2 Extreme desiccation tolerance involving the capacity of cytoplasm to rehydrate and then function normally (poikilohydry).

3 Maintenance of an internally hydrated environment by biochemical and anatomical modifications (homoiohydric).

Extant land vegetation includes representatives of all major groups; cyanobacteria, algae, bryophytes and tracheophytes. The last are usually considered most successful and are homoiohydric — possessing xylem (with lignin) for water transport, a waxy cuticle (cutin) for reducing evaporation, stomata and an intercellular space system for gaseous transport (Raven 1984). The poikilohydric life style of cyanobacteria, algae, and bryophytes is usually considered more primitive, is of particular significance in the colonization of unstable 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/or dispersal units such as spores. The latter, impregnated with sporopollenin, a complex fatty polymer, also occur in tracheophytes. Thus although there is no direct record of thallophytes (cyanobacteria and algae) colonizing moist land surfaces in the Early Palaeozoic, it seems likely that they were present. A possible limiting, physical factor may have been high ultraviolet (UV) radiation correlated with low atmospheric oxygen. Indeed it has been postulated that lignin evolved from precursors involved in UV absorbance, and that cutin and sporopollenin initially had a similar role in UV reflectance.

With regard to higher plants, attempts to demonstrate the vascular status of megafossils, thus pro-

viding unequivocal evidence for land vegetation, have traditionally dominated research. However, more recently the affinities of Ordovician and Silurian microfossils have been rigorously appraised in the search for alternative pioneering colonizers.

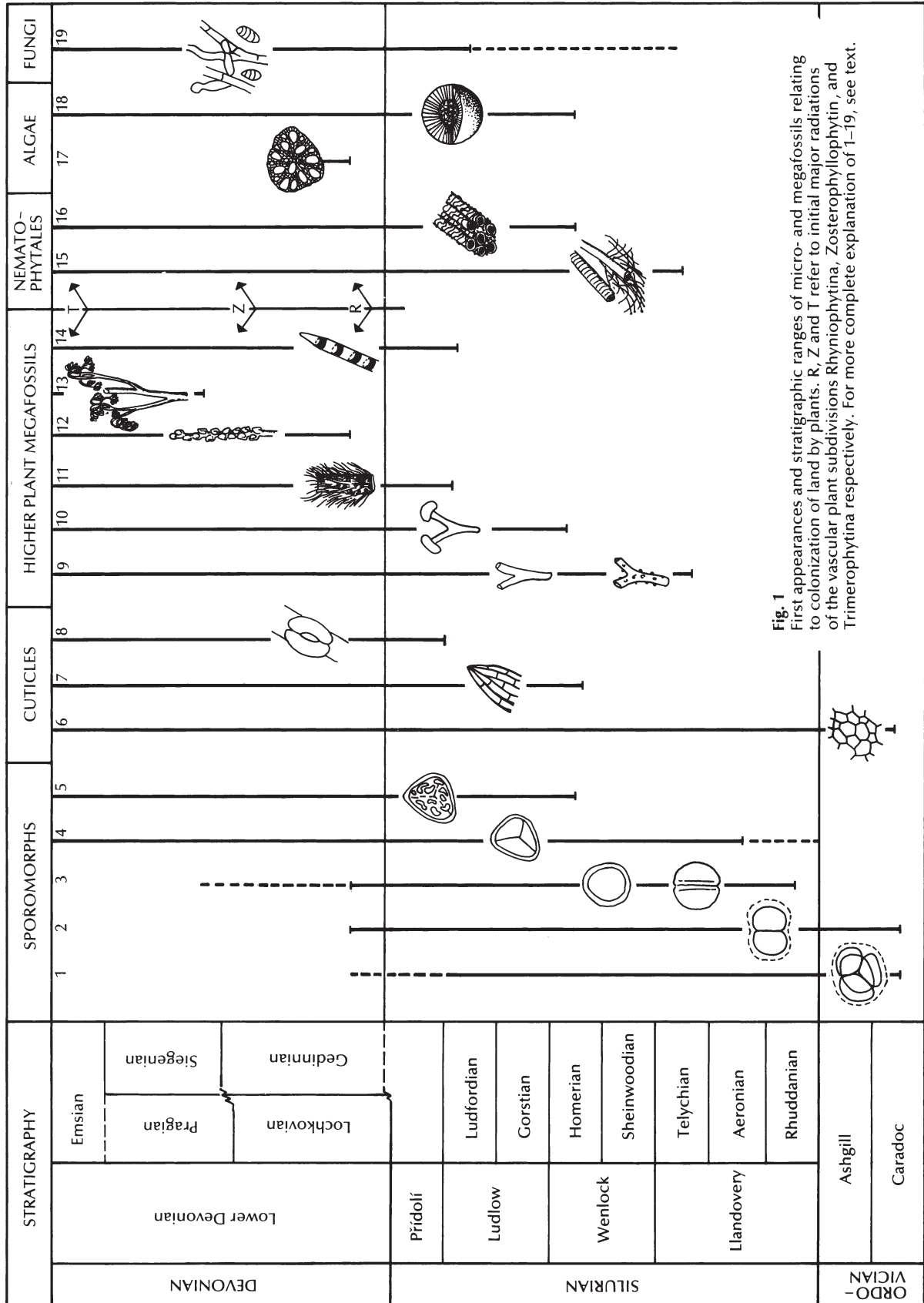
The first records and ranges of all fossils thought relevant to terrestrialization are documented in Fig. 1, and numbers below refer to that figure.

Sporomorphs

1, 2. *Cryptospores*. (lacking trilete (Y) or monolete (l) marks; after Richardson & Edwards 1989.)

Obligate permanent tetrads (1), so named because they do not split into four spores (monads) on dispersal, possess durable, smooth, unornamented walls thought to be impregnated with sporopollenin, although this has not been chemically proven. They are thus considered to derive from land plants. Those characterizing Upper Ordovician spore assemblages are smaller, smooth walled, and often lack the enveloping smooth or sculptured 'membrane' typical of most early Silurian forms. Its absence may result from poorer fossilization potential. Such tetrads increase in numbers and diversity, dominating assemblages until the end of the Llandovery. Thereafter they become relatively less common and occur only rarely in Lower Devonian sediments, where they are probably reworked. Gray (1985) has argued most persuasively that as comparable tetrahedral tetrads (sometimes membrane enclosed) occur in certain living liverworts, they thus derive from poikilohydric plants with bryophyte physiology and life histories. It is also possible that they belonged to freshwater or marine algae for which there are no modern analogues, or that they were shed by intermediate extinct forms that lived in ephemeral water bodies producing spores when these dried up. Membrane enclosed *monads* and *obligate dyads* (2) have similar ranges to tetrads and were probably of similar derivation.

3. *Dyads*. Habitually lacking a membrane, and believed to split into the consistently associated alete (lacking trilete or monolete marks) spores with thinner proximal faces and identical distal features, these are distally smooth walled in earliest records (Rhuddanian) and sculptured from the Homerician. They persist throughout the Silurian and are relatively common in basal Devonian assemblages. Dyads occur in *Salopella*-like sporangia in the Přídolí. The affinities of that genus remain



obscure, as vascular tissue has never been demonstrated.

4, 5. *Monads with triradiate marks*. The earliest monads not derived from obligate tetrads are smooth walled, usually with equatorial thickening, e.g. *Ambitisporites* which is later recorded in Přídolí *Cooksonia pertoni* sporangia. Sculptured monads occur continuously from the Homeric, showing rapid diversification and increases in numbers in the Ludlow and Přídolí. For the most part their origins, be they bryophyte or tracheophyte, are unknown, but their presence in Silurian and Gedinnian *Cooksonia pertoni* (Fanning *et al.* 1988) indicates that some of the producers may have been rhyniophytoid (10).

Cuticles

6. '*Nematothallus*'. Associated with the earliest tetrads are small cuticular fragments, thought analogous to vascular plant cuticles. They lack stomata and are usually imperforate, with smooth outer surface. Ornamented forms appear in the Wenlock and continue into the Gedinnian. A reticulate pattern represents the outlines of surface cells in the underlying tissue. In *Nematothallus*, such cells were \pm isodiametric in tangential section, while in the cuticles of higher plants they are elongate vertically. Lang (1937) suggested that they covered *Nematothallus*, a thalloid plant composed of tubes which he placed in the Nematophytales (15, 16), a taxon for plants with organization neither algal nor higher plant.

While there may be some doubt that all durable spores derive from land plants, this is not the case for cuticles, although being imperforate and hence relatively impermeable to gases, their function and even composition in *Nematothallus* might have been different from that in tracheophytes, e.g. primarily as UV screens, facilitating runoff, or in defence. It is unlikely that they belonged to the tetrad producers because, although the first records are coincident, cuticles persist into the Emsian and are sometimes quite common constituents of Lower Devonian assemblages.

7, 8. *Higher plant cuticles*. Homeric fragments with larger, more strongly demarcated and aligned cells are interpreted as sporangial from comparison with dispersed and *in situ* Gedinnian rhyniophytoid examples (10). Cuticles without stomata deriving

from sterile axes occur in the northern hemisphere Ludlow. The earliest *direct* evidence for stomata (with two guard cells) comes from sterile axes at the base of the Přídolí, with examples on *Cooksonia* and *Zosterophyllum* recorded in the Gedinnian. However, since stomata were described on Canadian Emsian *Baragwanathia abitibiense* they were probably also present on the earlier Australian Ludlow *B. longifolia*, where cells are not preserved.

Higher plant megafossils

9. *Sterile axes*. It is usually accepted that those with dichotomous branching and peripheral support tissues (sterome), the earliest being Llandovery *Eohostimella*, are derived from erect land plants. Late Silurian and early Devonian examples (e.g. *Hostinella*) possess a central strand composed 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, while others may possess conducting tissues of bryophytic nature (cf. Lower Devonian *Aglaophyton* (*Rhynia*) *major* which exhibits many homoiohydric characters, and would be assigned to the Tracheophyta but for the moss-like conducting tissues).

10–13. *Fertile tracheophytes*. Wenlock *Cooksonia* (Rhyniophytina: 10) is generally accepted as the earliest erect pteridophyte-like plant (Edwards *et al.* 1983). Reservations as to its affinity stem from a complete lack of anatomy. Spores occur in Přídolí, and stomata and sterome in Gedinnian *C. pertoni*. Tracheids have never been demonstrated in central strands. Thus although *Cooksonia*, *Salopella* and *Steganotheca* are usually assigned to the Rhyniophytina because of general morphological similarity to later examples, e.g. *Rhynia gwynne-vaughanii*, they are better called 'rhyniophytoid' to emphasize our ignorance. A major radiation is recorded in the early Gedinnian, but they then became insignificant constituents of land vegetation (Edwards & Fanning 1985).

Baragwanathia longifolia (11) in Australian Ludlow strata is morphologically similar to Lower Devonian examples, with sufficient anatomical as well as morphological characters to indicate lycophte affinity. Thus, even in the absence of anatomy in Silurian representatives, its vascular status is unquestioned. The earliest lycophte with typical

sporangium/sporophyll organization is the late Emsian *Leclercqia*.

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

Nematophytales

15. *Microfossils of tubular organization*, either as isolated tubes or wefts, are recorded from the Telychian into the Lower Devonian. The most conspicuous tubes are internally sporadically thickened ('banded'), broadly resembling tracheids in their ornament, but there is no direct evidence that they were lignified. The source plants are problematic: they occur with smaller tubes in *Nematothallus* (Lang 1937) and have been found in plants with organization otherwise typical of *Prototaxites* (16). The habitats of such organisms, be they freshwater or terrestrial, remain as conjectural as their affinities. In that some tubes (but not banded forms) 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. Some of the associations may belong to *Nematothallus* or *Nematoplexus*.

16. *Prototaxites* (Wenlock–Upper Devonian) is included because it is sometimes cited as a land plant largely due to its occurrence in tracheophyte assemblages in freshwater sediments. Its organization, in which narrow filaments enclose wider smooth tubes, is unique, and hence in the absence of reproductive organs its affinities, possibly algal or fungal, remain unknown, and speculation on the functions of its tissues unrewarding.

17. *Parka*, best known from the Scottish Gedinnian, 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*. Comparative biochemical and ultrastructural studies suggest that among the green algae the Charophyceae show closest similarities with bryophytes and tracheophytes while *Coleochaete*, with its parenchymatous organization, and protection, nutrition, and prolonged retention of the zygote, possesses the greatest number of advanced features.

18. *Pachytheca* is exceedingly common in certain marginal fluvial and lacustrine facies in the Lower Devonian. 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 here 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). Resting spores of presumed mycorrhiza in some Rhynie Chert axes are frequently cited as supporting evidence, but the abundant spheres and hyphae may just indicate saprotrophism (i.e. decomposition of dead organisms) in peat development. Further evidence for terrestrial fungi is the record of ascomycetes remains (hyphae, probable conidia, and ascospores) from the Ludlow of Gotland (Gray 1985), 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 cyano- and eubacteria, later joined by filamentous and unicellular algae. Such an encrusting layer would have both physically stabilized and chemically broken down the substrate, releasing nutrients and, in stable environments, resulting in the build-up of humus (see also

Section 1.8.1). From the middle Ordovician onwards microfossils morphologically convergent with those from later tracheophytes suggest a novel vegetation, possibly with thalloid organisms covered by cuticle and spore producers with liverwort life-style; aerial dispersal indicates the attainment of some stature. The appearance of *Ambitisporites* in the Llandovery heralded a new phase — the advent of pteridophyte-like plants with axial organization, possibly forming a 'turf' just a few centimetres high. The larger size permitted by homoiohydric, 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 is an increase in axis diameter and length of fragments: 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 of the Emsian trimerophytes attained a height of over 1 m. As to habitats, the best direct evidence comes from the Rhynie Chert, but as all these early pteridophytes were homosporous (i.e. with spores of one size), the free-living gametophyte would have required moist conditions both for vegetative growth and reproduction. With regard to route of terrestrialization for higher plants, physiological considerations support transmigration from fresh water on to land.

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1.8.3 Invertebrates

P. A. SELDEN

Introduction

The diversity of invertebrate species on land greatly exceeds that in the sea; this is almost entirely due to the terrestrial insects which form 70% of all animal species alive today. However, of over 30 invertebrate phyla, only the arthropods, the molluscs, and the annelids have significant numbers of macroscopic terrestrial representatives. A greater number of phyla include very few terrestrial species, cryptobiotic representatives, or internal parasites on terrestrial organisms. The body plans of some highly successful marine phyla have apparently 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 taxon has become extinct, as far as is known.

Outstanding questions on terrestrialization are: what physiological mechanisms enabled invertebrates to emerge onto land; did each taxonomic group use similar mechanisms; were their routes onto land the same; did they all come onto land simultaneously, suddenly or gradually, or in different invasions? The hardest evidence comes from comparative physiology, but palaeontology has the power to test theories based on living material, and uniquely adds the dimension of time.

Invertebrates moving from seawater to land experience profound changes in all aspects of life (Little 1983). On land, water supply is at least variable, and commonly seasonal. To invertebrates, whose air breathing mechanisms utilize diffusion to a far greater extent than ventilation, oxygen is more available in air than in water because the diffusion coefficient (partial pressure per unit length, in ml/[min × cm² × cm × atm]) of oxygen in

water is 0.000034, but in air is 11.0. Support is more problematical in the less viscous aerial medium than in water, but once overcome, locomotion is 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 invertebrates. On land, internal fertilization is the norm, and greater protection (e.g. from drought) is afforded to the developing embryos. Changes in nutrition, ion balance regulation, and excretion are also necessary for terrestrialization.

Some land animals avoid the difficulties of water supply by living in soil interstitial water; strictly, such animals (e.g. protozoans, ostracodes, and nematodes) should not be regarded as terrestrial. Poikilohydry is used only by small terrestrial animals, such as protozoans, tardigrades, nematodes, and rotifers, whose habitat is subject to seasonal drought periods. Many soil, litter, and crevice dwellers are able to take advantage of the high humidity in such habitats, and though they are often able to foray in drier situations (e.g. woodlice across the kitchen floor), retreat to the humid home base is essential to prevent desiccation. In addition to woodlice, the centipedes, millipedes, flatworms, leeches, and earthworms are included in this group. Some animals, such as many land snails, can withstand desiccation during dry periods by aestivation, but require water or high humidity for activity at other times. Finally, the true invertebrate conquerors of the terrestrial habitat, not requiring a humid environment in which to flourish, but active in dry, and even desert, conditions, are the majority of insects, many arachnids, and a few crustaceans. All terrestrial arthropods have waterproofing in the cuticle, but the form this takes differs in each arthropod group and is not always well studied. The differences may be important for palaeontology, however, since the preservation potential for different cuticles is not the same.

The fossil record

The fossil record of terrestrial invertebrates is shown in Fig. 1 (Rolfe 1980; Chaloner & Lawson 1985). There is no fossil record of terrestrial flatworms, nemerteans, or nematodes, although fossil examples of parasitic and aquatic nematodes are known (Conway Morris 1981). Oligochaete annelids are known from the Carboniferous. Their traces, in-

cluding burrows and faecal pellets, occur in palaeosols from the Carboniferous onwards. They may have emerged onto land with the first humic soil (Section 1.8.1).

Land snails, both helicid prosobranchs and stylommatophoran pulmonates, are recorded from the Upper Carboniferous, indicating that they had already become significant members of the land fauna by that time. The earliest basommatophoran pulmonate is Late Jurassic in age; this contradicts evidence from comparative morphology, which suggests that basommatophorans were ancestral to the other pulmonates. Possibly the development of ground shade and deciduous leaf litter (probably Lower Carboniferous) was necessary before land snails could be assured of the damp conditions necessary for colonization (Solem 1985).

All extant insects are terrestrial or secondarily aquatic, and there were no terrestrial trilobites, as far as we know. The record of Onychophora, which includes the Recent *Peripatus*, appears to begin with *Aysheaia* from the marine, Middle Cambrian Burgess Shale. Terrestrial uniramians (myriapods and insects) were thought to have evolved from land-living onychophorans, but there is new evidence that the earliest myriapods were marine. This comes from myriapod-like fossils in marine sediments from the Silurian of Wisconsin and the Middle Cambrian of Utah. By the Devonian, millipedes, centipedes, and arthropleurids had appeared in terrestrial faunas, and some reached giant proportions in the Carboniferous forests. The earliest apterygote insects occurred in the Devonian, but the first pterygotes were Carboniferous in age.

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. They illustrate a failed attempt at terrestrialization using a method now being tried by the Crustacea. Their close relatives, the scorpions, succeeded however, by changing their gills into lungs. All other arachnids are primarily terrestrial today, and the evidence from comparative morphology suggests that each arachnid group emerged onto land independently. The oldest are the trigonotarbid: extinct, close relatives of spiders, with good terrestrial features, from the Lower Devonian of Rhynie, Aberdeen. In the Devonian are also found mites, pseudoscorpions, and possibly spiders, and by the Carboniferous there were more arachnid orders than today; only the spiders have radiated more dramatically in later periods.

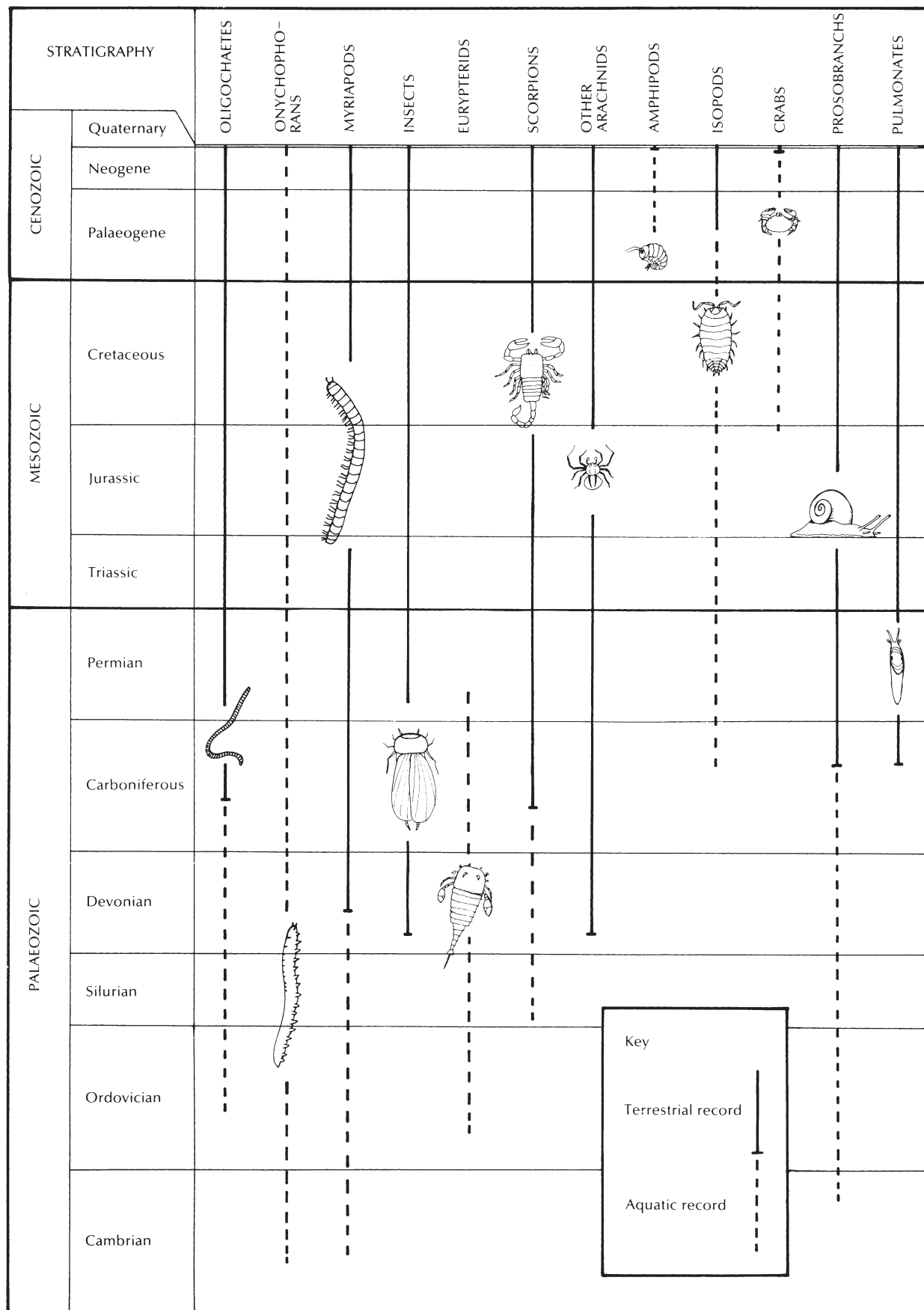


Fig. 1 The fossil record of terrestrial invertebrates and their forebears.

The fossil record of crustaceans is generally good because, like the trilobites, they have a mineralized exoskeleton. 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 Middle to Late Mesozoic at least. The terrestrial talitrids, with no fossil record, are considered by some to have emerged onto 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 Oniscoidea are known only since the Eocene. Although crabs and crayfish first appeared in the Jurassic, the important crab radiations did not occur until the Cretaceous and the Eocene; families with terrestrial representatives first appeared in the Palaeogene, but true terrestrial forms not until the Late Neogene.

Morphological adaptations for life on land

A major problem for terrestrializing animals is that both oxygen and carbon dioxide molecules are larger than the water molecule, so that any membrane across which the respiratory gases are diffusing will leak water. This may not be too disastrous in moist environments like the soil, in which animals such as earthworms can use cutaneous respiration, but inhabitants of dry habitats need a waterproof skin and have developed special respiratory organs to reduce water loss. Respiratory organs can be broadly classified into gills, (evaginations) used primarily in water and lungs (invaginations used primarily in air). A great many animals utilize cutaneous gas exchange in conjunction with gills or lungs. Aquatic animals which venture onto land for short periods of time may use their gills for air breathing, but if much time is spent on land, accessory lungs are usually developed. Many examples of animals with both lung and gill can be found among the gastropods and the Crustacea. In some instances, the lung developed not for land life, but to withstand poorly oxygenated water or drought periods (cf. lungfish).

True lungs among the invertebrates are found only in gastropod molluscs and arthropods. Among gastropods the pulmonates (land snails and slugs), and a few prosobranchs (e.g. helicids), are the only truly terrestrial forms. The gastropod lung is formed from a highly vascularized part of the mantle cavity, which in pulmonates opens by a small pore

(the pneumostome) to the outside. In the arthropods, book-lungs, tracheae, and pseudotracheae are all types of lung which have evolved independently in a number of groups. The book-lungs of arachnids are homologous with the gills of the aquatic chelicerates, and appear to have been derived from them simply by sealing the edges of the gill covers and leaving a hole (the stigma) to connect to the outside. The early scorpions (Silurian to Carboniferous) were aquatic and gills are known in the Devonian *Waeringoscorpia* from Germany; but by the Lower Carboniferous, pulmonate scorpions had appeared alongside the aquatic forms. In the related, extinct eurypterids, the so-called gills actually resemble some crustacean air-breathing organs, which suggests that this was their real function, and that true gills, being thin membranes, have not been preserved or recognized in fossils. As in the pulmonate gastropod lung, dendritic structures resembling insect tracheae have developed within the book-lungs of some arachnids; additionally, some arachnid groups have developed tracheal systems. Among the chelicerates, therefore, respiratory organs developed independently in each group by modification of various pre-existing organs according to need.

The insect tracheal system is a dendritic pattern of tubes arising from apertures (spiracles) in the body wall, and penetrating to every tissue in the body to supply oxygen directly to the cells. Since the insects appear to have evolved from terrestrial myriapods, the problems of terrestrialization have never troubled them, which may explain their success. A variety of tracheal systems occurs among the myriapod groups. Several independent terrestrial lines are found in the Crustacea (Powers & Bliss 1983), principally the talitrid amphipods, the isopods, and the land crabs. In the land crabs, secondary lungs are developed that work alongside the gills (which are never lost). The isopods are more terrestrialized than the crabs, and their pleopods (gills) bear invaginations (termed pseudotracheae, from their resemblance to insect tracheae) for air breathing.

For small animals, hydrostatic skeletons work as well on land as in water; witness the success of the slug form. Arthropods moving onto land evolved the hanging stance for stability, and additionally use some form of leg 'rocking' or jointing mechanism to prevent the plantigrade foot from twisting on the ground (with consequent abrasion and loss of grip) during walking; such features can be seen in fossils. Arthropods become vulnerable during

moulting, and it is possible that pioneer terrestrial forms returned to the water for ecdysis. Sense organs on fossils can give clues to terrestriality: trichobothria (fine hairs which respond to air vibrations) found on Devonian arachnids prove their terrestrial mode of life, and stridulatory organs on the same animals at least suggest it. Complex copulatory organs preserved in fossils suggest a terrestrial habitat and their absence is evidence for an aquatic life.

Routes onto land

The physiological barrier between sea and land can be crossed by a number of routes. Invertebrates which moved onto land across the marine littoral environment include the talitrids, the isopods, and most crabs, within the Crustacea, and possibly the chelicerates and the uniramians. There is evidence that some terrestrial forms emerged via brackish water (some crabs) or salt marshes (some pulmonate snails). The freshwater route was used by the oligochaetes, leeches, prosobranch gastropods, and the burrowing potamonid crabs and crayfish. Interstitial forms have utilized both fresh- and salt water routes, and it is possible that the very earliest land animals followed this route. Indeed, a late Ordovician palaeosol from Pennsylvania is full of coprolite-bearing burrows which have been attributed to the activities of microarthropods, possibly myriapods (Section 1.8.1).

From the fragmentary record, it would appear that most terrestrial invertebrates arrived on land with, or shortly after, the Silurian plant invasion (Section 1.8.2). The first records are of fully adapted land animals (the Rhynie Chert of Aberdeen, the Alken fauna of Germany, and the Gilboa fauna of New York), which points to a pre-Devonian terrestrialization period for most groups. The major exception is the Crustacea, which are attempting terrestrialization now. The pressures, or advantages, which cause terrestrialization are undoubtedly various (e.g. escape from predators, more abundant food supply) and invite speculation. What is clear, however, is that animals came onto land together with their biotic interactions, and hypotheses should seek to explain the invasion of the land by biotas rather than individual taxa.

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1.8.4 Vertebrates

A. C. MILNER

Introduction

The earliest terrestrial radiation is presumed to have been of fish-like tetrapods (four-legged land vertebrates — amphibians, reptiles, birds, and mammals) capable of moving on land and breathing air. Modification of structure, function, and physiology in subsequent radiations led to a monophyletic group of truly terrestrial vertebrates, the amniotes. The amniotes comprise two sister groups: therapsids, which include mammals; and sauropsids, which include reptiles and birds. Amniotes evolved a totally terrestrial life cycle, eliminating an independent aquatic larval phase by means of a relatively waterproof extraembryonic membrane (amnion) which encloses the developing embryo in fluid, and a shelled egg. This reproductive strategy enabled colonization of the terrestrial environment, and early amniotes diversified into lineages leading ultimately to mammals and birds.

The earliest tetrapod record

Tetrapod remains first appear in the fossil record in the Frasnian stage of the Upper Devonian. The only abundant skeletal remains are those of the ichthyostegals, discovered in the nineteen-thirties in the Famennian red beds of East Greenland (Jarvik 1980). Three genera have been recognized, *Ichthyostegopsis*

from skulls only, and *Acanthostega* and *Ichthyostega* from skull and postcranial material, although no complete skeleton has been described (Fig. 1). *Ichthyostega* is undoubtedly the most primitive tetrapod known and retains many fish-like characters. Specialized autapomorphies debar it from direct ancestry of all other tetrapods.

Tetrapod–fish relationships

The orthodox view of the origin of tetrapods is that they derive from one particular group of bony fishes (Osteichthyes), the osteolepiforms, which are all fossil. This is currently in dispute and the subject of major contradictory reviews. Rosen *et al.* (1981) have argued that lungfish (Dipnoi) are the sister group of tetrapods, based on the shared derived character of a choana (internal nostril) and other supporting homologies. Panchen and Smithson (1987) reappraised the same data and concluded that lungfish do not share a true tetrapod choana; they support the traditional view that osteolepiform fishes are the sister group of tetrapods and, therefore, that the extinct taxa contained in that group are more closely related to tetrapods than are the lungfish.

Both osteolepiforms and dipnoans first appear in the Lower Devonian and if either is the sister group of tetrapods then the earliest tetrapods must also have been present in the Lower Devonian (Bray 1985; Milner *et al.* 1986). It is now generally accepted, however, that the tetrapods are monophyletic. A diphyletic origin from two separate groups of fossil osteichthyan fishes has been proposed by Jarvik (1980). His theory derives living urodeles (salamanders) from porolepiforms, and all other tetrapods (amphibian and amniote) from osteolepiforms;

it has not received support outside the Swedish school.

Morphological adaptations for life on land

The classical scenario painted a picture of terrestrial vertebrates emerging onto land from freshwater, argued on physiological grounds. Such a transition was thought to be in response to periodically arid environments, as interpreted from the sedimentology of the Devonian red beds. Recently, a number of authors (references in Bray 1985) have argued that the geological evidence favours a marine origin both for vertebrates as a whole and for tetrapods. Devonian osteichthyans are mainly associated with marine or nearshore continental environments and, indeed, the ichthyostegalian may be associated with coastal tidally-influenced sediments (Bray 1985).

Air breathing, by means of internally positioned inflatable airsacs with moist linings (lungs), is a basic character for osteichthyan fishes found also in tetrapods. It may also have been, primitively, an adaptation to the marine environment for all jawed fishes (gnathostomes) (Bray 1985). Ureotelic nitrogenous excretion (production of urea to minimize osmotic dehydration) is found primitively in marine vertebrates. Thus two important physiological adaptations to the terrestrial environment, air breathing and the ability to cope with dehydration, were already present in the osteichthyan fishes from which tetrapods evolved.

An alternative and completely opposite scenario then, is that the environmental pressures leading to terrestrialization might have been the drive to escape from freshwater influx (and the inherent physiological problems of maintaining water

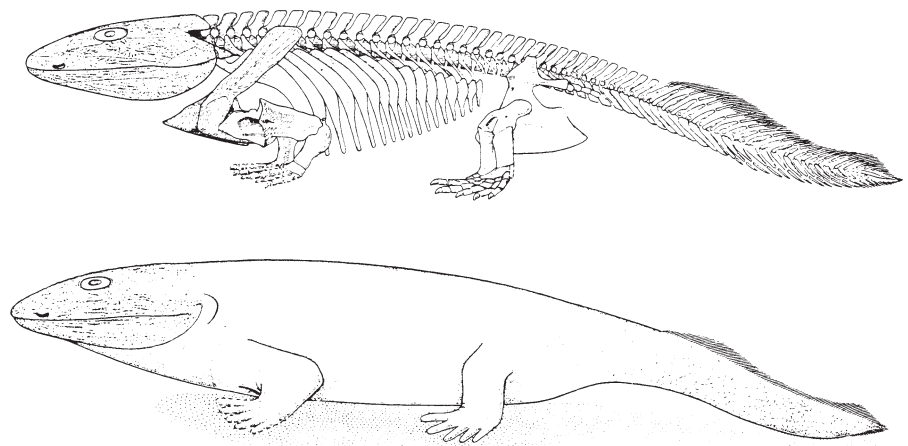


Fig. 1 Composite skeletal reconstruction and flesh restoration of *Ichthyostega*, the most primitive terrestrial tetrapod known. Length about 65 cm; the largest specimens attained a length of about 1 m. (From Jarvik 1980.)

balance in hypo-osmotic conditions) into shallow marine environments during a wet season (Bray 1985).

Major structural and functional adaptations are implicated in the terrestrialization of vertebrates, among them modifications of the systems involving movement and support, sensory perception, and reproduction.

A complex of limb and limb girdle characters, autapomorphic for tetrapods (Rosen *et al.* 1981; Panchen & Smithson 1987) reflect the interwoven functions of supporting body weight and transmitting muscular locomotor forces to the distal regions of the limbs. *Ichthyostega*, which inevitably serves as the primitive tetrapod model, displays the following characters which demonstrate the acquisition of fully functional walking limbs and sprawling gait (Jarvik 1980): pelvic girdle connected to the vertebral column; form of the jointed limbs with a hinge joint at the wrist and knee and a rotary ankle joint; and load bearing digits with articulated phalanges (Fig. 1). The derivation of the tetrapod limb from the fin skeleton of either a lungfish, as argued by Rosen *et al.* (1981), or an osteolepiform, preferred by Panchen & Smithson (1987), presents complex problems of homology which cannot be resolved satisfactorily from the present fossil record.

The ability to receive airborne sound is an important adaptation to life on land. Tetrapod autapomorphies in the middle ear, namely the presence of a fenestra ovalis in the otic capsule (part of the braincase housing the semicircular canals of the inner ear) and a stapes (an unsutured rod-like bone providing a connection between the otic capsule and the body wall) indicate that early land vertebrates were able to receive low frequency airborne or water-borne sound. Structural adaptations to receive and process high frequency sound, with a slender stapes acting as a sound conductor in an impedance-matching middle ear, had developed by Visean times in temnospondyl amphibians (from which modern amphibians derive). An impedance-matching middle ear developed independently in amniotes and is observed first in some Permian forms.

The configuration of the ear region offers clues to the evolutionary transition from amphibians to reptiles (i.e. amniotes). Soft structure autapomorphies are not reflected in the skeleton of early land vertebrates that were related to amniotes; they cannot be categorized satisfactorily on skeletal characters. The relative size of the semicircular canals (organs of hearing and balance in the inner ear), proportion-

ally much larger in small animals, led Carroll (1970) to propose that the transition from an amphibian (non-amniotic) to a reptilian (amniotic) reproductive pattern occurred through a filter of small adult body size. Reproductive patterns of living terrestrial amphibians suggest that there was an intermediate stage in the development of terrestrial reproduction when non-amniote eggs were laid on land. Non-amniote eggs are restricted in size for physiological reasons, imposing in turn a strict limit on adult body size (Carroll 1970). It is also a recognized reproductive strategy for small terrestrial amphibians to produce a small number of relatively large yolky eggs. This permits the offspring to reach an advanced stage before hatching and is a more efficient energy investment in small forms. Whatever the underlying cause, the process of miniaturization involved remodelling of the skull and braincase to accommodate the still relatively large semi-circular canals. Thus the structure of the ear region is fundamentally different in amniotes and anamniotes.

The earliest tetrapod that can be unequivocally characterized as an amniote, *Hylonomus*, is Westphalian (Middle Silesian) in age. It possesses a suite of characters highly adaptive for a fast-running small insectivore, including slender limbs and long, slender manus (hand) and pes (foot). It might therefore be concluded that this condition represents the primitive amniote ecological niche. However, a recent review of early amniote relationships concluded that the early amniote ecological niche was filled by small, slow-moving general invertebrate feeders (Heaton & Reisz 1986). There is a striking correlation between the appearance of slenderly-built cursorial insectivores, exemplified by *Hylonomus*, in the late Carboniferous and the increasingly diverse fauna of running and flying insects.

Early tetrapod biogeography and ecology

In addition to the ichthyostegals, the geographical range of Devonian forms has been extended recently by discoveries of tetrapod footprints from the Frasnian Stage in Australia and from the Upper Devonian in Brazil. A possible tetrapod lower jaw is also known from Australia and a partial skeleton, unequivocally tetrapod and more advanced than the ichthyostegals, has recently been described from the Upper Famennian of European Russia (Milner *et al.* 1986). The Upper Devonian tetrapod

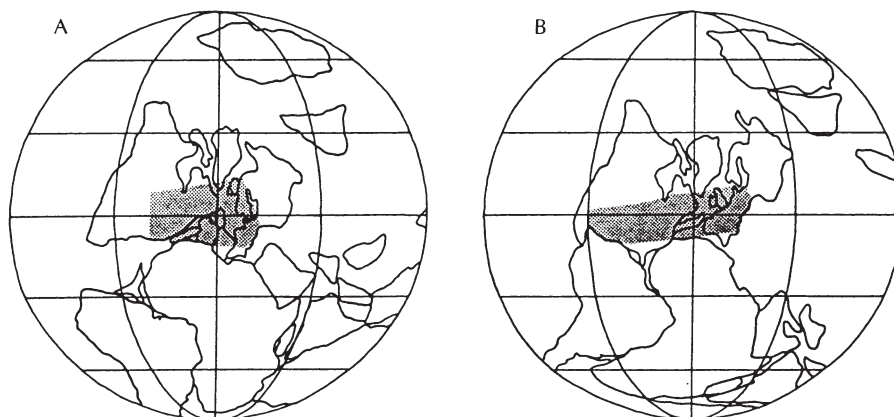


Fig. 2 The world in A, Tournaisian–Namurian and B, Westphalian time, showing the known range of fossil tetrapods (stippled) in relation to contemporaneous continental positions. (After Milner *et al.* 1986.)

record is thus very sparse; it demonstrates that tetrapods were present by the late Devonian in the palaeoequatorial regions of Euramerica and Gondwanaland but information on structural and ecological diversity is lacking.

Our knowledge is likewise restricted geographically and ecologically during the Carboniferous. For discussion of the tetrapod record, the Carboniferous is most usefully divisible into two coherent units (Milner *et al.* 1986). In the Tournaisian/Visean/Namurian (360–315 Ma) most of the dozen or so families recognized are of large specialized aquatic forms, and a few specimens of small terrestrial tetrapods hint at almost unrepresented terrestrial faunas. All the tetrapods known from this period occur in a band across the southern coastal region of Euramerica from Iowa to West Germany (Fig. 2A) and most derive from lake-bed or estuarine deposits, hence the predominance of specialized aquatic forms. A recently discovered Scottish Dinantian terrestrial fauna (Milner *et al.* 1986), albeit very late Visean in age, is revealing a wider structural diversity among terrestrial tetrapods and increases the probability that they were already structurally and ecologically diverse in the late Devonian.

All Westphalian tetrapod faunas known, with the exception of one trackway recorded from the late Carboniferous of Chile, also derive from the southern margin of Euramerica in a slightly wider longitudinal belt from Arizona to Czechoslovakia (Fig. 2B). Some 30 families are recognized, apparently an explosive increase in diversity compared with the pre-Westphalian record. However, this phenomenon is an artifact of the existence of a few highly productive Westphalian localities which represent three major environments and tetrapod associations (Milner *et al.* 1986). These are: (1) an open-water fish-dominated habitat with specialized lake dwell-

ling tetrapods; (2) a swamp pool association, a pond-like environment where small amphibians predominated but with occasional lake and terrestrial erratics; and (3) terrestrial associations found as erratics in swamp pools, deltaic fans or as the major assemblages in burnt hollow upright lycopod stumps. This last preservation, from sites in Nova Scotia, has yielded remains of small animals that had been either entrapped or used the stumps as refuges. These animals show obvious terrestrial adaptations and they include the earliest known reptile, *Hylonomus* (Milner *et al.* 1986).

It is evident from the above brief survey that virtually all that is known of the first quarter of tetrapod history (374–296 Ma) derives from an apparent succession of faunas in a geographically restricted area — the southern equatorial coastal belt of the Euramerican plate. This has been interpreted variously as the centre of origin and diversification of terrestrial vertebrates, and as the result of a concentration of collecting activity in Europe and North America. Likewise it appears, from literal interpretation of the fossil record, that the origin and early radiation of terrestrial vertebrates was a chronological sequence of faunas evolving in response to environmental changes. The record may equally represent local succession of ecological communities along the southern coast of Euramerica. The poverty of the fossil record in the Devonian and Carboniferous severely restricts our perspective on these problems.

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1.9 Flight

1.9.1 Arthropods

R. J. WOOTTON

Introduction

Although mites and small spiders are frequently carried passively by air currents, insects are the only arthropods to have developed the power of active flight. Flight had already evolved by the early Namurian, when insects first appear in the fossil record. Namurian insects are rare, but Westphalian deposits — in particular the spectacular beds of Mazon Creek, Illinois (Westphalian C–D) (Section 3.11.5) — display large, developed faunas of winged insects, diverse enough to indicate that flight may have arisen by the end of the Devonian. A handful of primitively wingless (apterygote) Carboniferous insects are known; but there are no convincing ‘protopterygotes’ to indicate the nature of the transition — leaving ample scope for speculation.

Debate has focused on two areas: the homology, nature, and functions of wing precursors; and the circumstances and means by which flight arose.

The homology and functions of the pro-wings

Two hypotheses, both with their roots in the 19th century, are still in contention:

1 *The paranotal lobe theory* maintains that wings arose by enlargement of the second and third thoracic pairs of a segmental series of fixed, flat dorso-lateral outgrowths, the paranotal lobes. Supporting

evidence is provided by the presence of such lobes on the first thoracic segment and sometimes the abdominal segments of adult Palaeozoic insects in several orders (Fig. 1A), of a few later and extant forms, and of several Carboniferous nymphs in which the wing pads appear as part of a continuous series of lateral lobes on thorax and abdomen (Fig. 1B). This was the orthodox view until the late nineteen-seventies and is still widely supported, sometimes in a modified form (Rasnitsyn 1981; Quartau 1986).

2 *The tracheal gill theory*, revived by Wigglesworth (1976) and developed by Kukalova-Peck (1978, 1983), claims that wings are homologous with the abdominal gills of juvenile mayflies (Ephemeroptera), and that both are ultimately derived from articulated projections of ancient basal leg segments, now incorporated into the sides of the body. Kukalova-Peck has quoted considerable supporting evidence from fossil and extant insects, including Carboniferous and Permian mayfly nymphs with strikingly wing-like gills (Fig. 1C). The theory, though by no means universally accepted, has now to be taken seriously.

There is an important distinction between the two hypotheses. In the paranotal theory the lobes are presumed to have been immovable, and only later to have developed a mobile articulation with the thorax, as flapping flight evolved. In the tracheal gill theory the wing precursors are seen from the first as actively movable appendages whose form, articulation, and musculature altered progressively with their functions. Movable or not, the fore-runners of wings would not have begun to generate useful aerodynamic forces until they had reached a certain size and shape, and it is necessary to find

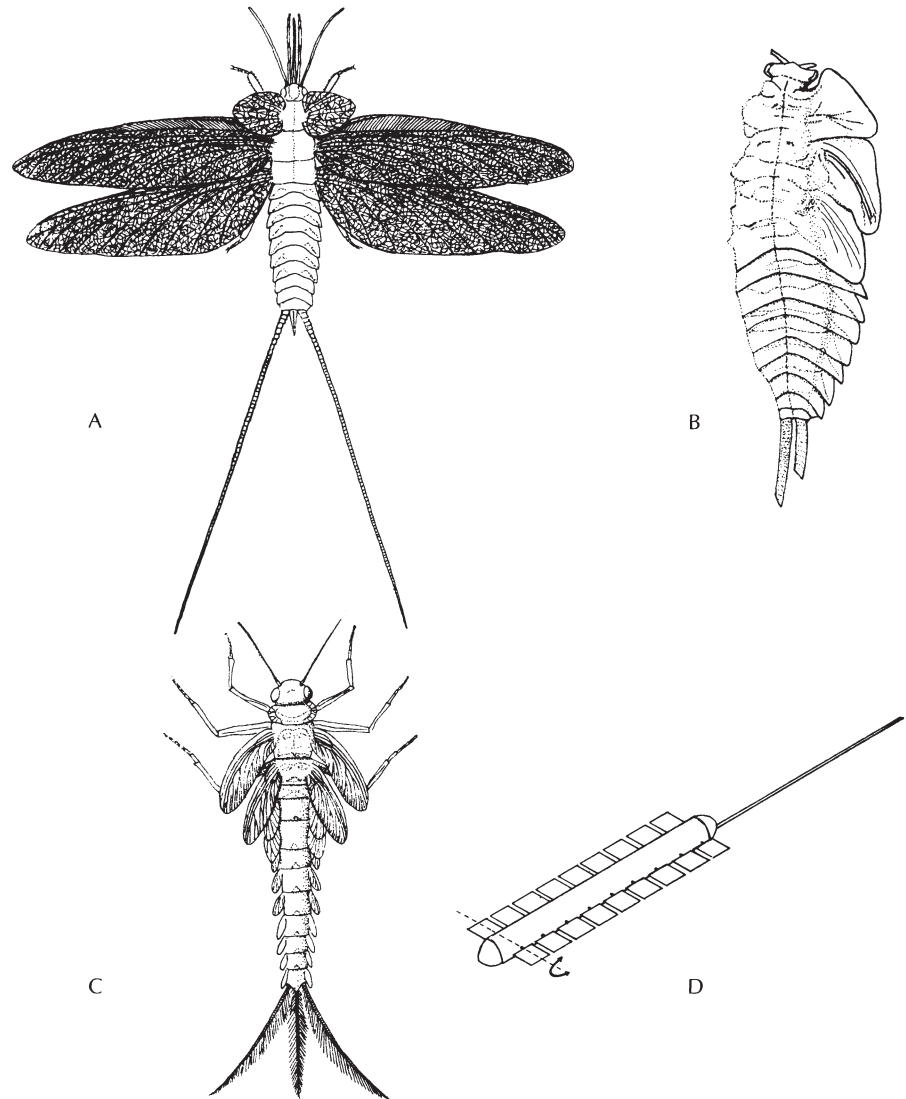


Fig. 1 A, *Stenodictya* (Order Palaeodictyoptera), reconstruction based on several species. Body (minus cerci and mouthparts) c. 60–70 mm long. (After Kukalova 1970.) B, *Rochdalia parkeri* (Order Palaeodictyoptera), nymph. Upper Carboniferous. Length (excluding cerci) 22 mm. (After Wootton 1972.) C, *Kukalova americana* (Order Ephemeroptera), nymph. Lower Permian, Oklahoma. Length 21 mm. (Reconstruction after Hubbard & Kukalova-Peck 1980.) D, Balsa model, as tested by Wootton and Ellington (1991). Lengths 80 mm and 160 mm. The winglets could be twisted around their mounting to alter the angles of attack.

some earlier functions to account for their reaching this stage.

Fixed lateral lobes — most of them certainly not homologous with wings — occur in many modern insects, particularly in juveniles. They act variously: to streamline sedentary aquatic insects pressed to a substrate; and in several kinds of defence — in mimetic camouflage, as armament, or to obscure outlines or reduce shadows. All these have been suggested as possible pro-wing functions. A recent candidate is thermoregulation. Kingsolver and Koehl (1985), experimenting with model insects of three sizes equipped with several sizes of thoracic winglets, found that the latter increased heat uptake — up to a certain size beyond which no further effect could be detected. This size corresponded well with that at which aerodynamic

effects became detectable in wind tunnel experiments. In the authors' view pro-wings developed as thermoregulatory structures, and were so pre-adapted for flight.

The functions proposed for the forerunners of wings in the tracheal gill hypothesis are more straightforward. The basal segments of the legs of modern apterygote insects bear articulated styles, homologous with neither gills nor wings but similar in form to those envisaged as early wing precursors. Their function is sensory. The flattened plate-like gills of many mayfly nymphs serve in gaseous exchange and can usually be flapped, increasing the rate of water flow over the body and providing ventilation, and in some cases propulsion.

Gills are aquatic adaptations, whereas wings function in air. All variants of the tracheal gill theory

assume that the ancestors of winged insects were aquatic or semiaquatic, at least as juveniles, and that the gills persisted in forms which became terrestrial, at least as adults. Rather inconveniently for this theory, extant apterygotes are predominantly terrestrial; but there is no reason why protopterygotes should not have evolved by way of a secondarily aquatic line. The adoption, or readoption of terrestrial habits then needs to be explained. Wigglesworth (1976) and Kukalova-Peck (1983) proposed that aquatic or semiaquatic protopterygotes took to climbing up emergent or waterside vegetation, perhaps to feed on the energy-rich sporangia, and so became available for aerial dispersal.

The development of flight

The many theories which have been put forward on the circumstances of the origin of flight fall into three groups. Variants of each were current when the paranotal lobe theory held exclusive sway, but some recent versions take account of the new factor of pro-wing mobility inherent in the tracheal gill hypothesis:

1 *The running/jumping theory.* Protopterygote insects gained the speed necessary for flight by running or jumping into the air, perhaps to escape from predators, and planed or flapped to a landing.

2 *The floating theory.* Flight evolved in insects small enough to be carried up by winds or thermals. Pro-wing enlargement was favoured by selection for high surface/volume ratio, and thus high drag.

3 *The parachuting/gliding theories.* Arboreal insects falling or jumping from a height used their pro-wings initially for parachuting, then progressively for gliding and powered flight.

In each hypothesis it is assumed that selection for improved aerodynamic efficiency led to the enlargement of the pro-wings on the second and third thoracic segments, and to the reduction and eventual loss of the remainder; and that performance was further enhanced by the development or improvement of the power of flapping, with its associated morphological and physiological adaptations.

One theory can be ruled out. Running and planing over level ground would be pointless, since even if take-off speed were reached the insect would begin to slow down as soon as it left the ground. Choice

between jumping, floating and paragliding is a matter of estimating relative probabilities. The hypotheses are not entirely mutually exclusive — an insect jumping from an eminence into rising air would have features of all three — but their implications are rather different.

The jumping theory requires that a protopterygote with a small pro-wing area could generate enough lift, with or without flapping, to achieve useful, stable, shallow flight, within the speed range which could be reached in a leap.

The floating theory implies that an insect small enough to be carried by air currents would develop the morphological characteristics appropriate to powered flight.

The parachuting/gliding theories require that pro-wings should initially maintain the insect in a stable attitude which would enable it to generate some lift in falling, and so glide or fly to a lower level slowly enough to avoid being damaged in landing.

Several of these criteria have been investigated by Wootton and Ellington (1991), by dropping appropriately scaled cylindrical balsa models with serial winglets which could be rotated to particular angles relative to the body axis (Fig. 1D), so testing the effects of one aspect of pro-wing mobility. They found that models scaled to be dynamically similar to an insect c. 25 mm long parachuted stably and relatively slowly at steep glide angles, if the winglets were rotated backward so as to be fully stalled at angles of attack around 85°, but were incapable of shallow glides. However, larger models corresponding to insects c. 70 mm long — well within the size range of Palaeozoic forms — were capable of fast shallow glides, the speed and angle of which could be adjusted by minor changes in the angle of attack of the winglets. Removal of 'abdominal' winglets destroyed stability in the pitching plane, but this was readily restored by adding slender tail filaments, such as are found in many primitive winged insects (Fig. 1A).

These results appear to favour the parachuting/gliding hypothesis, since shallow glides only proved possible at speeds well in excess of those normally achieved in a jumping take-off; a period of acceleration in free fall is needed. The evidence also indicates that the ability to change the angle of attack of the pro-wings would have been valuable in controlling glide angle and speed, and perhaps in ensuring stalled soft landings. Preliminary unpublished calculations suggest that flapping would have had negligible effect on flight performance in the

early stages of flight evolution, but would have become increasingly effective as the pro-wings enlarged in association with improved gliding.

The evolution of powered flight from passive floating is far harder to envisage. Selection for drifting efficiency might favour the enlargement of body appendages, but with a high-drag morphology which would not adapt them for active flight. Selection would, however, favour small size, which would necessitate uncomfortably high flapping frequencies even when the wings had become fully developed. The advantages of flapping at the pro-wing stage would be infinitesimal.

Conclusion

Recent discoveries notwithstanding, hard information on the origin of insect flight is still rather scarce. On balance, the combined evidence from palaeontology, comparative morphology and experimental biomechanics suggests that flight probably evolved in the Devonian, in medium to large arboreal insects initially bearing serial lateral appendages which may have been capable of being actively twisted, and perhaps flapped. The appendages may at first have served to stabilize and slow the insects' falls, but came to provide lifting surfaces, allowing shallow fast glides. There followed enlargement of the winglets closest to the centre of mass, to a size where flapping became effective in generating thrust and weight-support; and reduction of the remaining winglets, accompanied by enlargement of caudal appendages to prevent loss of stability.

Though in no way proven, a scenario of this kind is both feasible and fairly parsimonious. No evolutionary 'quantum leaps' would be required. Given the initial presence of small articulated lateral appendages, the insects could pass from winglessness to active flight by gradual stages, all of which make functional sense.

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1.9.2 Vertebrates

K. PADIAN

Introduction

Three groups of terrestrial vertebrates have evolved flight independently: pterosaurs (Late Triassic–Late Cretaceous), birds (Late Jurassic–Recent), and bats (Eocene–Recent). By 'flight' is meant flapping flight; parachuting, gliding, and soaring are other, different modes of flight. Parachuting is descent slowed mainly by drag; in gliding, lift predominates and the angle of descent tends not to exceed 45°. Soaring, as opposed to these two passive modes of flight, actively uses the energy of rising thermals and air currents to maintain height, even though the wings are fixed. Soaring habits seem to have evolved only in active flyers, not in passive ones, although aerodynamically there seems to be no reason why passive flyers could not soar; however, their wings are not long and narrow like those of other soarsers.

Three principal factors are important in understanding the origin of flight and its evolutionary history in each flying group:

1 Aerodynamic considerations define the physical requirements for flight and restrict the morphological and ecological possibilities for animals that fly. Aerodynamics of living vertebrates are well enough known to shed considerable light on parameters for fossil forms (Rayner *in* Hecht *et al.* 1985; Rayner 1988). Most important is the generation of sufficient thrust to create a vortex wake that propels the animal forward. Wing design, planform, and muscle physiology are instrumental in quantifying flight capabilities, and can to some extent be modelled in fossil forms by comparison with living ones.

2 Functional considerations are important in understanding the evolution of the flight apparatus and the generation of the flight stroke, the latter being the single property that defines powered flight (Padian 1985). All three groups of flying vertebrates use a vertical or down-and-forward stroke of the forelimbs to generate thrust. Each group, although built on the general tetrapod plan, has modified its basic equipment in different ways (Fig. 1). For example, the wing is functionally divided into three segments, of which the outermost is principally supported by the fourth finger in pterosaurs, the wrist and fused fingers in birds, and the unfused fingers in bats. But despite differences in the equipment, the flight strokes are essentially the same.

3 The evolution of flight is also influenced by phylogenetic factors. Organisms have to use what they inherit in order to solve evolutionary and ecological problems; their past history dictates in large measure what they are capable of doing in future. Therefore, understanding the phylogeny of organisms in detail helps us to understand the ecological milieu from which they evolved. As a result, complex adaptations may be dissected part by part simply by assembling the evolutionary sequence of forms that evolved the adaptation. Of course, this must be done by reference to other, functionally independent character sets (Gauthier & Padian *in* Hecht *et al.* 1985; Padian 1987).

In studying the evolution of flight, then, the aerodynamic factor provides us, in effect, with the laws that bound the possible solutions to the problem. The functional factor shows how the problem is solved. The phylogenetic factor shows much about why a given animal solved the problem in the particular way it did. With these three approaches in mind, the evolutionary histories of flight in pterosaurs, birds, and bats may be considered.

Pterosaurs

These first flying vertebrates were archosaurs very closely related to dinosaurs, and the common ancestor of the two groups seems to have been a small, lightly built, bipedal form of the Middle Triassic. Typically, pterosaurs have been pictured as bat-like lizards with poor terrestrial capability, but a large suite of features suggests that they were instead agile bipeds that moved much more like birds and other dinosaurs (Padian 1985). The wings were narrow and could not have been attached to the legs without spoiling vortex patterns over the wing.

Pterosaurs have been divided historically into two groups: the earlier, paraphyletic 'Rhamphorhynchoidea' and the later, monophyletic Pterodactyloidea (Wellnhofer 1978). The 'rhamphorhynchoids' retained the long tail of their archosaurian ancestors, hyperelongated the metacarpus and (especially) the fourth finger for flight, and stretched a wing of skin behind the forelimb running along the body wall to the tail. The wing membrane was invested with countless stiffening 'fibres', which were intercalated and oriented through the wing like the feather shafts of birds or the fingers of bats (Padian 1985). 'Rhamphorhynchoids' also hyperelongated the two phalanges of the fifth toe; adaptations for grasping or perching have been suggested without close argument, but the elongation was equally likely to have been merely a developmental consequence of elongating the outer digit of the hand.

It is often observed that in the history of any flying animals (including humans), early designs are highly stable aerodynamically. In more advanced forms, on the other hand, the designs become inherently unstable as the neurological control systems become more sophisticated. Pterodactyloid pterosaurs, like post-*Archaeopteryx* birds, lost the tail, a primary mechanism of dynamic stability. Pterodactyloids also shortened the humerus (the first functional segment of the wing), lengthened the metacarpus (much of the second section), and tended to shorten the wingfinger slightly (the third section). Aerodynamic reasons for this are not yet understood, but stability was probably involved. Large size and soaring habits characterized several lineages within Pterodactyloidea, including those of *Pteranodon* and *Quetzalcoatlus* (Late Cretaceous, North America), and these represented most of the latest known forms in the fossil record. No known pterosaurs show particular arboreal specializations, but it must be remembered that the terrestrial fossil record is biased toward aquatic environments and against forest and upland habitats.

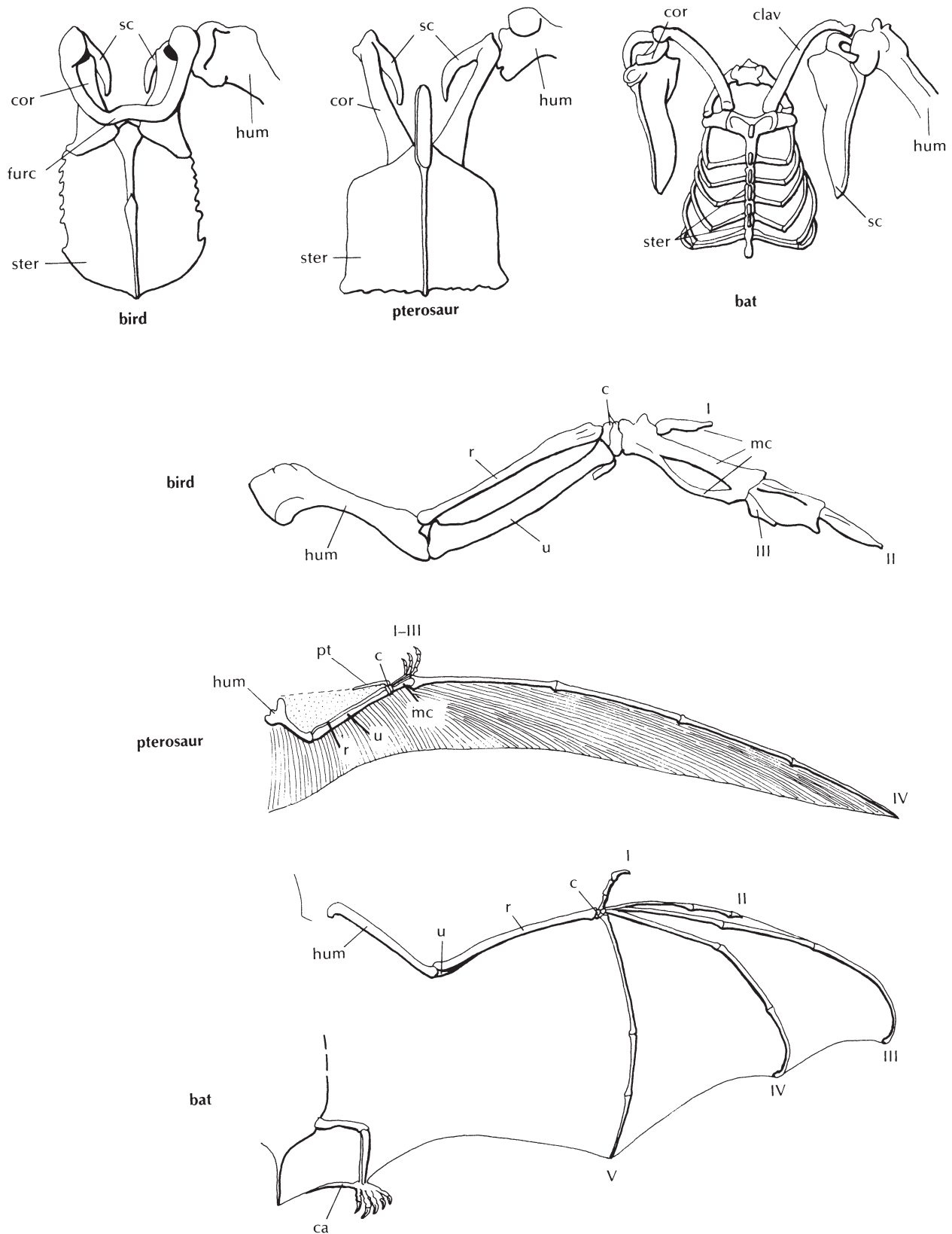


Fig. 1 Diagrammatic comparisons of the thoracic regions and forelimbs of the three groups of vertebrate flyers. Thoracic regions (above) are seen from the front; left forelimbs (below) in ventral view. Structurally, the coracoids of pterosaurs and birds seem to be functionally analogous to the clavicles of bats, as do the furcula of birds, the cristospine of pterosaurs, and the manubrium of bats. Abbreviations: *c*, carpus; *ca*, calcar; *clav*, clavicle; *cor*, coracoid; *furc*, furcula; *hum*, humerus; *mc*, metacarpus; *pt*, pteroid; *r*, radius; *sc*, scapula; *ster*, sternum; *u*, ulna; *I–V*, numbered digits. Not to scale. (From Padian 1985.)

Birds

Archaeopteryx, from the Late Jurassic Solnhofen Limestone of Bavaria (Section 3.11.7) is the first known bird, recognized by its flight feathers. In the nineteen-seventies J.H. Ostrom established its ancestry from among small carnivorous (coelurosaurian) dinosaurs, an idea first advanced a century ago by T.H. Huxley. Gauthier (1986) used over 200 nested synapomorphies to document the sequence of acquisition of characters that not only show how the major archosaurian groups are related to each other, but also how those characters relevant to flight evolved. Some features considered typically 'avian', such as the furcula (fused clavicles) and calcified sterna, appeared in carnivorous dinosaurs at a more general level than Aves. Other features, such as the perching foot, the reduced tail and teeth, and the fused carpometacarpus, appeared well after *Archaeopteryx*. Little is known of Cretaceous birds apart from a few open-water forms. The loon-like *Hesperornis* and the tern-like *Ichthyornis* (Late Cretaceous, Western Interior, North America) are not members of the orders of living birds; most of these have their first records in the Eocene or later. The refinement of flight adaptations in avian evolution is poorly known and must be reconstructed mainly with reference to living forms. Recent discoveries of Early Cretaceous birds from Spain show that by that time the dorsal vertebrae were reducing in number, the tail had been shortened to a pygostyle, the coracoids were strut-like and braced to the sternum, and the furcula (wishbone) had a prominent hypocleidium. A perching foot with trenchant recurved claws appears to have been well developed.

Archaeopteryx is perhaps the world's most famous fossil; it is the basis for a great diversity of approaches and viewpoints on the origin of birds and the early evolution of their flight (Hecht *et al.* 1985). The traditionally favoured view is that birds evolved in trees and passed through a fully gliding stage on the way to active flight (Bock *in* Hecht *et al.* 1985). It is easiest to evolve flight in this way (Rayner; Norberg; *in* Hecht *et al.* 1985), but this does not exclude other possibilities. The view that flight evolved from a small terrestrial animal that ran and leaped into the air, gaining flight gradually by the elaboration of 'proto-wings,' has recently been advocated (Ostrom; Gauthier & Padian; Caple *et al.*; *in* Hecht *et al.* 1985). The advantage of this view is that it is rooted in the evolution and ecology of avian ancestors, whereas the 'arboreal' theory is not; but

the disadvantage is the relative difficulty of evolving flight 'from the ground up'. Terrestrial speeds needed for take-off are uncomfortably high, judging from small living bipeds (Rayner *in* Hecht *et al.* 1985), whereas speed is easily gained by dropping out of a tree. It is difficult to see what evidence could resolve this question; most likely, some compromise between the two extremes will be most fruitful.

Bats

Little is known about the early evolution of bats; like pterosaurs, when they first appear in the fossil record (the Eocene *Icaronycteris*: Jepsen 1970) they are fully formed flyers, and the evolution of their flight can only be reconstructed from the skeletons of the earliest forms. Like gliding mammals, and unlike birds and pterosaurs, bats incorporate the hindlimbs in the wing membrane, which explains why their terrestrial ability is so poor: their fore- and hind limb locomotory systems are not independent, and stress has clearly been placed on the forelimb system. In all respects, bats seem to have followed the model for evolution from gliding forms (Rayner; Norberg; *in* Hecht *et al.* 1985). Based on analyses of the general distribution of their characters, bats appear to have evolved from a group of generally nocturnal, arboreal, insectivorous-omnivorous placentals. Some facility for echolocation and hanging upside down would seem to have appeared at an early stage in bat evolution. A nocturnal, arboreal form that could glide and hang upside down (thus freeing its forelimbs from most locomotory functions) would be a reasonable ancestor (Padian 1987).

For this reason, recent studies of the phylogenetic position of Chiroptera have generated considerable excitement and controversy. Although several workers have claimed that the Chiroptera are diphyletic (separate origins of megabats and microbats), cladistic studies by Novacek and his colleagues (e.g. Wible & Novacek 1988) have provided a consilience of skeletal and molecular evidence that appears to support chiropteran monophyly. Moreover, a suite of cranial and postcranial characters suggests that the closest sister-taxon to Chiroptera is Dermoptera, the so-called 'flying lemurs' now restricted to Southeast Asia. If Novacek and his co-workers are correct, some habits of the living dermopteran *Cynocephalus*, coincident with those discussed in the preceding paragraph, may shed light on the ecology of the common ancestor of the two groups.

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1.10 Angiosperms

M. E. COLLINSON

Introduction

The angiosperms or flowering plants are the most diverse living plant group with over 250 000 species. They dominate world vegetation, with the exception of moss-lichen tundra and high latitude northern hemisphere coniferous forest. They exhibit a wide range of life form and strategy, ranging from tiny free-floating aquatic duckweeds through epiphytes and lianas to tall forest trees. This diversity and dominance has, however, been attained relatively recently in terms of Earth history, apparently within the last 120 million years. The origin and subsequent diversification of the flowering plants has influenced community structure and the evolution of all other biotas.

Early fossil evidence

Several synapomorphies of the angiosperms (Crane 1985; Doyle & Donoghue *in* Friis *et al.* 1987) are features of reproductive biology not amenable to recognition in the fossil record. Characteristic pollen, wood, and leaves (Fig. 1) may, however, be easily detected. Like other plants, angiosperms are largely represented in the fossil record by organs (like pollen, leaves, seeds) which are dispersed or shed during life. The smallest and most widely

dispersed are most likely to be preserved. It is to be expected, then, that the earliest recognizable angiosperm fossils are pollen grains with the tectate/columellate wall (Fig. 1G). These monosulcate pollen, named *Clavatipollenites* (Fig. 2B), occur in the Early Cretaceous (Barremian) of England, West Africa, Argentina, and eastern North America (Muller; Walker & Walker; *in* Dilcher & Crepet 1985). *Clavatipollenites* pollen are very similar to grains produced by modern members of the magnoliid dicotyledon family Chloranthaceae, e.g. *Ascarina* (Walker & Walker *in* Dilcher & Crepet 1985). As pollen of other magnoliid plants lack the diagnostic wall structure and plant organs may evolve at different rates, there is no reason to assume that *Clavatipollenites* pollen represent either the earliest or the most primitive flowering plants.

Cladistic analyses

Recent cladistic analyses of fossil and modern seed-plant groups (Crane 1985; Doyle & Donoghue 1986; Doyle & Donoghue *in* Friis *et al.* 1987) imply a pre-Cretaceous origin of angiosperms, possibly as early as the Triassic. In these analyses an anthophyte clade can be defined (Fig. 3B), for which the sister group may be one of several Mesozoic seed plants

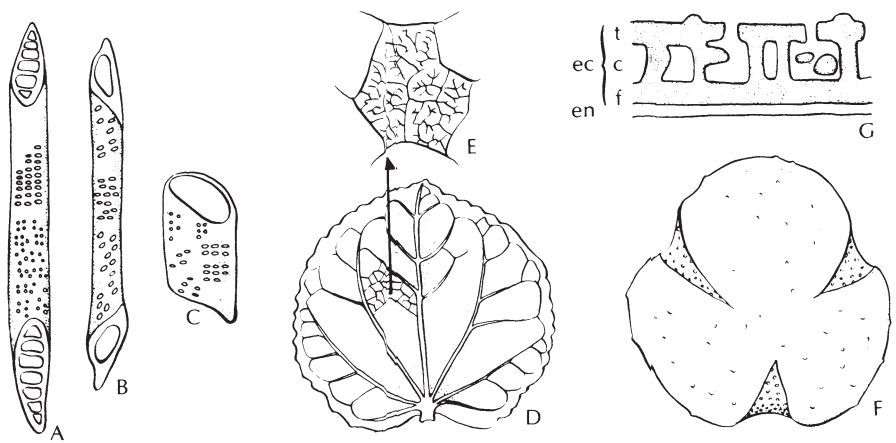


Fig. 1 Characteristic features of angiosperms detectable in the fossil record. A–C, vessel elements (lengths vary from about 200–1000 μm). D, E, dicotyledon leaf (length about 5 cm) with venation detail. F, tricolpate pollen grain (diameter about 30 μm). G, section of pollen wall (thickness about 1–3 μm) showing endexine (en) and ectexine (ec) divisible into footlayer (f), columnar layer (c), and tectum (t). (From Friis *et al.* 1987.)

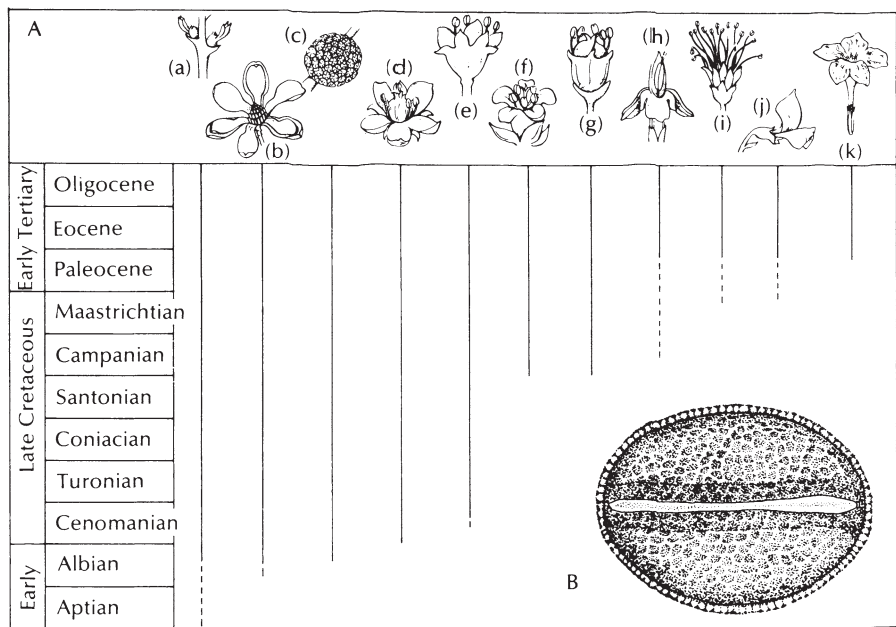


Fig. 2 A, Time of appearance of major floral types. Solid lines based on flower fossils, dashed lines on indirect evidence — mostly pollen. (From Friis & Crepet in Friis *et al.* 1987.) B, *Clavatipollenites*, monosulcate pollen (length 20 μm). (From Stewart 1983.)

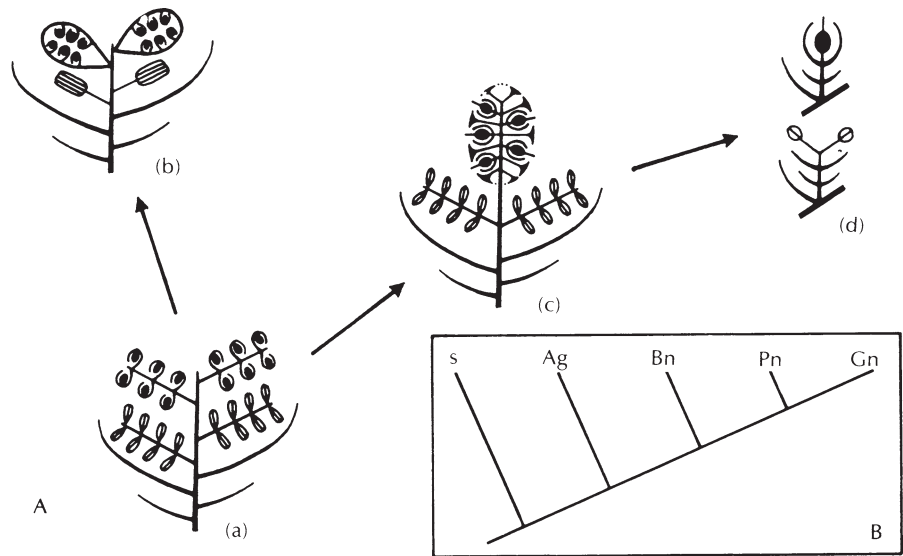
(*Caytonia*, glossopterids, corystosperms) that exhibit varying degrees of ovule protection, net leaf venation, fused pollen sacs, etc. (all later elaborated upon in members of the anthophyte clade). Flower-like organization of reproductive structures (Fig. 3A) typifies members of the clade, hence the proposed term anthophyte. This feature can no longer be seen as a uniquely angiosperm attribute. Fig. 3A represents the inferred character transformations in the reproductive structures of members of this clade. In angiosperms the microsporophyll (= stamen) is reduced but the megasporophyll (= carpel) remains complex. In Bennettitales the megasporophyll is reduced to a uniovulate unit but the microsporophyll remains complex. In Gnetales both micro- and megasporophyll are reduced.

According to these cladistic analyses the Gnetales are the closest living relatives of the angiosperms and these two groups share a common ancestry (along with Bennettitales and *Pentoxylon*) amongst Mesozoic seed plants. Careful study of these, especially Triassic representatives, and a clearer understanding of the fossil record of Gnetales, will clarify the phylogenetic history of the anthophyte clade.

Early radiation

Following the widespread appearance of *Clavatipollenites* pollen during the Barremian, other angiosperm pollen types occur in later Barremian and Aptian strata. These include probable

Fig. 3 A, Major character transformations in reproductive structures inferred from Fig. 3B and present in: (a) hypothetical ancestor; (b) angiosperm; (c) Bennettitales; (d) Gnetales. (From Friis *et al.* 1987.) B, The angiosperm clade: Ag = angiosperms, Bn = Bennettitales, Pn = *Pentoxylon*, Gn = Gnetales, s = sister group involving one or more of corystosperms, glossopterids or *Caytonia* according to author. (After Doyle & Donoghue in Friis *et al.* 1987.)



Chloranthaceae; forms similar to those of modern monocotyledons; and forms referable to the Winteraceae, another family of the magnoliid dicots. In the Aptian, tricolpate pollen (Fig. 1F) first indicate the presence of non-magnoliid ('higher') dicotyledons (Hamamelidae or Ranunculidae). In the Albian, pollen with endoapertures (tricolporate) signal the occurrence of probable Dilleniidae or Rosidae. Angiosperm pollen accounted for only up to 1% of palynofloras in the Barremian. By the late Albian they accounted for up to 70% in some low palaeolatitude areas, with lower proportions in middle palaeolatitudes. In the Turonian, angiosperms dominated palynofloras from many areas of the world (Muller; Walker & Walker; both in Dilcher & Crepet 1985).

Details of the early phase of angiosperm leaf diversification are largely based on material from eastern North America. Angiosperm leaves may be characterized by reticulate venation, in a hierarchical system often with free ending veinlets (Fig. 1D, E). Most Aptian angiosperm leaves are small, entire-margined and simple with pinnate venation, sometimes with a poorly developed hierarchy. Middle to Late Albian assemblages show an increase in diversity of leaf form, including pinnatifid and palmately lobed forms and cordate leaves. Forms similar to those of modern magnoliid (Chloranthaceae), hamamelid (Platanaceae), and rosid dicotyledons are recorded from the Albian (Upchurch in Dilcher & Crepet 1985; Upchurch & Wolfe in Friis *et al.* 1987).

A statistical assessment of the proportion of different plant groups in leaf floras (see Fig. 5) clearly

demonstrates the rapidity with which angiosperms became dominant elements, replacing cycadophytes and pteridophytes during the Early and earliest Late Cretaceous. The replacement generally took place later at higher palaeolatitudes. Angiosperm floral provinciality was well established by the Late Cretaceous.

Angiosperm herbs and small woody plants first entered early successional habitats such as stream sides, coastal plains, and other disturbed areas in a similar manner to the weeds of today (Retallack & Dilcher 1986; Crane in Friis *et al.* 1987). During the Late Albian they diversified into full aquatics, forest understory shrubs and riparian trees. Early in the Late Cretaceous angiosperms (probable shrubs and small trees) remained effective colonizers and expanded first into environments previously dominated by cycadophytes (including Bennettitales) and ferns.

The rise of angiosperms may have influenced certain dinosaur feeding strategies, reflected in the Late Cretaceous radiation of ornithischian herbivores (Coe *et al.* in Friis *et al.* 1987). Although angiosperms clearly dominated vegetation in many areas by the early Late Cretaceous, several significant advances took places later (see below).

Early floral biology

Recently, data on fossil flowers and, more rarely, on partially reconstructed whole plants has added to that from dispersed pollen and leaves (Friis & Crepet; Crepet & Friis; in Friis *et al.* 1987). Amongst the earliest known fossil flowers from the early

Late Albian of eastern North America are forms (Fig. 2A(a)) which are very similar to modern members of the Chloranthaceae, e.g. *Chloranthus*. The floral morphology suggests insect pollination, as does their similarity to modern insect pollinated *Chloranthus*. In contrast, the abundance of the early Cretaceous pollen *Clavatipollenites* suggests wind pollination, as in modern *Ascarina*. In the same fossil flora unisexual platanoid flowers also occur (Fig. 2A(c)).

These small, platanoid and chloranthoid flowers are usually considered derived by comparison with large showy bisexual flowers which also occur in the Albian (Fig. 2A(b)). The best known example is from the Albian/Cenomanian boundary of the Western Interior of North America (Fig. 4; Dilcher & Crane in Dilcher & Crepet 1985). This plant has been reconstructed using organic connection, attachment scars, and association evidence, from a suite of fossil organs occurring in one thin sedimentary unit. Its multifollicular fruit (named *Archaeanthus*) represents the primitive condition as predicted from, but not represented in, modern flowering plants. Other features of the flower (numerous free, spirally arranged parts) also conform to the traditional, hypothetical angiosperm archetype. However, certain aspects of the whole plant, e.g. the lobed leaf, are more advanced. The '*Archaeanthus* plant' shares most features with members of the Magnoliales, amongst living plants, but it cannot be assigned to a modern family. Strata of the same age have also yielded a more derived flower form (Fig. 2A(d)) with parts in whorls of five. Clearly all of these floral forms (Fig. 2A(a–d)) were represented very early in the evolution of flowering plants. They confirm the pattern of rapid diversification as inferred from pollen and leaves, and the early differentiation of 'higher' dicotyledons (Crane 1989). They also suggest the early existence of wind pollination and a range of insect pollination strategies.

Pollination biology and dispersal strategy

Insect pollination may characterize all members of the anthophyte clade and was therefore not a controlling factor in angiosperm origins. The enclosing carpel (megasporophyll enclosing ovules) and the receptive stigmatic surface on the carpel are, however, unique to the angiosperms. Together these permit control of pollen germination, hence fertilization, and allow for the exploitation of incompatibility mechanisms. Such mechanisms permit or

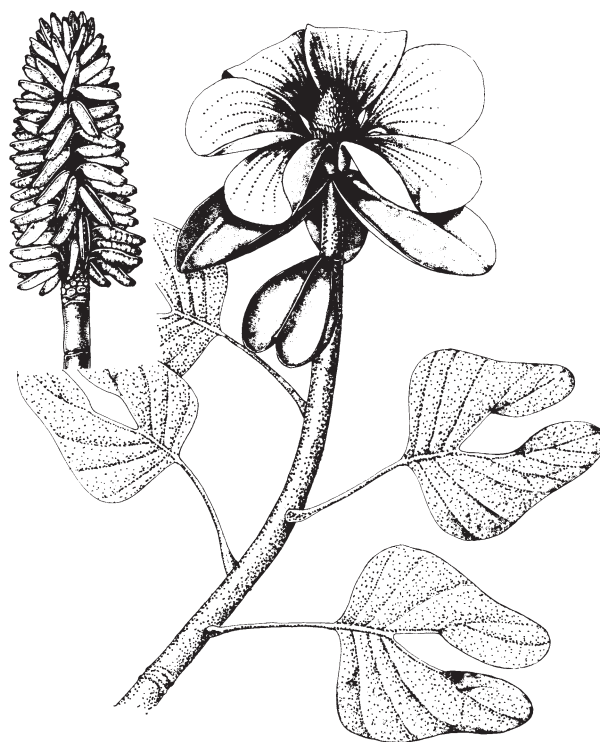
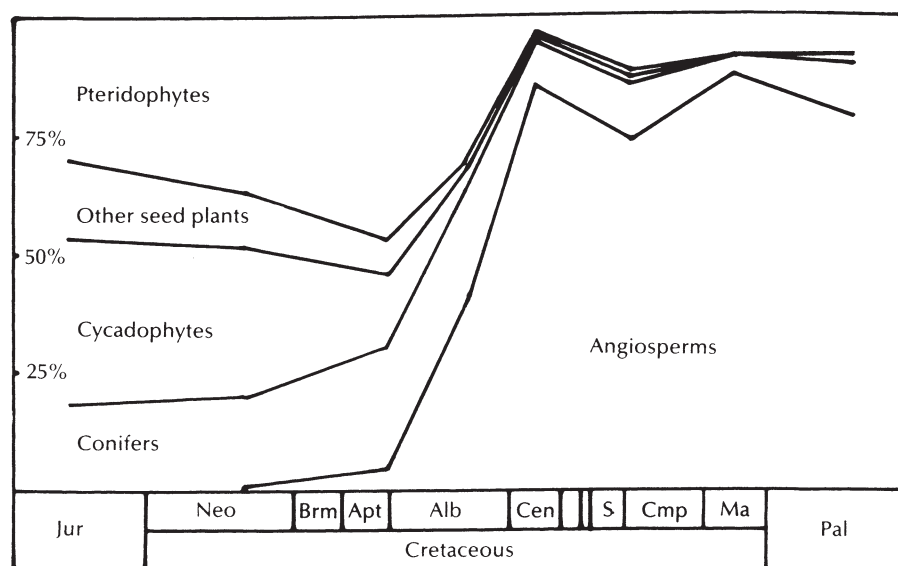


Fig. 4 Reconstruction of one of the best known Cretaceous angiosperms, '*Archaeanthus*' from the Dakota Formation, Albian/Cenomanian boundary, Kansas, U.S.A. External flower diameter about 130 mm. (From Dilcher & Crane in Dilcher & Crepet 1985.)

enforce cross fertilization with resultant enhanced variation. The carpel also provided for new means of seed dispersal through a range of fruit structures. Combined, these features increase speciation rates and reduce extinction rates, resulting in increased diversity and potential dominance in vegetation. Such features can be best exploited through controlled (biotic) transfer of pollen to the stigma rather than the more haphazard wind pollination.

The late Cretaceous and Early Tertiary evolution of floral form (Fig. 2A) reveals the continued elaboration associated with new pollination vectors. The earliest insect pollinated angiosperms probably possessed generalist flowers visited by a range of insects. Specialization for beetle pollination is indicated by the large robust magnolialean flowers with prolific pollen production (Fig. 2A(b)). Early Late Cretaceous flowers with reduction and fusion of whorled parts and nectar glands in discs (Fig. 2A(d–f)), along with inferior flowers with stout styles (stigmatic stalks) (Fig. 2A(g)), suggest increasing specialization for more specific insect pollinators, including those feeding on nectar as well as pollen. In the latest Cretaceous and Early

Fig. 5 Percentage contribution of major plant groups to ancient leaf floras from Jurassic to Palaeocene. (From Crane *in* Friis *et al.* 1987.)



Tertiary further elaborations such as zygomorphy (bilateral not radial floral symmetry, Fig. 2A(h, j)), brush flowers (Fig. 2A(i)), and long corolla tubes (Fig. 2A(k)) were developed. These are associated with advanced pollinators like bees and butterflies. Some of the more specialized 'faithful' plant-pollinator relationships were established by the Eocene (Crepet & Friis *in* Friis *et al.* 1987).

Fruiting structures also diversified to include fleshy fruits, along with a range of dry nuts and winged fruits (Tiffney *in* Dilcher & Crepet 1985; Friis & Crepet *in* Friis *et al.* 1987). The fruits not only indicate a range of dispersal types but also a range of establishment strategies. Large seeds, able to establish in shaded, canopy covered forest, became more widespread in contrast to the smaller seeds of the earliest angiosperms. This is consistent with an early Tertiary origination of angiosperm-dominated forests with angiosperms as the tall canopy trees, inferred from the fossil record of leaves and wood (Crane; Upchurch & Wolfe; *both in* Friis *et al.* 1987).

Later radiation

The fossil records of pollen, leaves, fruits, seeds, flowers, and wood all point to a major radiation and modernization of flowering plants in the latest Cretaceous and Early Tertiary (Fig. 5). This may in part have been in response to the Cretaceous/Tertiary event, followed by the diversification of mammals replacing dinosaurs as the main large vertebrates on land (Section 2.13.7). Extinction of the dinosaurs, whether gradual or sudden, resulted in the removal of large herbivores which were not

replaced by an equivalent diversity of large herbivorous mammals until the end of the Eocene (Coe *et al.*; Collinson & Hooker; Wing & Tiffney; *in* Friis *et al.* 1987). The later Tertiary saw a further radiation of angiosperms, particularly of the herbaceous groups which represent much of their modern diversity. Grasslands, for example, probably originated in the latest Oligocene or Miocene, perhaps in response to grazing mammals (Section 1.11).

Plant communities reconstructed from Early Tertiary floras are often said to be similar to those of the present day, although in reality none was identical in composition. Instead they combined elements whose nearest living relatives are widely separated ecologically and geographically (Collinson & Scott 1987; Crane *in* Friis *et al.* 1987). Some wetland herbaceous and wooded communities have a good fossil record which may eventually permit reconstruction of their evolution. In other cases, e.g. grasslands and montane forests, the record is far less promising.

Future studies should emphasize the sedimentological and taphonomic context of angiosperm fossils. This, together with more critical comparative studies of fossils and their living relatives, will lead to a fuller understanding of angiosperm evolution.

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1.11 Grasslands and Grazers

J. R. THOMASSON & M. R. VOORHIES

Grasslands

Modern grasslands cover more than 30% of the Earth's land surface and contain more than 10 000 species of grasses that provide more than half the calories consumed by animals (including humans) every day. Yet, in spite of their obvious importance, the origin and evolution of grasslands has remained relatively obscure until recent decades when evidence from fossil grasses, vertebrates, and soils (palaeosols) has increased significantly.

A review by Thomasson (1987) of the history of palaeoagrostology indicates that undoubted fossil grasses are more widespread in the fossil record than previously thought, having been reported from most continents and many stratigraphic levels dating from the Oligocene; reports of probable fossil grasses may extend the age of the oldest grasses to the Eocene. The macromorphological remains of undoubted fossil grasses include anthoecia (husks) and caryopses, leaves, stems, roots, and rhizomes; many show external and internal micromorphological details (Fig. 1) that provide extensive information about phylogenetic relationships in several groups of grasses, the physiological pathways of photosynthesis in certain grasses, and diet in some herbivores. Macrofossils also ultimately constitute the most direct evidence for understanding the origin and evolution of grasslands. Microfossils, in the form of pollen and silica bodies (phytoliths), generally are less reliable for documenting the origin and spread of grasses and grasslands.

The most complete and remarkable record of fossil grasses comes from Late Oligocene–Miocene strata in central North America (Thomasson 1987). By the Late Miocene, all subfamilies of the Gramineae are present in these deposits (along with abundant remains of grazers), clearly indicating the widespread presence of grasslands in that region since at least the Middle Miocene.

The spread of grasslands in central North America during the Tertiary is evidenced by a dramatic increase in both numbers and varieties of fossil grasses (Thomasson 1987). From a comparatively limited Late Oligocene record of one genus (*Berriochloa*, including *Stipidium*) with only two or three species, a rich Late Miocene record comprises at least six genera (*Archaeoleersia*, *Berriochloa*, *Graminophyllum*, *Nassella*, *Paleoeriacoma*, and *Panicum*) with as many as 20–30 different species. Although living descendants of these Late Miocene grasses (e.g. *Nassella* and *Piptochaetium*) are especially common in open grasslands of Central and South America, some are found throughout the world (e.g. *Panicum* and *Stipa*). Tertiary grasslands undoubtedly disappeared under the harsh climate of the Pleistocene and were replaced by boreal forests and taiga; consequently modern grasslands are a post-Pleistocene development in central North America.

Fossil evidence for grasslands in other parts of the world is limited. Palmer (1976) provided conclusive evidence from grass cuticles for the presence

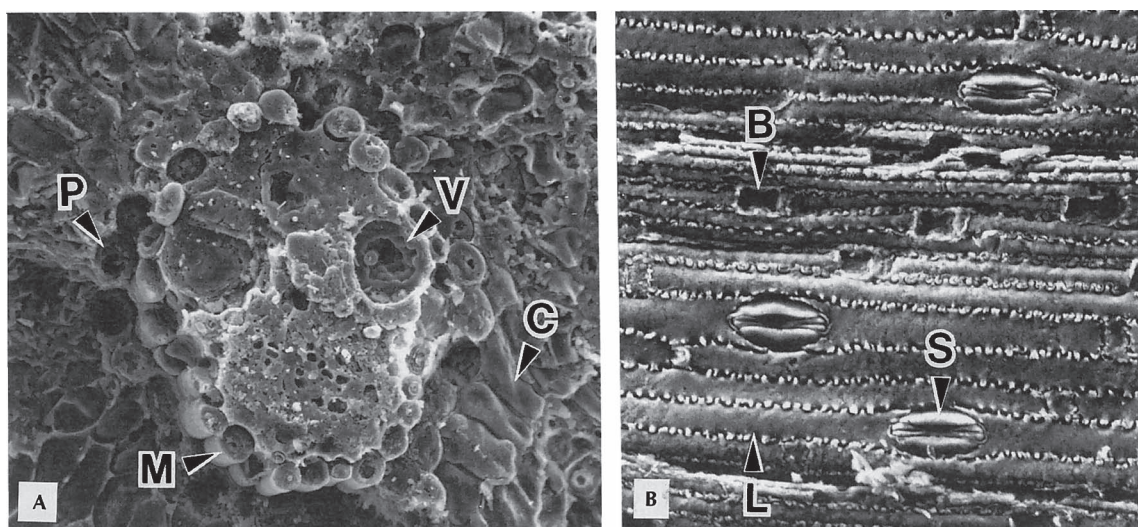


Fig. 1 A, Cross-section of vascular bundle in a grass leaf from Minium Quarry, Late Miocene, Northwest Kansas, $\times 500$. Note the double bundle sheaths. M = mestome, P = outer parenchyma, V = metaxylem vessel elements, and C = slightly radiate chlorenchyma. B, Surface of a grass leaf from locality KO45 in the Late Miocene Lukeino Formation, Kenya, $\times 620$. L = long cells with sinuous walls, S = stomata, and B = silica body cavities. (Photograph A by J. R. Thomasson, B by B. Jacobs.)

of open grasslands during the late Pleistocene in Africa; and B. Jacobs and G. J. Retallack independently (personal communication) have recently discovered fossil grasses in Miocene strata in Kenya that show great potential for elucidating the role of grasses during the Late Tertiary in Africa (Fig. 1B). Although well preserved grasses are known from Europe, they have not been studied sufficiently to suggest a specific habitat (e.g. grassland, woodland, etc.).

Next to fossil grasses themselves, the strongest indirect evidence for the origin and evolution of grasslands comes from studies of the dentition and skeletal structure of fossil vertebrates. Some studies of the vertebrate evidence suggest that grasslands first appeared in South America during the Eocene or Oligocene, in Africa during the Oligocene, in North America during the Late Eocene to Early Oligocene, in Central Asia, China, and Western Asia during the Miocene, and in Australia during the Pliocene (Webb 1977; Wright 1986). Other studies (see below) of large, mobile herbivores such as horses suggest that true grasslands (i.e. savannas, as opposed to woodlands with patches of grass) did not appear until the Middle Miocene.

Finally, palaeosols (fossil soils) provide clues to the emergence of grasslands. Fossil grassland soils can be recognized by the presence of calcic horizons, phytoliths (silica bodies), and grass-like root traces (the biological nature of the latter has only occasionally been documented by cellular details).

Palaeosols provide evidence for many features of ancient environments, including the nature of the plant community (i.e. grassland vs. forest) (Wright 1986). Contrary to most vertebrate evidence, palaeosols suggest that grasslands of a savanna or pampas type may have appeared during the Oligocene in North and South America; that small areas of relatively treeless prairie may have emerged in central North America (South Dakota) by the Late Oligocene; and that grasslands may have appeared in Northern Pakistan and India, and the Rift Valley in Kenya and Tanzania during the Miocene.

Grazers

One of the most striking features of the later Cenozoic (Neogene) terrestrial fossil record on all continents is the appearance of hooved mammals with limbs adapted for high speed running and dentitions adapted for dealing with a diet high in cellulose and/or grit. In the modern world these adaptations occur in such herbivorous animals as horses, bison, and certain antelopes and kangaroos that inhabit open grasslands and subsist exclusively or primarily on a diet of grasses. These 'grazers' contrast with the 'browsers' (e.g. moose, tapir) that consume primarily the leaves of dicotyledonous plants. Modern ecological studies have shown that many herbivores both graze and browse and are thus 'mixed feeders', but the end members are

none the less sufficiently distinct to be useful categories in discussing the evolution of the ungulates, or hooved mammals.

Structural features of the limbs and dentitions that distinguish modern grazers from browsers have been used to separate fossil ungulates into feeding categories, and to document the fact that the grazing habit has arisen independently in many families, primarily during and since the Miocene (a time of world-wide climatic deterioration; Janis 1984). Most published studies have identified as grazers those ungulates with hypsodont teeth (high crowned, where the height of the enamel-covered crown exceeds its length or width). Complex infoldings of the tooth crown and the presence of reinforcing cement on the occlusal surface are additional features characterizing the hypsodont teeth of nearly all living grazers. The postcranial skeletons of fossil ungulates with hypsodont teeth, where known, usually exhibit elongate limbs, especially in the distal segments (below the wrists and ankles). The correlation between grazing habit and hypsodont teeth and long limbs is good, but not perfect; an exception is the hippo, which does not have exceptionally high-crowned teeth and certainly lacks long limbs, but is clearly a grazer in the strictest sense, consuming only grass. (Would-be palaeo-ecologists can perhaps take some small comfort from the fact that the hippo feeds only on tender new growth — in contrast to the zebra, a more orthodox grazer, which consumes the older, tougher tops of plants).

With these qualifications in mind the most frequently cited example of a progressive adaptation to grazing — the evolution of the horse — may be examined. The accepted dogma among vertebrate palaeontologists has been that extensive grasslands appeared in the Miocene simultaneously with the first horses having high-crowned teeth and reduced lateral digits ('side toes') on the feet. Since it was first stated in the nineteenth century by R. Kowalevsky, the hypothesis of a coevolutionary relationship between the spread of siliceous grasses and the diversification of the horse family has received support from an increasingly well documented fossil record of the Equidae, especially in North America.

In the Eocene and Oligocene all horses had relatively short, strongly tridactyl feet and very low-crowned teeth, although a trend toward increased lophodonty ('ridginess') of the tooth crowns can be observed in the transition from Early Eocene *Hyracotherium* through Late Oligocene *Miohippus*.

Recent study of microwear facets on the cheek teeth show that these early horses ate relatively soft, low-fibre vegetation that required crushing and a limited amount of slicing, but little or no grinding (Rensberger *et al.* 1984). This interpretation is consistent with the palaeobotanical evidence for extensive forests and woodlands in western North America in the Early Tertiary.

The first hypsodont equids are included within *Merychippus* (*sensu lato*) from the Middle Miocene, some 17–18 Ma. Their habitat should probably be characterized as savanna woodland rather than open grassland, judging by the palaeobotanical evidence and by the fact that most contemporary ungulates (oreodonts, camels, protoceratids, dromomerycids, tapirs, rhinos, chalicotheres) had low-crowned dentitions. By 12 Ma, however, the *Merychippus* stock had diversified to such an extent that fossil beds in the central Great Plains frequently contain as many as five additional genera of 'grazing' horses [*Protohippus*, *Pliohippus*, *Calippus* (Fig. 2), *Pseudhipparion*, *Neohipparion*] as well as three 'browsing' genera (*Anchitherium*, *Hypohippus*, *Megahippus*), which are essentially much enlarged but otherwise little modified derivatives of the Oligocene *Miohippus*. *Parahippus*, morphologically intermediate between the 'browsing' and 'grazing' groups, is also found in the same death assemblages, making the Late Middle Miocene the time of greatest generic diversity within the Family Equidae. Stratigraphically higher deposits in the same area exhibit sedimentological and palaeobotanical evidence for a drier climate, fewer trees and more extensive grassland, facts that accord well with the extinction of the last genus of browsing horse 9 Ma, when eight well demarcated hypsodont genera were still thriving.

It is perhaps during this interval that the closest analogies can be drawn between North American savanna ecosystems and those of modern Africa (Webb 1983). Later Miocene deposits (5–8 Ma) record increasing aridity and further restriction of woodlands in the Great Plains. Selective extinctions of browsers occurred (all North American rhinos, dromomerycids, protoceratids, and gelocids) and hypsodont taxa also declined in diversity; all but two generic lineages of horses became extinct. By the Early Pliocene, surviving equids included only *Equus* (which remained abundant through the Pleistocene in North America and into the Recent of the Old World as zebras, asses, and horses) and *Nannippus* (a diminutive, extremely hypsodont form that probably still retained lateral digits) which became extinct at the end of the Pliocene.

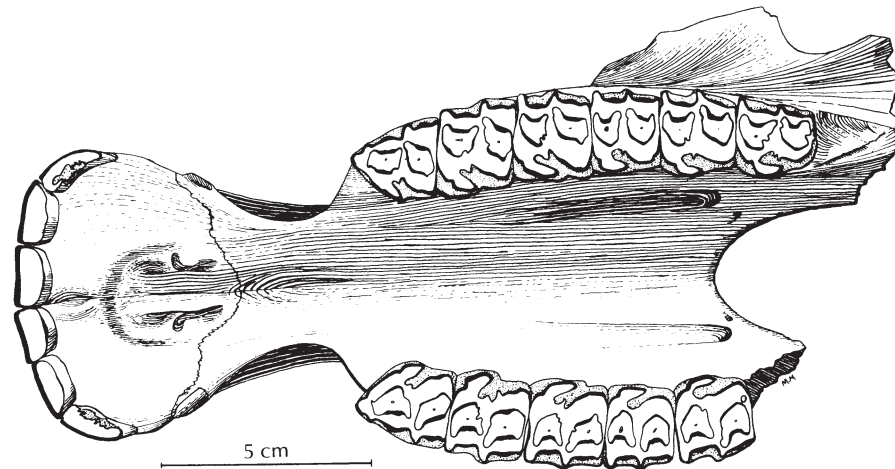


Fig. 2 Skull of extinct North American horse, *Calippus*, in palatal view showing laterally expanded muzzle and linear arrangement of incisors, presumably an adaptation for close cropping of siliceous grasses at ground level. Cheek teeth are prismatic, hypsodont, and heavily invested with cement in this genus, further indications of a grazing habit. *Calippus* was the first equid to evolve cheekteeth with a hypsodonty index (height/length of unworn teeth) exceeding 2.5, achieving this by the Middle Miocene, 14 Ma. It may not be coincidental that proboscideans (both mastodons and gomphotheres) reached North America at almost exactly the same time; like modern elephants, these early tuskers probably opened up areas of forest and woodland, thus encouraging the spread of grasslands and grazers.

The Late Tertiary decline of the Equidae has been much discussed. Some authors have pointed to parallel increases in diversity and abundance of contemporary ruminants (bovids, antilocaprids) and have suggested a causal relationship, attributing the differential evolutionary success of the cloven-hoofed ungulates to their remarkable ability to digest cellulose in the forestomach. Equids, in contrast, with their 'hindgut fermentation' were considered less efficient. Recent studies have complicated the picture, however. It appears that in some situations — namely an overabundance of high-fibre, low quality grass — horses may be more efficient than ruminants in utilizing grasslands (Janis 1984). Perhaps this accounts for the fact that horses, despite their decline in generic diversity, continued numerically to dominate Great Plains assemblages of large mammals from the Pliocene until well into the Late Pleistocene.

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1.12 Hominids

R. L. SUSMAN

Early hominids

Hominid evolution begins roughly 4 Ma with the first bipedal ape-men and ends with the origin of our own species (Fig. 1). The first stage is characterized by the appearance of *Australopithecus afarensis*, an ape-man that lived between 4 and 3 Ma in Eastern Africa. *A. afarensis* was highly sexually dimorphic, with males weighing as much as 80 kg and females as little as 30 kg. These earliest hominids had small brains (350 cm³), long upper limbs and short lower limbs compared with later hominids; their fingers and toes were long and curved by human standards. Many anatomical features suggest that at this stage of hominid evolution our ancestors still climbed trees while, at the same time, they were becoming bipedal (Stern & Susman 1983). There is no archaeological record at this time nor is there any anatomical evidence from the hand of *A. afarensis* that these early hominids used bone or stone tools.

Between 3 and 1.75 Ma there is a profusion of hominid species, including *Australopithecus africanus*, *Paranthropus robustus*, *P. boisei*, and *Homo habilis*. *A. africanus* had a brain size of 450–500 cm³ (measured in six individuals) and weighed, on average, around 50 kg (females c. 30 kg and males up to 65 kg). *A. africanus* was notable in having very large teeth, particularly the premolars and molars which are used to grind food; the surface area of premolars averaged 123 mm², compared to 107 mm² in the premolars of *A. afarensis*.

While some authors view *A. afarensis* and *A. africanus* as very similar (and perhaps even members of the same species), others maintain that *A. africanus* is the successor to *A. afarensis*. Morphologically, there are good reasons to conclude that *A. afarensis* was both specifically distinct from, and ancestral to, *A. africanus*. These include a progression in brain size, an increase in tooth surface area, and changes in the hip which may reflect an increasing (but not yet complete) reliance on bipedalism as a means of moving on the ground.

P. robustus occurs slightly later in the fossil record (> 2–1.2 Ma) than *A. africanus*. *Paranthropus* had huge teeth with premolars of 179 mm², and a brain averaging 500–550 cm³. Although these robust australopithecines are traditionally considered to have

been much larger than their gracile counterparts, the former may have been larger only with respect to their jaws and teeth; body weight in the two groups did not differ as much as their jaws and teeth might suggest. New palaeontological evidence uncovered at the Swartkrans, South Africa, suggests that *P. robustus* possessed a hand that was morphologically capable of human-like precision gripping, and may have used bone and stone tools to procure plant foods (Susman 1988). *P. robustus* was essentially a ground-dwelling, bipedal hominid — more adapted to life on the ground than either *A. afarensis* or *A. africanus*. The latest surviving members of this robust lineage became extinct 1.2 Ma.

Contemporary with *Paranthropus* were the first members of the genus *Homo*. The earliest was *Homo habilis*, a species that lived mostly on the wooded savannas, in the vicinity of large lakes or along rivers. Known principally from East Africa, *H. habilis* had a bigger brain than either *Australopithecus* or *Paranthropus*, with an average cranial capacity of 650–700 cm³. It had smaller teeth, with a premolar grinding surface of 109 mm², and correspondingly smaller jaws and chewing muscles. Its limbs (hands, feet, and leg) and limb proportions are decidedly human-like. In many details of the foot and hand *H. habilis* is similar to *P. robustus* as well as humans. *H. habilis* is found with stone artifacts, and its tool tradition is known as the Oldowan (Leakey 1971). The Oldowan consists primarily of flake-tools and tools made of quartzite and chert, trimmed on only one edge for the most part. There is no evidence from marks or indications of burning of animal bones at *H. habilis* sites to suggest that hunting was a major subsistence activity at this stage. At the same time plant remains (including pollen) at some sites indicate that plant food gathering was still a major occupation.

Homo erectus

At roughly 1.5 Ma *H. erectus* appears in the fossil record. *H. erectus*, thought to be the successor to *H. habilis*, represents a major adaptive shift. *H. erectus* is found throughout the Old World, from Africa to Europe and the Far East. There is a considerable

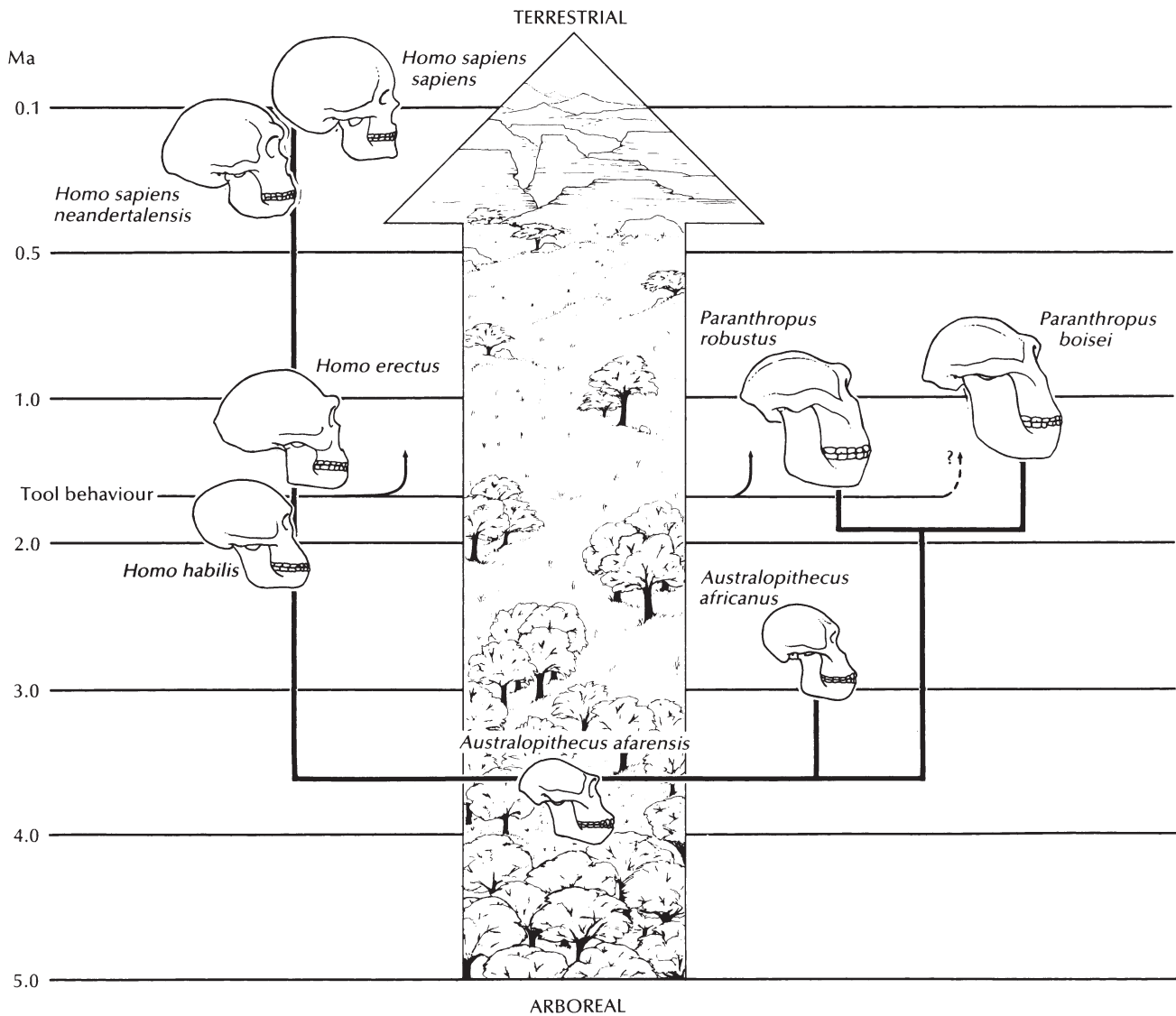


Fig. 1 Phylogeny of Plio-Pleistocene hominids from the earliest, *Australopithecus afarensis* (> 3 Ma) to the most recent, modern humans (*Homo sapiens sapiens*). Hominids continued to exhibit climbing adaptations until the appearance of *H. erectus*. Stone tools are firmly documented at c. 2 Ma (and may date back to 2.4 Ma) and were used by *Paranthropus*, as well as *H. habilis* and their descendants. The placement of *A. africanus* on the tree is equivocal.

increase in body size at this stage, a reduction in sexual dimorphism and in tooth size, and a considerable expansion of the brain. The skull of *H. erectus* is characterized by a very thick braincase with a volume of 1100 cm³, a long, low profile, very thick brow ridges, a well developed ridge on the occipital bone, a skull that has its widest diameter low down on the vault, and the absence of a chin.

With the advent of *H. erectus* there was a shift in subsistence from vegetarianism (and perhaps some scavenging) to hunting. Also at this time the first clear associations of hominids and charred animal

bones occur suggesting that *H. erectus* used fire to prepare, and possibly cook and/or preserve game. The stone artifacts recovered with *H. erectus* show technical improvement over the earlier Oldowan. This stage of cultural evolution has been called the Acheulean, and is characterized by large (35 cm long) hand axes. Although in Asia and Eastern Europe a modified Oldowan (pebble-chopper) industry persists into *H. erectus* times, in Africa and Western Europe hand axes characterize the Acheulean industry. Hand axes were made by flaking a stone core on two sides and creating a tool

that was sharp over most or all of its circumference. These tools not only indicate enhanced skills in perceiving a final form unlike the shape of the raw stone, but also greater selectivity in the choice of raw materials. As the Acheulean industry progressed, there is evidence of refined flaking techniques and the use of soft hammers including wood, horn, and bone. Use of soft hammers allowed the manufacture of finer edges on cutting and chopping tools. The remains of selected large mammals with cut marks, and indications of burning at *H. erectus* sites, suggest that hunting was a major subsistence activity at this stage. At the same time plant remains (including pollen) at Acheulean sites indicate that plant food gathering was still a major part of the subsistence activity of *H. erectus*.

Archaic *Homo sapiens*

The *H. erectus* grade existed for more than one million years. Their successors have been called archaic *H. sapiens*, and early representatives have been unearthed principally in Africa and Europe. Fossils indicate that by 300 000 years ago the earliest *H. sapiens* had spread throughout the Old World. There are conflicting views as to where *H. sapiens* originated from its geographically dispersed predecessor, *H. erectus*. Some suggest that local populations of *H. erectus* in different parts of the world evolved separately into the different races of *H. sapiens*. Another theory is that only a single population gave rise to *H. sapiens* and that this population eventually replaced the others. Confounding a better understanding of this phase in hominid evolution is a dearth of both firm radio-metric dates and good archaeological sites, and the fragmentary condition of hominid fossils.

Fossils from this time period include a distorted skull from Steinheim, West Germany, a partial braincase from Swanscombe, England, a skull from Kabwe, Zambia, and a partial skull from Bodo, Ethiopia. The cranial volume of archaic *H. sapiens* reached 1200–1300 cm³ (within the range of modern humans). The braincase is also thinner than that of *H. erectus*, with a somewhat higher forehead and a shorter face.

The stone tool industry associated with archaic *H. sapiens* indicates that as early as 500 000 years ago Acheulean tools became smaller and at 220 000 years ago a new technological innovation was introduced. The new method of tool making consisted of first preparing a cylindrical core, then striking long blades from it. This is known as the Levallois tech-

nique, and the new culture, called the Mousterian, first appears in Europe. The Mousterian is thought to have evolved from the advanced Acheulean. The transition from Acheulean to Mousterian was a gradual one, with considerable overlap between them.

The Neanderthals

Following the archaic *H. sapiens* of the Middle Pleistocene came the Neanderthals. One popular definition of Neanderthal is that group of hominids that occupied Europe and the Near East from 100 000 to 40 000 years ago. This stage is known from fragmentary skeletal remains of only 100 or so individuals. Neanderthals are distinguished from earlier archaic *H. sapiens* by their thin skull, rounded forehead, reduced brow ridges, prominent, broad nose, rounded orbits, flattened cheek bones, enlarged cranial volume (1500 cm³ and more), large pulp cavities in their small molar teeth, and a space between their last molar tooth and the vertical part of the jaw bone. Some Neanderthal skulls had a bun on the back where neck muscles attached, but others lacked this feature. Some Neanderthal jaws had a very weak chin, while others had a prominent mental eminence. Neanderthals were stockily built, with very thick-walled long bones even in the very young.

The Mousterian culture is closely associated with Neanderthals of the later Pleistocene, a period marked by increased cultural diversity. There were dozens of different types of stone implements in the Mousterian tool kit. Very specialized blade-tools were fashioned from pre-flaked cores, and pressure flaking was used to sharpen their edges. The Mousterians hunted large mammals and gathered plant foods. Our knowledge of their subsistence is aided by the fact that Mousterian artifacts and Neanderthal remains are found in cave sites (unlike earlier excavations of archaic *H. sapiens* that are found in fluvial deposits and in open-air sites).

Archaeological evidence reveals that Neanderthals buried their dead. Evidence of magico-religious beliefs comes from excavated grave goods. Hunting practices involved the exploitation of relatively few large species and the year round occupation of sites (rather than seasonal migration). Other cultural practices included the construction of shelters, the application of surgical procedures to the sick and injured, and the widespread use of fire. Around 40 000 years ago Neanderthals disappeared from the fossil record.

Modern humans

The remains of modern humans in the Upper Palaeolithic are far more common than those of Neanderthals, because of the increased practice of burying the dead. Hominid fossils in the 40 000 year time range are virtually indistinguishable from modern humans (some earlier remains dated c. 90 000 are also very modern looking). They had small, broad, non-projecting faces, high foreheads, protruding chins, and large (1500 cm³) cranial capacities. Their stature was similar to that of modern humans, in the 168–182 cm range. Jaws and teeth recovered from Europe suggest that they had widely varying diets. There are also Upper Palaeolithic fossil remains from Asia, Africa, and the Pacific.

Modern humans of the Upper Palaeolithic possessed a range of stone tool industries. The refined Upper Palaeolithic industries produced blade tools that were finished by soft hammers and pressure, rather than percussion flaking. Many of the stone tools were hafted onto arrow or spear shafts; other projectile points were made from bone and tusk. Scrapers, borers, and small cutting tools were fashioned for the preparation of shafts, skins, as well as food-stuffs.

Humans of the Upper Palaeolithic hunted, fished, and gathered plant foods in a wide range of environments from warm and humid to cold climates. In some areas, such as Northern Europe, there is evidence of seasonal exploitation of migrating game. Fossil evidence also reveals that rhinoceros, mam-

moth, and bear were hunted. In coastal areas there was heavy exploitation of marine resources. At two sites in Germany over 99% of the mammalian faunal remains consist of reindeer.

There is a considerable amount of cave art and plastic art beginning about 30 000 years ago in Europe. The functional significance of cave and chattel art has been debated but most subscribe either to the theory that art is related to hunting rituals occasioned by periodic (seasonal) shortages of food, or that the symbolism had sexual-reproductive connotations.

Humans in the Upper Palaeolithic survived injuries and disease to a greater extent than earlier hominids. The life expectancy of humans in the Upper Palaeolithic had improved over that of the earlier Neanderthals, although it was still low by modern day standards. Roughly half of European and Asian individuals reached the age of 21 years, and only 12% reached 40 years old.

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