have arisen early in Earth history, either directly from the progenote or later from archaebacterial 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 globines 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, Nimbia and Paliella* (Fig. 2H).

The class Inordozoa 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 Inordozoa and Cyclozoa. The Inordozoa includes *Hallidaya, Lorenzinites, Rugoconites, Hiemalora* (Fig. 2G), *Elasenia, Evmiaksia,* and *Pomoria.*

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, Tribrachidium, 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 *Ichnusina, Persimedusites* and *Staurinidia.*

It is noteworthy that as the symmetry of the Precambrian Coelenterata is reduced, their organization becomes more complicated: from primitive,
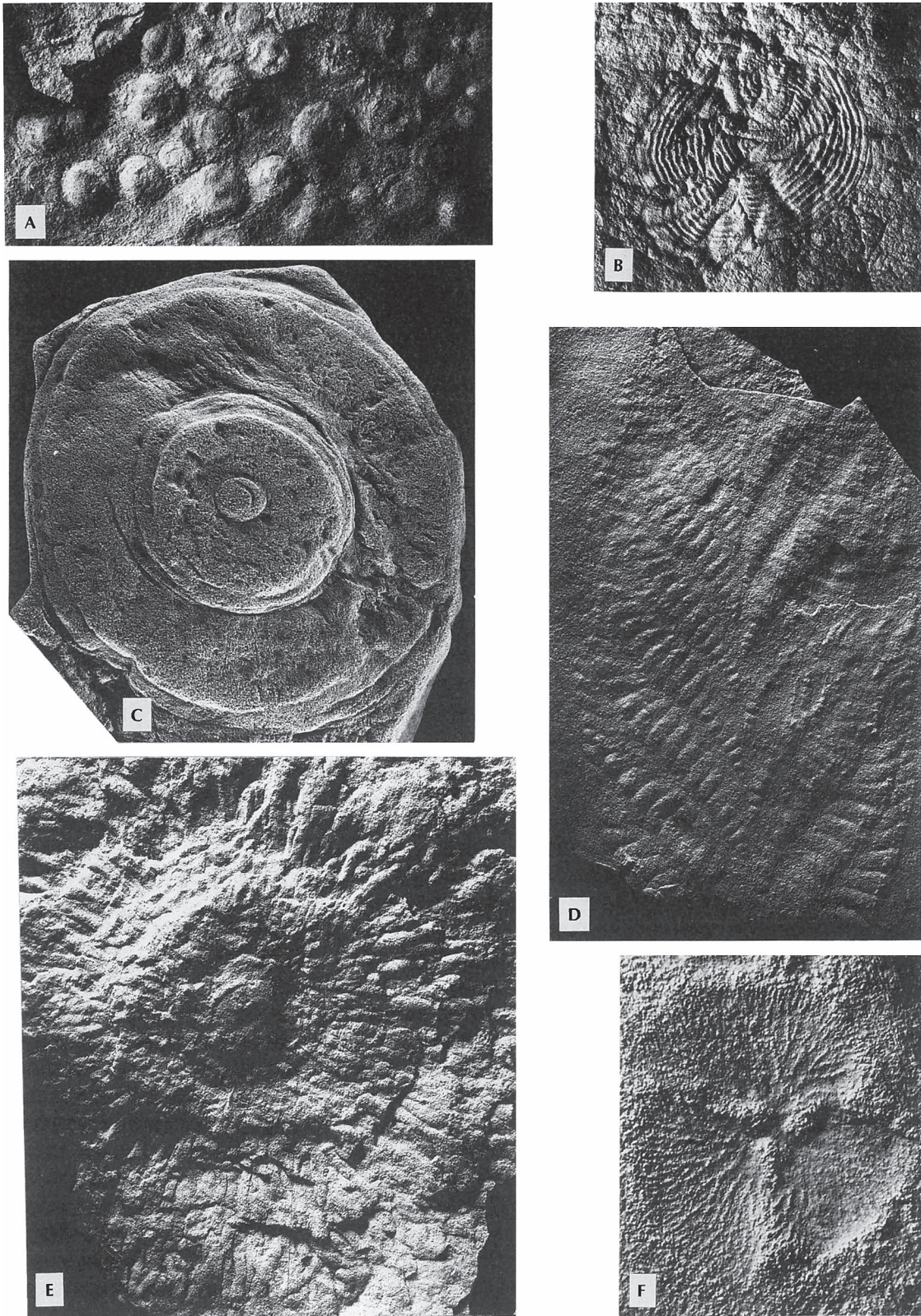
Fig. 1 Vendian metazoans. A, *Nemiana simplex*, × 0.5. B, *Ovatoscutum concentricum*, × 1. C, *Ediacaria flindersi*, × 1. D, *Charnia masoni*, × 1. E, *Eoporpita medusa*, × 1. F, *Albumares brunsae*, × 4. Specimens in A and D are from the Khatyspyt Formation, Northern Yakutia, U.S.S.R. Specimens in B, C, E and F are from the Ust—Pinega Formation, southeast of the White Sea region, U.S.S.R.
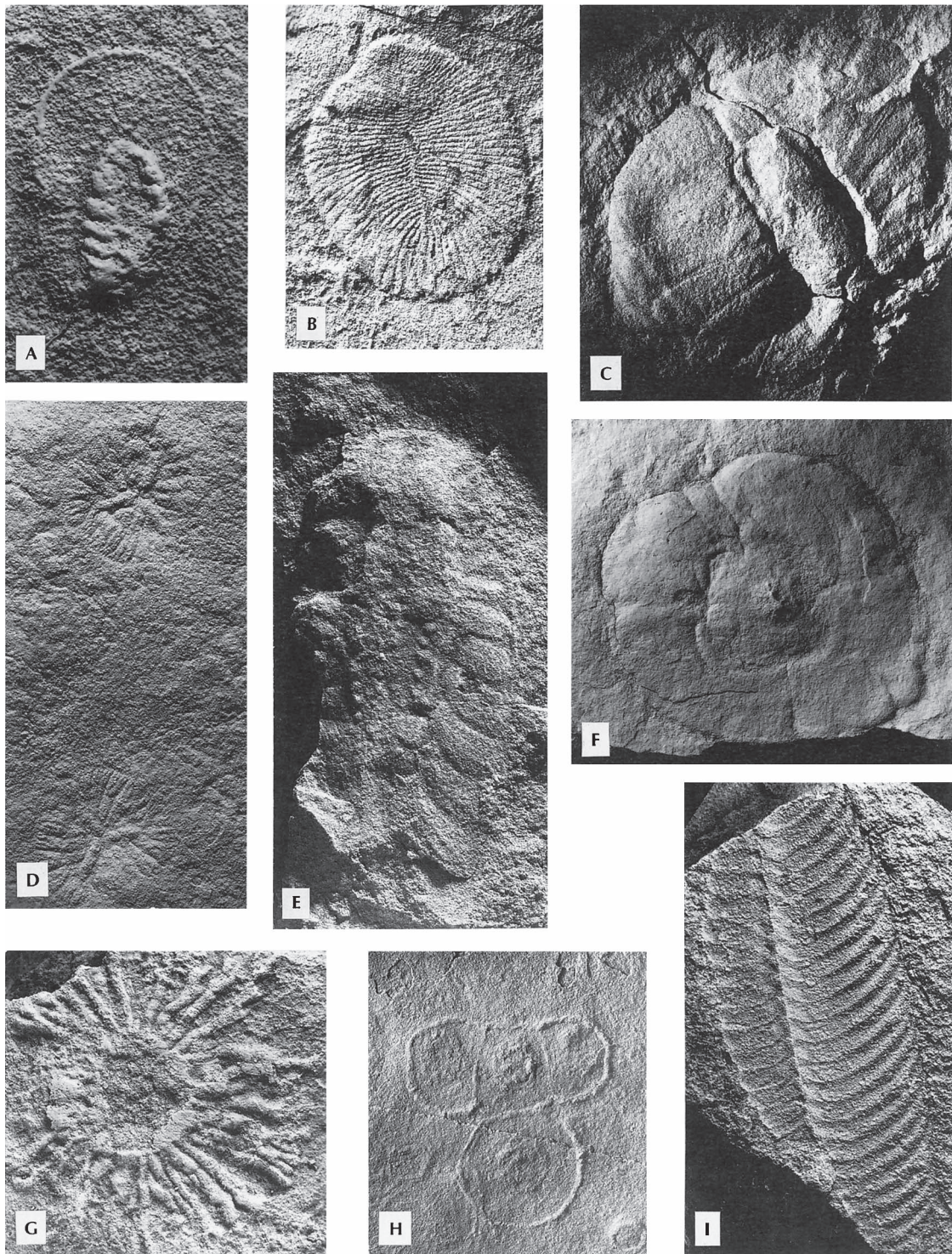
Fig. 2 Vendian metazoans. A, *Onega stepanovi*, × 5. B, *Dickinsonia costata*, × 1. C, *Mialsemia semichatovi*, × 1. D, *Anfesta stankovskii*, × 1.1. E, *Bomakellia kelleri*, × 0.7. F, *Conomedusites lobatus*, × 1. G, *Hiemalora stellaris*, × 1. H, *Paliella patelliformis*, × 0.7. I, *Pteridinium nenoxa*, × 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 polymerous (consisting of numerous anatomically identical body parts) forms in the Dickinsoniidae as well as among oligomerous (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 chitinoid, comb-like jaws. Chitinoid 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 polymerous 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

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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
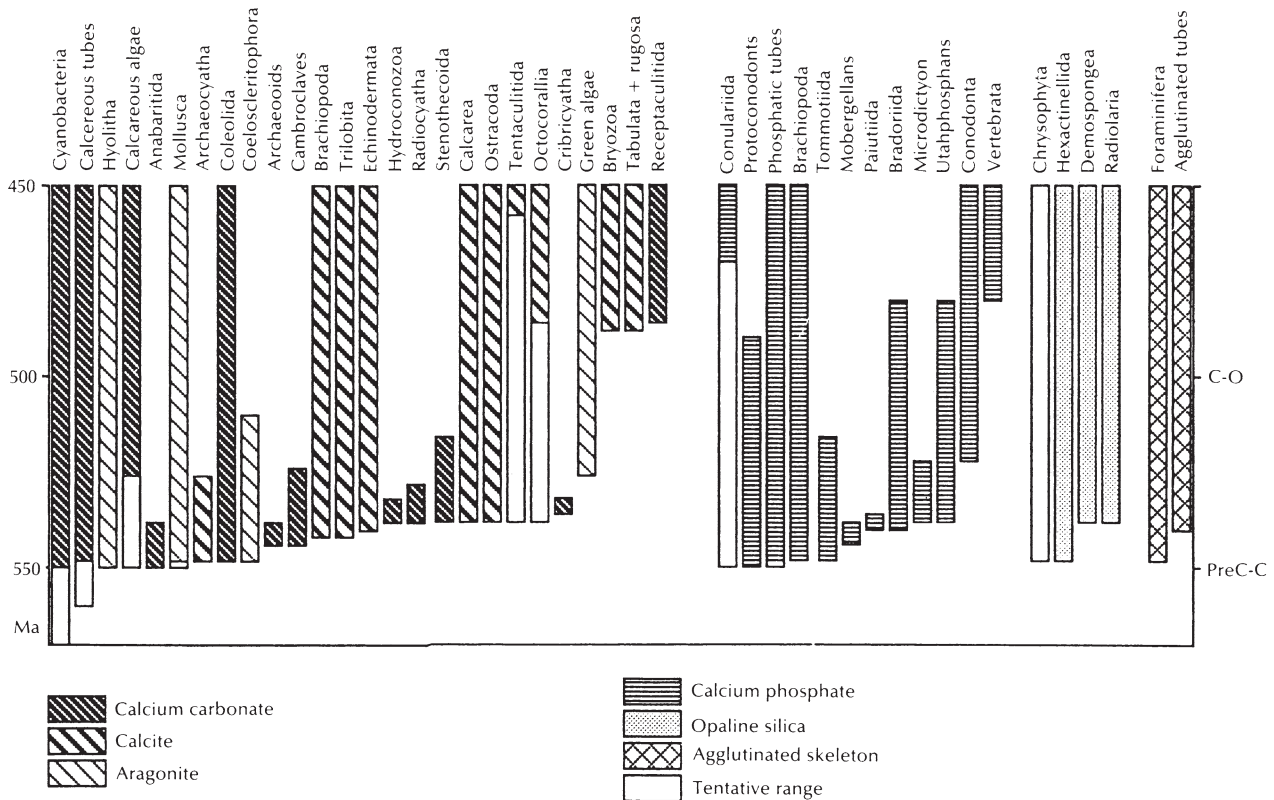
Fig. 1 Temporal distribution of clades of biomineralizing and agglutinating organisms in the Late Precambrian to Late Ordovician, compiled from various sources. Precambrian—Cambrian boundary (PreC—C) arbitrarily placed at the appearance of the *Protohertzina—Anabarites* assemblage and assigned an age 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 micro-granular 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 special-ized sclerocytes, sometimes originating intracellu-larly 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 skel-etons of pennatulacean and a few alcyonarian octo-corals. 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 *Obru-chevella*, 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 photosyn-thetic removal of CO_2 from the water in which they lived (Riding 1977). Fossils that may be true cal-carous 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 paiutiids 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 tommotiids — 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 utahphosphans 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.

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

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, Brachiopoda, 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
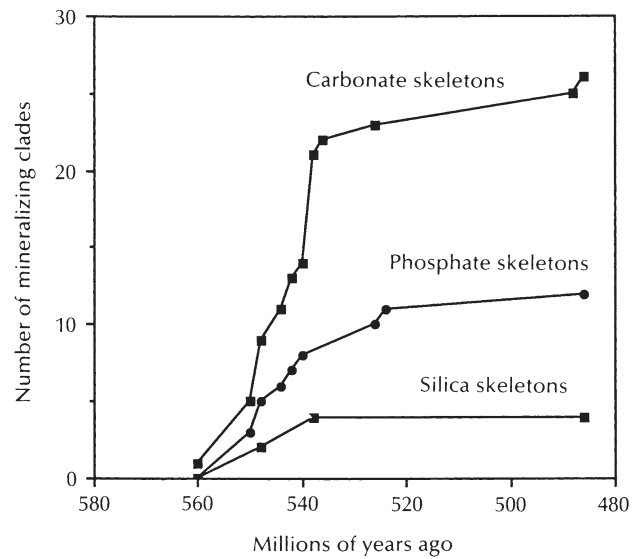
these clades, do not appear to support such views.

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 P_{O_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

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Introduction

Life on this planet is customarily divided into six kingdoms, the prokaryotic archaebacteria and eubacteria, and the four eukaryotic kingdoms of protoctistans, 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 protoctistans, 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