

ORIGINS AND EARLY EVOLUTION OF PREDATION

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ABSTRACT—Predation, in the broad sense of an organism killing another organism for nutritional purposes, is probably as old as life itself and has originated many times during the history of life. Although little of the beginnings is caught in the fossil record, observations in the rock record and theoretical considerations suggest that predation played a crucial role in some of the major transitions in evolution. The origin of eukaryotic cells, poorly constrained to about 2.7 Ga by geochemical evidence, was most likely the ultimate result of predation among prokaryotes. Multicellularity (or syncytiality), as a means of acquiring larger size, is visible in the fossil record soon after 2 Ga and is likely to have been mainly a response to selective pressure from predation among protists. The appearance of mobile predators on bacteria and protists may date back as far as 2 Ga or it may be not much older than the Cambrian explosion, or about 600 Ma. The combined indications from the decline of stromatolites and the diversification of acritarchs, however, suggest that such predation may have begun around 1 Ga. The Cambrian explosion, culminating around 550 Ma, represents the transition from simple, mostly microbial, ecosystems to ones with complex food webs and second- and higher-order consumers. Macrophagous predators were involved from the beginning, but it is not clear whether they originated in the plankton or in the benthos. Although predation was a decisive selective force in the Cambrian explosion, it was a shaper rather than a trigger of this evolutionary event.

THE EARLY WORM CATCHES THE—WHAT?

THE ORIGIN of predation is veiled in as much uncertainty as is the origin of life. Perhaps even more: Life, as we know it today, has a common origin, but predation—in the broad sense of an organism killing another organism for nutritional purposes—has originated many times at different levels of organismal interactions. We can assume, however, that whenever predatory lifestyles evolved they became a strong evolutionary force. Predation introduces hazard into complacency, expands food webs, redistributes resources, recombines characters, and stimulates responses that cascade into an ever-expanding and never-ending series of evolutionary thrusts and ripostes. Predators and prey may enter into symbiotic relationships and emerge as new organisms. Current theories on a number of major transitions in evolution (non-cellular to cellular; prokaryote to eukaryote; non-sex to sex; small to large; unicellular to multicellular; multicellular to tissue-grade; sessile to motile; soft to hard; smooth to

spiny) tend to focus on the introduction of predation as a decisive factor.

The broad definition of predators alluded to above is in common use (e.g., Levinton, 1982; Woodin, 1983; Menge, 1995; Abrams, 2000). It involves much more than fanged beasts that pounce with a roar upon the hapless leaf-muncher. It includes organisms eating those that are smaller, of the same size, or larger. It includes grazing, whether the organisms being grazed are grass, plankton, or microbes in mats. The central aspect of the definition of predation is that it kills the victim. Leaf munching is not predation—not because the leaves are plants, but because browsing them usually does not kill the plant. Parasitism is not predation, for the same reason. Scavenging also is not predation, for the “prey” is already dead. Obviously, there are fuzzy lines between predation and other kinds of interactions—browsing and parasitism may kill the victim in the end, and the distinction between grazing (predation) and browsing (not predation) is blurred by the diffuse boundaries between individuals and clonal colonies. Scavenging and predation are often two

sides of the same behavior, and detritus feeders are bound to engulf countless living microbes. Most organisms are not confined to a single mode of life, so the same organism may be predator, scavenger, parasite, etc.—and, of course, prey. Phenomena in nature tend to have fuzzy edges, and terminology should not lead us to forget that.

Neither predator nor prey has to be an animal, so the definition allows for a discussion of the evolutionary mechanisms that might have been present long before crown-group animals were around. The definition encompasses so much of organism–organism interactions, however, that constraints are necessary to keep the chapter within bounds. The constraints will mainly be practical—I will deal with processes that either have left direct evidence among fossils or at least have the potential to have influenced the fossil record recounting the early history of life on Earth, up till about 500 million years ago. Also, emphasis will shift from prokaryote and protist predators during the early part of the interval covered, to multicellular suspension/filter feeders and grazers on planktic and benthic microbes, and finally to macrophagous predators—animals eating animals.

Because successful predation by definition leads to the death of the prey, its selective importance is considerable. Interactions between organisms are generally regarded as a major factor in evolution (though see Gould, 1985, 2002), and such interactions that lead to the failure of individuals to reproduce should have the strongest effect of all. The evolutionary effects are stronger in prey than in predator taxa (Dawkins and Krebs, 1979; Vermeij, 1987; Abrams, 2000), because of the unequal nature of the interactions—at each encounter the prey risks its life, the predator only its meal (the “life–dinner principle” of Dawkins and Krebs, 1979). Experimental work in modern ecosystems confirms that the introduction of predators may cause a rapid evolution of various defensive characters in the prey species (Thompson, 1998; Agrawal et al., 1999). When the predators respond by evolving more efficient means of predation, the feedback loop sets up the familiar “arms-race” (Dawkins and Krebs, 1979)

or escalation (Vermeij, 1987, 1994, 2002) scenario.

Nonetheless, our ability to identify the evolutionary effects of predation in the fossil record is limited, because evolution is the sum of all effects, and controlled experiments are generally not possible. We have very incomplete information about the nature of the encounters between predator and prey, and in most cases we know the identity of only one of the participants. We know equally little about population structure, competition levels, environmental stress, etc. The fossil record may yield trends through time, but interpreting them is similarly difficult. For example, trends toward larger size in both predators and prey may be interpreted as causally related but may equally well be responses to the same external factors.

For the vast stretches of pre-Phanerozoic time covered in this chapter, matters would seem even worse. Fossils are scarce, they are mostly microbial, and their mode of life cannot in general be deduced from their morphology. For most of the time period, direct evidence of predation is lacking. The fossil record is generally silent with regard to animals older than about 600 million years, and only indirect evidence suggests that animals or animal-like organisms and predatorial modes of life existed earlier. Clearly, formulating and testing ecological/evolutionary hypotheses in this setting is difficult or impossible. Nonetheless, theoretical considerations of the role(s) of predation in early evolution, set against paleontological data, help us to interpret the sparse early fossil record and to evaluate hypotheses regarding the role of predation as a driving force in the evolution from an almost exclusively microbial biosphere to one characterized by multicellular organisms and the complex food webs of modern ecosystems. Although the causalities and triggers of this process are far from understood, the evolution of predatory modes of life is likely to have played a central role, certainly in determining the course of evolution in a number of lineages and perhaps also as a major shaping force in the radiation of multicellular and unicellular organisms during the Cambrian explosion, one of the most significant and certainly the most manifest restructuring of the biosphere during Earth history.

PREDATION AND DIVERSITY IN THE EARLY BIOSPHERE

An imaginary biosphere without predators would be very different from what we are acquainted with. There would be various kinds of photo- and chemoautotrophs making use of available energy gradients to reduce carbon for energy storage and constructional/physiological purposes. There would be organisms scavenging excess organic matter, but there would be no organisms directly interrupting the lives of others by pilfering their tissues.

Leaving aside the question of whether such a Shangri-La for primary producers and decomposers is even theoretically possible, the selective pressures would be very different from those that affect most organisms today. Survival requirements would center around positioning oneself with respect to chemical, temperature, and light gradients, and the only need to move would be in order to adopt to shifting gradients—for example, varying light intensities or redox boundaries. Although competitive interactions would not be excluded, they would mostly be related to relative efficiencies of energy conversion systems. Under such circumstances diversities would be low and stable. The most complex benthic ecosystems would likely be layers of physiologically differentiated microbes, i.e., microbial mats. In the plankton, diversities would possibly be even lower because of the movement and mixing of water masses, which reduces spatial heterogeneity.

The cropping principle (Stanley, 1973a, 1976b) suggests in its general form that the introduction of predation into a low-diversity ecosystem will create a self-propagating feedback system of diversification. Stanley specifically discussed the appearance of cell-eating heterotrophy among planktic protists, which in his view may have been the driving force behind the eventual burgeoning of multicellular organisms and the Cambrian explosion. The phenomenon of predation-induced variability is well established in different kinds of ecosystems (see references in Stanley, 1973a, 1976b; as well as Porter, 1977; Kitchell, 1983;

Richards et al., 1999), and we may ask the more general question of whether some of the major diversity changes in the early fossil record were predator-induced.

Theories to that effect abound. At the base of the bush of life, the origin of cells has been interpreted as a symbiotic or predatory event (Maynard Smith and Szathmáry, 1995; Scudo, 1996; Cavalier-Smith, 2001). The origins of eukaryotic cells, multicellularity, and hard tissues are commonly interpreted to be primary results of predation (see below). These evolutionary innovations clearly had a great effect on diversity by introducing new kinds of organisms with unexploited capabilities of diversification.

Less dramatic, but perhaps stronger in long-term effect, are the diversity effects caused by the dynamics of predator–prey interactions at established levels of organization. Although the diversity effects of such interactions are commonly described in the ecological literature in terms of equilibrium models (where the predator–prey ratio is drawn toward a stable value), this may not be a good description of natural systems. Predators may drive their prey to local extinction (Katz, 1985) or make them more susceptible to extinctions by other agents (Schoener et al., 2001). The net effects on diversity are dependent on a number of factors, such as the existence of refuges, the selectivity and intensity of predation, etc., but as a general rule, selective predation on dominant species increases diversity (Kitchell, 1983). Competitive interaction may also influence diversity, though its effects may have been overstated in the past (Gould and Calloway, 1980; Benton, 1983). In the end, diversity may be less dependent on direct effects, such as those of predator–prey interactions, than on more-or-less complex cascades of indirect effects of biotic interactions (Menge, 1995).

There are of course also environmental (sea level, temperature, oxygen level, nutrient availability) and preservational parameters that affect diversity, and these may or may not be independently analyzed. Predation itself may bias the apparent diversity in the fossil record. Prey eaten by predators may be totally destroyed and

thus escape fossilization, although it is not likely that this will remove the record of the preyed-on species altogether. On the other hand, in some circumstances predation may enhance the possibilities of fossilization, thereby boosting the diversity record of the prey. Fecal-pellet transport via planktic predators is today the dominant mode of transfer of plankton to the sea floor, and indigestible tests of the prey are thereby protected from dissolution by the seawater (Honjo and Roman, 1978; Kitchell, 1983).

Sampling artifacts may have considerably stronger effects on fossil diversity curves than is generally recognized, and it is not unlikely that most of the short-term diversity changes reported from the fossil record are in fact a function of differential preservation in the rock record (Raup, 1976a, 1976b; Peters and Foote, 2001, 2002).

In conclusion, various effects of predation on diversity may be postulated, but general diversity data cannot be used to argue levels of predation. We may have to be content with “asking what is plausible in theory and what is interesting in the measurable fossil record of diversity” (Sepkoski, 1996). The “interesting” aspects of diversity may in this case be related not to clades or grades but to convergent adaptations to predator–prey interactions (spinosity, burrowing habit, tube-dwelling, spiculation, sclerotization, etc.) in comparable environments. Such data are generally not directly available from the literature, and will have to be specially compiled to be useful. Later in this chapter I will discuss, however, how some of the available diversity curves, in particular for stromatolites and protists, may be of use as proxies for predatorial activities in the early evolution of life.

SIZE INCREASE AS A RESPONSE TO PREDATION

Predators either penetrate their prey or swallow it. In our imaginary Shangri-La, there would be little need to get big. On the contrary, efficiency in the exchange of gases and nutrients is a function of an organism’s surface-to-volume ratio, and so smaller organisms have the advantage. Any

increase in size would have to be accompanied by an exponential increase in surface complexity to keep the surface-to-volume ratio stable.

Enter a predator. Now a large surface area may become a vulnerability—the more exposed surface, the more there is for the predator to attack. Increase in size may then be a better option, not only because it reduces the surface-to-volume ratio thus protecting against penetration, but also because it makes the potential prey more difficult to swallow (cf. Guillard and Kilham, 1977). Conversely, it is advantageous for a swallowing predator to be larger than its prey (see Hansen et al., 1994), so a positive feedback loop is created.

Also (with the exception of the large land animals, for which gravitation becomes the major obstacle), larger organisms can move faster than small ones (Bonner, 1965, 1993). Although movement may be an advantage also for an organism seeking out suitable energy gradients, there is no compelling reason to move quickly unless someone else does too. Thus, increasing motility, a corollary of size, may also be selected for in predator–prey interactions.

Other effects of larger size are division of labor and hence differentiation of tissues and the development of organs that would have no function in smaller organisms: respiratory, digestive, circulatory, and muscular structures, for example. These effects may be seen as secondary to the primary phenomenon of size increase (Bonner, 1965, 1993, 1998). They also have a much wider significance than merely being involved in predator–prey interactions, so at these higher levels of organization the connection between predation and size increase becomes weak.

Although increase in cell/body size, at least for simpler organisms, may thus be a more useful proxy for predation pressure than taxonomic diversity, a caveat is needed also here. The tendency toward larger body size and complexity in evolution is so prevalent that it has been regarded as a general law (Cope’s Rule). Whereas individual instances of size increase may be due to specific selection pressures, the general phenomenon does not have to be explained as anything more than an increase in

variance during the course of evolution: if you start small and simple, the only direction to go is toward large and complex (Stanley, 1973b; Gould, 1988; Bonner, 1993, 1998). Thus any event of diversification is likely to bring with it an increase in variance and, hence, an average size increase.

Two major advances in the early evolution of life, however, are inseparably connected with size increase: the origin of eukaryotes and the origin(s) of multicellularity. Both of these probably are in fact direct results of predation.

ORIGIN OF EUKARYOTES

Whereas prokaryotic organisms (bacteria and archaea) represent almost all of the biochemical diversity of the biosphere, eukaryotic cells are the basis for most of the structural and morphological diversity, most particularly with regard to multicellular organisms. In current theory, predation was a main factor behind the origin of eukaryotes. Molecular and structural evidence suggest that eukaryotes evolved through a series of endosymbiotic events in which prokaryotes engulfed or invaded other organisms, eventually leading to an amalgamation of several lineages into daughter organisms representing a higher level of co-operational complexity (Margulis, 1970, 1981; Cavalier-Smith, 1987a, 1987b; Martin and Müller, 1998; Gray, 1999; Lang et al., 1999; Roger, 1999). In particular, mitochondria and chloroplasts, containing as they do their own genome, show strong evidence of having been derived from free-living α -proteobacteria and cyanobacteria, respectively (Gray and Spencer, 1996). The probable origin of these endosymbiotic relationships is predation by means of phagocytosis and the survival of some prey within the predator (McFadden et al., 1994; de Duve, 1995; Roger, 1999). Thus the origin of eukaryotes may be seen as a direct consequence of predatorial interactions among prokaryotes (e.g., Maynard Smith and Szathmáry, 1995).

The same may be true of the origin of eukaryotic sex. The classic interpretation of sex in eukaryotes is that it arose from a single organism as a means of reshuffling genomes. Maynard Smith and Szathmáry

(1995) propose that alternating meiosis and endomitosis in this organism produced a haploid-diploid life cycle, and that (isogamous) syngamy eventually replaced endomitosis for the production of the diploid phase (because of the double advantages of repressing deleterious mutations and allowing for recombination); anisogamy was a later development. However, as commonly acknowledged (Williams, 1975; Maynard Smith, 1978; Maynard Smith and Szathmáry, 1995), the evolution of sex is far from well understood. A radical alternative to the classical model (Walther, 2000) is original anisogamy through the fusion of two prokaryotic organisms in a predatorial/symbiotic event. This would mean that eukaryotic sex, like eukaryotes themselves, is the result of predation.

Does the fossil record have anything to say about this? Although the record is fundamentally inadequate to illuminate processes at the level of organelles, some important information about early eukaryote evolution is in fact available. Cavalier-Smith (1987a) proposed that the original bacterial symbiotic host, in order to be capable of engulfing other organisms, must have lost its polysaccharide cell wall and compensated this by evolving an internal cytoskeleton and sterol cell membranes. Sterols (a group of steroid lipids) are an important and characteristic component of eukaryote cell membranes. The degradation products of eukaryotic sterols, C_{27} – C_{29} steranes, have been discovered in 2.7 billion-year-old organic matter together with 2-methylhopanes, a known degradation product of cyanobacterial membrane lipids (Brocks et al., 1999; Summons et al., 1999). Thus there is fossil chemical evidence that by that time at least two of the organismal groups that participated in the symbiotic events leading up to eukaryotic cells were present in the biosphere.

With regard to body fossils, the generally larger size of modern eukaryotic cells with respect to prokaryotic cells was used in a pioneering attempt to date eukaryote origins based on the size distribution of Precambrian microfossils (Schopf and Oehler, 1976). The earliest fossil now commonly attributed to eukaryotes is the 1.85 billion-year-old (Hoffman, 1987; Morey and

Southwick, 1995; P.F. Hoffman, pers. comm., 2002) Paleoproterozoic *Grypania*, a coiled, cylindrical organism that may attain half a meter in length and 2 mm in diameter (Han and Runnegar, 1992; Runnegar, 1994). Because of its complexity and size, *Grypania* is commonly interpreted to be a eukaryotic alga. Runnegar (1994) speculated that it may be a unicellular or coenocytic organism similar to some modern dacycladaceans (*Acetabularia* and relatives). Advanced unicellular eukaryotes, including spinous forms, are present in the Mesoproterozoic (Samuelsson et al., 1999; Javaux et al., 2001), although higher diversities (several tens of taxa or more) do not appear to have been attained until the Neoproterozoic (Vidal and Moczydlowska-Vidal, 1997). The diversification of unicellular phytoplankton, starting at about 1 Ga, is generally considered mainly related to predation types and levels (Knoll, 1992; Vidal and Moczydlowska, 1992; Knoll, 1994a, 1994b; Butterfield, 1997, 2001; Vidal and Moczydlowska-Vidal, 1997; Smetacek, 2001). Alternatively, Schopf (Schopf et al., 1973; Schopf, 1999) has proposed that it reflects the origin of sexuality about 1.1 billion years ago. Butterfield (2000), however, recently presented convincing evidence for sexually reproducing multicellular red algae already at 1.2 Ga, and argued that the origin of sexuality is linked to that of multicellularity.

ORIGIN(S) OF MULTICELLULARITY

In the living biota there are at least 13 lineages, eukaryotic as well as prokaryotic, in which multicellularity has been attained independently (Bonner, 1998, 2000). Although the selective pressures behind multicellularity may be complex, multicellularity as a general phenomenon can be seen as a consequence of size increase (Bonner, 1998). As discussed above, size increase in small unicellular organisms has its primary advantage in predator-prey interactions. An example is provided by the Myxobacteria, soil-living bacteria the cells of which aggregate in motile swarms to concentrate enzymes that digest other bacteria (Shimkets,

1990). This is a classic predatorial behavior, though this type of aggregating multicellularity (seen also in slime molds) is characteristic of terrestrial, not aquatic, organisms (Bonner, 1998, 2000).

In the absence of preserved cells, multicellularity in fossil organisms can usually only be inferred. Many of the possible multicellular organisms in the Precambrian fossil record may just as plausibly have been syncytial—consisting of a continuous protoplasmic mass with numerous nuclei but no cell walls. This does not matter much for our understanding of them, however; in modern animals some members of a group may be syncytial, others multicellular, and syncytial tissues may occur in otherwise multicellular animals. The first large presumed eukaryote in the fossil record, the 1.85 Ga *Grypania* (see above), has been compared with syncytial algae (Runnegar, 1994); and megascopic carbonaceous compressions in 1.8 Ga rocks in China are reported to have preserved cellular tissue (Zhu et al., 2000). Fossils resembling traces of motile multicellular organisms have recently been reported from 1.2–2 Ga rocks in Australia (Rasmussen et al., 2002). Their mode of feeding is not known, however.

Although strictly not multicellular (though see Shapiro, 1988 for a view of bacterial colonies as multicellular organisms), microbial mat-forming communities will be considered in this context. They are very common Precambrian fossils, and they show a diversity pattern that, it has been suggested, relates to the evolutionary appearance of grazing megascopic animals.

STROMATOLITE DECLINE AND THE RISE OF GRAZING MACROFAUNA

Microbial mats are accretionary cohesive microbial communities, which are often laminated and found growing at the sediment–water (occasionally sediment–air) interface (Pierson et al., 1992). The communities may be quite diverse and complex, involving photo- and chemosynthesizers, autotrophs and heterotrophs, aerobes and anaerobes, the different types occupying different layers in the mats. Photosynthesizing cyanobacteria are often a

dominant constituent in the uppermost layers, and the mats may be sites of considerable primary production. Filamentous mat-building cyanobacteria are motile; they tend to dominate in areas of higher sedimentation rates because they are able to glide upwards through their sheaths to avoid becoming buried by sediment (Des Marais et al., 1992). The cohesiveness of the mats is mainly due to large amounts of extracellular polysaccharides, and commonly also to the presence of filamentous bacteria. This makes the mats effective in binding sediment. Mat microorganisms also commonly induce mineral deposition as a by-product of their metabolism (Burne and Moore, 1987). Mats thus may form buildups, typically assuming the shape of pillows, low mounds, or columns.

Because they act as sediment binders and commonly precipitate minerals, mats are easily fossilized, and their fossil record extends over life's known history on Earth. Laminated fossil mats, stromatolites, are particularly prominent in Precambrian sedimentary environments, mostly in carbonate rocks. In their most distinctive form, developing pillow- or column-like structures, they are easy to recognize; but flat laminated mats may be difficult to distinguish from non-microbial layered sediments. Also, because of the simple physical principles involved in the shaping also of more complex stromatolites, distinguishing biogenic stromatolites from chemical precipitates is sometimes difficult or impossible (Buick et al., 1981; Grotzinger and Rothman, 1996).

A number of metazoans graze on mats, thereby often disrupting their coherence. Stromatolites today are therefore a feature mainly of environments where grazing fauna is restricted (Garrett, 1970; Farmer, 1992; Steneck et al., 1998), such as hypersaline pools or lakes, hydrothermal springs, ice-covered lakes, and tidal environments. This has inspired the hypothesis that an observed decline of stromatolites during the Proterozoic is coupled to the advent of grazing fauna (Garrett, 1970; Awramik, 1971; Walter and Heys, 1985; Walter et al., 1992b; Walter, 1994; Awramik and Sprinkle, 1999). If true, this would provide a useful proxy for the evolutionary appearance of

macroscopic grazers during a time when more direct evidence for animal life is lacking. In the view of Walter (1994), grazing and burrowing metazoans are "the simplest and best explanation" for the stromatolite decline in the Proterozoic. The relationship between stromatolite decline and grazing fauna is far from simple, however, and a number of factors have to be taken into account.

WHAT IS STROMATOLITE "DIVERSITY"?

The idea that increasing levels of grazing would lead to an overall decrease in diversity of the grazed organisms over evolutionary time is contrary to the expectations from the cropping principle (Stanley, 1973a, 1976b) discussed above. This paradox may be only apparent, however, because stromatolite diversity, as measured, reflects the extent of distribution rather than true taxonomic diversity.

Diversity is a taxonomic measure, the basic parameter in a diversity index being number of taxa. Because the microbiota of stromatolites is only rarely preserved, the taxonomy of stromatolites is based mainly on gross morphology, lamina shape, and microstructure (Bertrand-Sarfati and Walter, 1981). As a crude rule-of-thumb, morphology largely reflects environmental influence, whereas microstructure is more dependent on the taxonomy of the participating microorganisms (Semikhatov and Raaben, 2000). Consequently, although stromatolite taxonomy makes use of Linnean binomina, it is not equivalent to biological taxonomy.

Because stromatolite taxa have proven useful in stratigraphy (Bertrand-Sarfati and Walter, 1981; Grey and Thorne, 1985; Grey, 1994), it is often assumed that the taxonomy as applied reflects some measure of evolutionary changes in the composition of the microbial communities. If so, stromatolite diversity may indeed be used as a proxy for biological diversity. Environmental trends through time, however, may also produce stratigraphically discernible changes in stromatolite diversity in a way that mimics biological evolution

(Fischer, 1965; Pratt, 1982; Grotzinger, 1990; Riding, 2000). Although not denying the existence of a Proterozoic decline, Pratt (1982) argued that it is in part a chimaera: Phanerozoic stromatolites are widespread but tend to be diluted by the sheer diversity of reef-building metazoans (Pratt, 1982; Riding, 2000). Unlike their Proterozoic counterparts, the younger stromatolites have therefore not been the focus of taxonomic and stratigraphic studies. Walter and Heys (1985), however, found no correlation between stromatolite diversity and number of authors publishing on the respective time interval in the Proterozoic.

Nevertheless, it is likely that the stromatolite diversity curves from the Proterozoic reflect not so much real changes in diversity as changes in the relative abundance of stromatolites. The low reported diversities of Phanerozoic stromatolites (cf. Awramik and Sprinkle, 1999) may partly reflect that fact that stromatolite taxonomy is largely a pre-Phanerozoic endeavor. Modern stromatolites even have a morphological variability similar to that of Proterozoic ones (Bauld et al., 1992; Walter et al., 1992a), but their more complex fabric and prominent protist components make them poor analogues of the Proterozoic forms (Riding, 2000).

As a measure of possible effects of disruptive activities by metazoans, stromatolite abundance in particular environments may be more significant than overall "taxonomic" diversity. Walter and Heys (1985) indeed included a measure of abundance, corresponding to the number of basins in which a certain taxon was recorded from a certain stratigraphic interval. Although this gives some information on how geographically widespread a taxon is, as a measure of the total relative abundance, the "abundance" as represented in Walter and Heys's (1985) curves is flawed, as in fact it incorporates diversity. The diversity and abundance curves are almost indistinguishable, and this may be because they basically measure the same thing. This "thing" is probably closer to abundance than to diversity.

Thus the apparent decline of "taxonomic" diversity in the Proterozoic may be rather an effect of decreasing abundance of well-preserved stromatolites. As such, it may actually be a more

direct measure than true taxonomic diversity of factors that prevent the growth of stromatolites. Measures of stromatolite numbers per unit of rock ("density" of Grotzinger, 1990) or of areal cover of stromatolites in different environments through time would be even more appropriate, but the collection of such quantitative data would be a momentous task.

THE CAUSAL CONNECTION BETWEEN METAZOAN ASCENT AND STROMATOLITE DECLINE

Declining stromatolite diversity in the Phanerozoic had been noted (Fischer, 1965; Cloud and Semikhatov, 1969), and Garrett (1970) proposed that this was due to non-competitive restriction from grazing and burrowing animals. Awramik (1971) noted a distinct decline in the diversity of columnar stromatolites already in the late Proterozoic, from a peak in the Upper Riphean (950–675 Ma), and associated this with the evolutionary appearance of bottom deposit feeders and burrowing metazoans in the subtidal environment. Data on Proterozoic diversities have subsequently been improved by various efforts, in particular those of Walter and Heys (1985), who included also non-columnar stromatolites and corrected the diversity values for the relative lengths of the stratigraphic intervals and the relative intensity of study. Their data confirm the pattern of late Proterozoic decline, but suggest that diversity peaked in the Middle Riphean (1350–1050 Ma), earlier than in Awramik's 1971 curve but consistent with his later published curve (Awramik and Sprinkle, 1999) (see Fig. 1). Schubert and Bottjer (1992) noted a brief resurgence of stromatolites in the Early Triassic and attributed this to the dearth of benthic grazers in the aftermath of the end-Permian marine extinction events. A similar effect may be present following the Late Devonian (Frasnian–Famennian) mass extinction (Schubert and Bottjer, 1992; Whalen et al., 1998).

Grotzinger (1990) stressed that the data of Walter and Heys (1985) show the decline of

stromatolite diversity to have set in already at about 1000 Ma, whereas the rise of Ediacaran metazoans was some 400 million years later. Following Cloud (1968b) and Stanley (1976a, 1976b), a view has become prevalent among paleontologists that the first crown-group metazoan (i.e., belonging to an extant branch of animals) appeared no earlier than about 600 Ma (for a contrary view, see Fortey et al., 1997; Knoll and Carroll, 1999; Valentine et al., 1999; Budd and Jensen, 2000; Conway Morris, 2000). This is in more or less stark contrast to molecular sequence comparisons (Runnegar, 1982; Wray et al., 1996; Nikoh et al., 1997; Bromham et al., 1998; Gu, 1998; Wang et al., 1999; Hausdorf, 2000), which suggest that the major animal lineages diverged considerably earlier, maybe around 1,500 Ma or even earlier (Wray et al., 1996; Bromham et al., 1998; Wang et al., 1999). The considerable spread of the molecular biology dates currently reduces their usefulness, but even the severest critics of the old-divergence estimates based on molecules (Ayala et al., 1998; Lynch, 1999; Cutler, 2000) agree that molecule dates, if anything, support a much older metazoan history than a literal reading of the fossil record suggests.

This discrepancy is still unresolved. It is tempting to use the stromatolite record as an indicator of cryptic early small and soft-bodied metazoans, and thus to overcome a major weakness of the fossil record of early animal evolution. There are some problems with this approach, however, that have to do with size and abundance of the grazing metazoans.

A number of ecological studies of living biota support the proposed connection between the development of modern microbial mats/stromatolites and the absence of grazing or burrowing fauna. For example, Steneck et al. (1998) investigated a stromatolite-reef complex in the Bahamas that represents a gradation from a stromatolite-dominated back-reef, to a macroalgal-dominated reef flat, to a reef front dominated by corals, algae, and fish. Stromatolites transplanted from their original site had twice as high a survival rate in the back-reef than in the reef front. Levels of herbivory by all kinds of organisms were high in

the reef front, but below detectable levels in the back-reef. Although the experiments could not be carried out under total environmental control, the results support the hypothesis that the presence of grazing fauna has a destructive influence on stromatolite fabric. Other examples in support of the hypothesis were summarized and discussed by Farmer (1992).

The problem is that animals less than a few millimeters in size tend not to disrupt the fabric of modern microbial mats, and so may co-exist with stromatolites (Farmer, 1992). This means that the kind of animals (small and soft), the exclusive dominance of which might have explained a long non-record of a Proterozoic metazoan clade, would probably be unable to disturb microbial mats sufficiently to cause a decline in stromatolite abundance/diversity. Similarly, to explain the decline of stromatolites by the actions of animals large and active enough to leave trace fossils would meet with the justified objection that trace fossils from the time of stromatolite decline are exceedingly rare or absent. Occasional trace-like fossils do exist in Meso- and Paleoproterozoic rocks (Faul, 1950; Kauffman and Steidtmann, 1981; Breyer et al., 1995; Seilacher et al., 1998; Rasmussen et al., 2002), hinting at the early presence of animal-like organisms large enough to displace sediment and disturb stromatolite fabric, but these traces are exceedingly scarce in comparison with the massive stromatolite decline that can be traced all over the Earth.

The pattern of ecological control of modern stromatolites is still persuasive enough to suggest that grazing metazoans are important for holding stromatolites and microbial mats at bay. As an explanation for stromatolite decline during the Neoproterozoic, the grazing hypothesis may be incomplete, but it seems to explain more of the demise and the present distribution pattern than do alternative or complementary hypotheses, such as geochemical trends, competition from eukaryotes, or taxonomic artifacts (Pratt, 1982; Grotzinger, 1990; Riding, 2000). At present, however, the pattern of stromatolite decline can only be taken as suggestive of widespread and abundant grazing organisms.

PREDATION ON AND BY PROTEROZOIC PROTISTS

Modern planktic predators are efficient grazers on phytoplankton (Steele, 1974; Stanley, 1976b), and most of the morphology of planktic protists is probably a response to predation (Smetacek, 2001). The development of spines or other external processes is widespread and is considered to be mainly a way for the potential prey to expand its exposed surface beyond the size that a predator of the same size order is able to handle, or to reduce its nutrient-to-volume ratio (Burzin, 1997; Butterfield, 1997).

Planktic ecosystems are often not very accessible to paleontological investigations, but fossil data are potentially of great value to test the several hypotheses that place important phases of early metazoan evolution in the plankton (Nielsen, 1985, 1995, 1998; Runnegar, 2000). One possible source of such data would be the demonstration of antipredatory devices in early phytoplankton, represented by acritarchs (loosely defined as organic microfossils of unknown and probably varied affinity; cf. Mendelson and Schopf, 1992a), as indicative of the presence of grazers in the water column.

There are a number of problems in the interpretation of such data. Acritarchs are a very disparate group of fossils, and their ecology is in many cases unknown. Not all are planktic (see discussion in Butterfield and Chandler, 1992; Butterfield, 1997), and all may not be protists. Processes may be of different kinds and of different functional significance (for example, they may also be selected for as a means to increase water friction or adhesiveness). The presence of process-bearing acritarchs is therefore not a definite indication of the presence of predators/grazers. Conversely, however, a biota of simple spheromorph acritarchs of consistently low diversity would be strongly suggestive of the absence of selective pressure from plankton-eaters.

Acritarchs undergo a dramatic diversification near the Precambrian–Cambrian boundary (e.g., Moczydlowska, 1991), with a wealth of complex

and process-bearing forms introduced. Diverse biotas of Neoproterozoic large process-bearing acritarchs have been discovered during the last decades (Chen and Liu 1986; Zang and Walter, 1989; Mendelson and Schopf, 1992a; Zang and Walter, 1992; Knoll, 1994b; Vidal and Moczydlowska-Vidal, 1997; Zhang et al., 1998). Occurrences of process-bearing forms before 1 Ga are exceedingly scarce, though weakly spiny acritarchs are known already from about 2 Ga (Hofmann, 1971; Mendelson and Schopf, 1992b). A recently reported 1.5 Ga biota with process-bearing acritarchs (Javaux et al., 2001) is a notable exception to an otherwise rather consistent series of Paleoproterozoic and Mesoproterozoic simple spheromorph assemblages. The total curve of acritarch species (Fig. 1) suggests that diversities were low between 2 and 1 Ga and then rose to a peak before a decline during the great Neoproterozoic ice ages (the “Snowball Earth” episodes of Kirschvink, 1992 and Hoffman et al., 1998). Another peak after the last of these ice ages was followed by an extinction event and a subsequent Cambrian bloom.

Though this evidence is tentative, it may be noted that the rise in acritarch diversity during the Neoproterozoic is an approximate reciprocal of the decline seen in stromatolite “diversity” (Fig. 1), and that both trends may reflect an increase of predatorial activity. An alternative explanation is that this dual pattern reflects a general diversification of protists, which ecologically displace the mat-forming prokaryotes. However, modern microbial mats usually incorporate protists (red, brown, and green algae, diatoms, etc.), which help to stabilize the sediment (Bathurst, 1967; Ward et al., 1992; Riding, 2000), so there is no evidence that mat-forming prokaryotes and protists are mutually exclusive.

Non-acritarch eukaryotes in the Neoproterozoic also show probable antipredatory morphologies. The “vase-shaped microfossils”, or melanocyrrillids (Bloeser, 1985), have flask-shaped tests and resemble modern testate amoebae (Porter and Knoll, 2000); plate-shaped microfossils of probably siliceous composition resemble scales of various Phanerozoic groups of biomineralizing

BENGTSON—ORIGINS AND EARLY EVOLUTION OF PREDATION

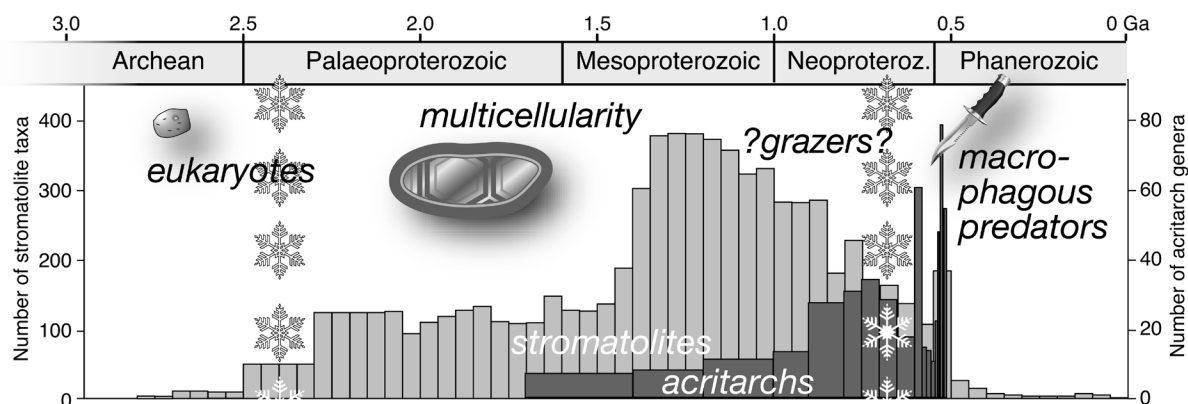


FIGURE 1—Time diagram showing diversities of stromatolites (after Awramik and Sprinkle, 1999) and acritarchs (after Knoll, 1994b), with timings of the predation-related evolutionary steps discussed in the text (knife tip points to the first appearance of macrophagous predators in the fossil record; other symbols show only approximate timings). Snowflakes indicate periods of global glaciations (“Snowball Earth”; Kirschvink, 1992, 2000; Hoffman et al., 1998).

protists (Allison, 1981; Allison and Hilgert, 1986; Kaufman et al., 1992).

THE ROLE OF PREDATION IN THE CAMBRIAN EXPLOSION

Following the massive glaciations in the late Neoproterozoic (Kirschvink, 1992; Hoffman et al., 1998; Eerola, 2001), the biosphere underwent a thorough restructuring. On the face of it, it was a burgeoning of multicellular life, but it has become clear that the event affected the biosphere at all levels, and also that the biological events were coupled with geochemical, oceanographic, tectonic, and atmospheric changes. The end result was that a modern type of marine biosphere, with complex food webs and diverse feeding strategies, was established for the first time. In the sedimentary record, it is expressed as profound differences between rocks below and above the transitional interval. This “Cambrian explosion,” which culminated between 550 and 540 Ma, has been and is the focus of intense and multifaceted research and speculation (recent reviews of the field are by Fortey et al., 1996; Butterfield, 1997; Vidal and Moczydłowska-Vidal, 1997; Knoll and Carroll, 1999; Valentine et al., 1999; Brasier, 2000; Budd

and Jensen, 2000; Conway Morris, 2000; Levinton, 2001, p. 443–494; Zhuravlev, 2001). A recent thematic volume (Zhuravlev and Riding, 2001) deals specifically with the ecological aspects of the Cambrian explosion.

The Cambrian explosion is, in its anatomy, thoroughly dependent on ecological processes. That predation had an important role might seem obvious; and already in the beginning of the last century the proposal was made that the sudden appearance of skeletal tissues in the Cambrian was due to the introduction of predators (Evans, 1912). At that time, the common understanding regarding the Precambrian biota was “not that animals did not exist in those early periods of the earth’s history, but that the scarcity of creatures having a resistant skeleton, precluded the preservation of their remains in such a form as to be easily recognizable” (Matthew, 1912). Interestingly, after Cloud (1948, 1968a) successfully argued for the opposite alternative, that the metazoans did not have a long Precambrian history and that the Cambrian explosion was not just a calcareous dress-up party, the role of Cambrian predators began to be downplayed. Evans’ idea about the crucial influence of predators for the origin of skeletons had lived on (Dunbar, 1960; Hutchinson, 1961), but when Cloud’s interpretation de-

emphasized the role of skeletons in the Cambrian explosion, the view started to become prevalent that predators were absent or at least of little importance in Cambrian ecosystems (Nicol, 1966; Glaessner, 1972; Valentine, 1973; Erben, 1975). As the evidence for Cambrian predators and predation mounted, however (Bengtson, 1968; Bergström, 1973; Alpert and Moore, 1975; Bengtson, 1977; Birkenmajer, 1977; Szaniawski, 1982; Whittington and Briggs, 1982), this view again gave way to the now-common acceptance of predators as a major and important part of the Cambrian ecosystems (e.g., Conway Morris, 1986; Debrenne and Zhuravlev, 1997). Let us look at a couple of questions:

1. Could the Cambrian explosion have been triggered by predators?
2. What was happening in the plankton?
3. How did macrophagous predation enter into the picture?
4. What were the responses to macrophagous predation?

COULD THE CAMBRIAN EXPLOSION HAVE BEEN TRIGGERED BY PREDATORS?

The Cambrian explosion has attracted as many explanation attempts as ever did the demise of dinosaurs, and no smoking gun has yet turned up. There has been a certain tendency to suggest that the proximal cause for the event is whatever object or phenomenon is under study, and predation has not escaped this trigger-happiness. There seems little reason to doubt that predators played an early and important role in the evolving Cambrian ecosystems (Stanley, 1976a, 1976b; Bengtson, 1977, 1994; McMenamin, 1986; Vermeij, 1987, 1990; McMenamin and Schulte McMenamin, 1990; Crimes, 1994; Butterfield, 1997), but more is demanded of a trigger for the Cambrian explosion than that things would have been different without it.

The search for a trigger may in fact be unfruitful: Any phenomenon relating to an event such as this can belong to one of three causal categories: prerequisite, trigger, and effect; or it could have no causal relationship at all with the event (Bengtson,

1994). Prerequisites for the Cambrian explosion are many (free oxygen, shelf space, regulatory genes, biominerals, etc.), and so are its effects. All these are parts of cascades, however, whereas a true trigger should be independent of them, an analogue to (and as elusive as) “free will”. It must either arise “spontaneously” or be introduced from the “outside”; i.e., it must have a timing independent of the integrated biological–chemical–physical system that determines the actual course of the event. Such a trigger might arise from, say, a cosmic event, but may not be in any way spectacular. An actual trigger is not even needed for the event to take place; the impetus may instead come from a critical accumulation of prerequisite conditions (see also Kauffman, 1989).

Predation is probably as old as (cellular) life itself, and it is likely to have existed in many different forms and at many different levels during the formative phases of the Cambrian explosion. What we can hope for is a better understanding of how predation interacted with other ecological/evolutionary forces to produce the specific biotas and food webs of the Cambrian and—in the end—in what way this came to determine the subsequent evolution of the biosphere.

WHICH WAY THE PLANKTON REVOLUTION?

Planktic ecosystems represent most of the marine biomass in today’s oceans, and predator–prey interactions are probably the single most important factor in their evolution (Kitchell, 1983; Signor and Vermeij, 1994; Verity and Smetacek, 1996; Butterfield, 1997; Smetacek, 2001). The evolution of diverse and complex acritarchs during the Neoproterozoic suggests activities by planktic and/or benthic predators, and the possibilities of open oceans even during extreme “Snowball Earth” events (Hyde et al., 2000) may have left the planktic realm as the only part of the biosphere relatively untouched by the global freezing (Runnegar, 2000).

Thus animal predators on protist photosynthesizers may have evolved during the Neoproterozoic, survived the “Snowball Earth”

bottleneck in the plankton, and later reinvaded the benthic realm as the shakers-and-movers of the Cambrian explosion. This idea would be consistent with a long metazoan prehistory of small animals, which did not leave a fossil record (Fortey et al., 1996; Peterson et al., 1997; Peterson and Davidson, 2000; but see Budd and Jensen, 2000). It has some weak points, however.

First, the elaborate acanthomorphic acritarchs of the Neoproterozoic are quite large, typically hundreds of micrometers (Zang and Walter, 1989), and Butterfield (1997) has argued that most or all of these were benthic, and that the only truly planktic acritarchs of that age are the undifferentiated small spheroidal forms. Secondly, the spiny processes are not unquestionably antipredatory adaptations. Thirdly, the Proterozoic predators need not be animals—they could be protists having no direct phylogenetic connection with the Metazoa. Finally, the open-ocean version of “Snowball Earth” (or “Slushball Earth”) has been strongly contested (Hyde et al., 2001; Schrag and Hoffman, 2001).

An alternative view holds that animal predators on phytoplankton had a much later origin. Signor and Vermeij (1994) stressed that the major groups of Paleozoic zooplankton and suspension-feeders originated in the Middle or Late Cambrian and diversified in the Ordovician radiation. They suggested that this indicates a relatively late expansion of animals into the pelagic realm. Butterfield (1997) pointed out, however, that the strong diversification of small spiny acritarchs (e.g., Moczydlowska, 1991) and the presence of filter-feeding apparatuses on zooplankton (Butterfield, 1994) already in the Early Cambrian indicated that the zooplankters were a prominent part of the Cambrian radiation.

In Butterfield’s (1997) view there was little or no animal presence in the Proterozoic plankton, but the key event that triggered the Cambrian explosion was “the expansion of metazoan activities into the plankton,” leading to “the evolution of small metazoans able to intercept and exploit a significant proportion of ... [the primary] production, thereby permitting the evolution of the large, active metazoans that define the Phanerozoic.”

Both these scenarios place emphasis on planktic predators. In the former case there was a long Neoproterozoic history of planktic/benthic predation followed by an ice-age bottleneck where the predators survived in a planktic refuge, and a subsequent recolonization of the benthic realm during which time macrophagous predators evolved from planktic predecessors into a major governing force in the Cambrian radiation. The latter (Butterfield, 1997) scenario implies that planktic filter feeders evolved from the benthic fauna near the beginning of the Cambrian and played a decisive role by harvesting the primary production of the water column and making it available to larger organisms.

ONSLAUGHT OF THE FANGED BEASTS

The importance of larger macrophagous predators is that they represent second- and higher-order consumers, signifying the advent of complex food webs and complex interactions between different kinds of multicellular organisms. In the Ediacara biota, the first possible macrophagous predators belong to the first skeletal assemblage—the Neoproterozoic *Cloudina-Namacalathus* assemblage (Germs, 1972; Grotzinger et al., 2000). These sessile organisms enclosed themselves within calcareous tubes and calices. Their general cnidarian-type morphology suggests that they might have had a predatory lifestyle like most modern cnidarians, but this is conjectural. More significantly, there is evidence of predatory shell borers in this assemblage (see below).

From the point of view of a possible derivation of the metazoans from planktic predators, it is interesting to note that the second oldest evidence of probable macrophagous predators are the protoconodonts (Missarzhevskij, 1973; Bengtson, 1976, 1977, 1983). These animals had slender teeth combined in a complex grasping apparatus (Landing, 1977; McIlroy and Szaniawski, 2000), and Szaniawski (1982, 2002) has convincingly argued for their close affinity to modern chaetognaths, arrow worms. Chaetognaths are one

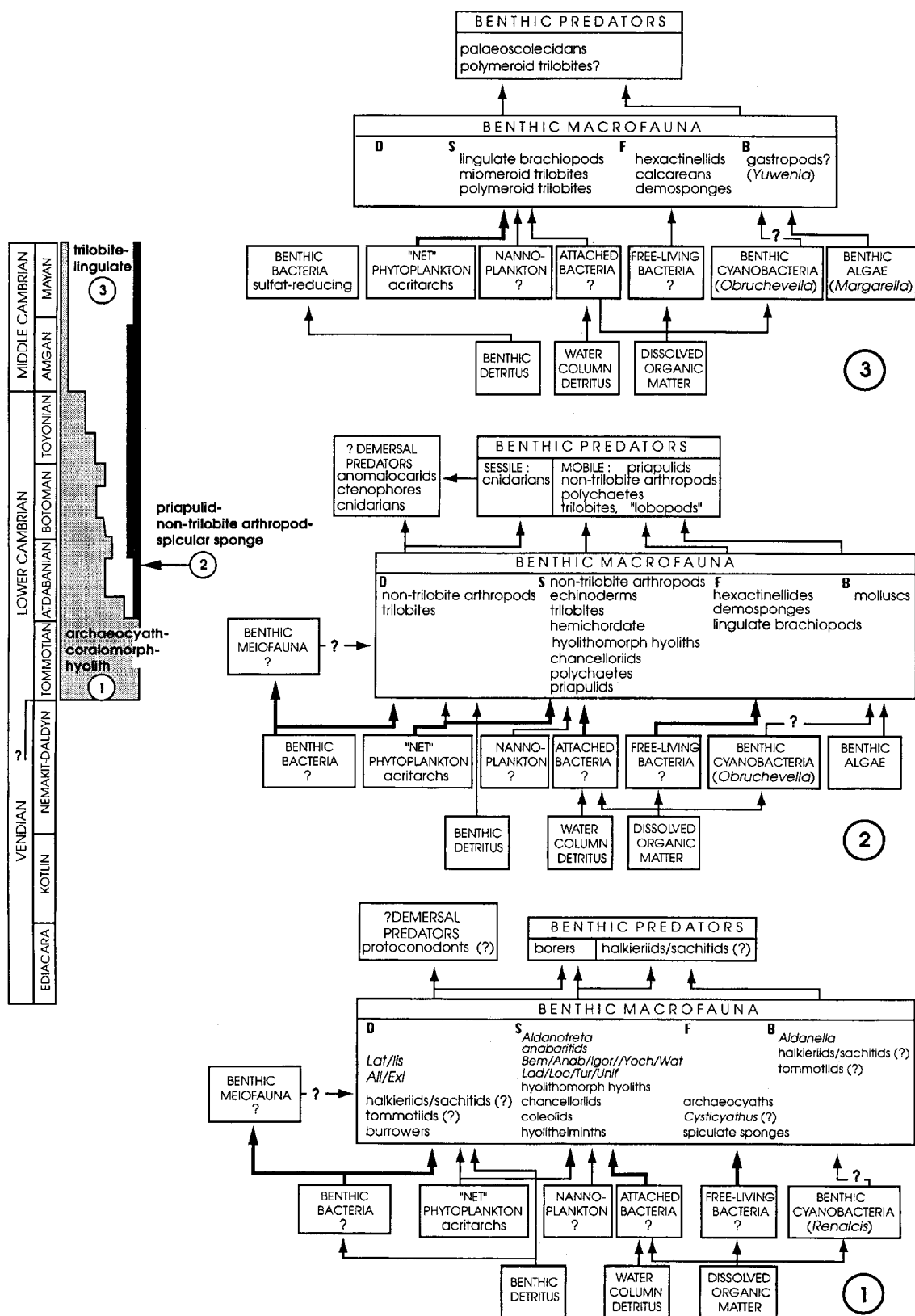


Figure 2

of the major groups of modern planktic macrophagous predators, and they are currently believed to occupy a basal position in the bilaterian phylogenetic tree (Telford and Holland, 1993, 1997; Wada and Satoh, 1994; Halanych, 1996).

The list of other Cambrian macrophagous predators identified as fossils is now long, in stark contrast to the commonly held opinion a few decades ago that predators were few or absent in the Cambrian (Glaessner, 1972; Erben, 1975). The quantitatively most important macrophagous predators appear to be arthropods (Budd, 2001; Hughes, 2001), though the relative predisposition of arthropods for fossilization, even in “soft-bodied” lagerstätten, may have enhanced their apparent dominance.

Conway Morris (1986) analyzed the community structure of the Phyllopod Bed in the Burgess Shale. His main conclusion was that the proportion of predators in Cambrian ecosystems had been severely underestimated in previous studies based only on hard-part preservation. Bengtson et al. (1992) tabulated metazoan genera through the Lower Cambrian and concluded that although predators (including herbivores) were of low diversity throughout this time period, the basic components of a modern marine ecosystem were present already from the beginning of the Cambrian. Zhuravlev and Debrenne (1996) and Debrenne and Zhuravlev (1997) reviewed the trophic structure of three types of Lower–Middle Cambrian benthic environments—reefal, level-bottom open-marine, and level-bottom dysaerobic (Fig. 2), suggesting short and simple food chains comparable with those of recent eutrophic areas.

ANTIPREDATORY RESPONSES

Of the many direct adaptations to counter predation pressure that are available to organisms, only a few types are potentially visible in the fossil record. Chemical defense, life-history modifications, migrations (or indeed any behavior that does not leave trace fossils), mimicry, and protective coloring are all unlikely to leave a recognizable fossil signature, and so must largely be left as a reminder to the paleontologist that the information is incomplete.

Skeletons.—The once-common interpretation of the Cambrian explosion as a biomineralization event (see quote from Matthew, 1912, above), an “explosion of fossils” rather than of organisms, is now largely in disrepute. This is partly because of the massive evidence for an equally rapid evolution of non-skeletal organisms; partly because of the realization that biomineralization as such is widespread among organisms (Lowenstam and Weiner, 1989). Bengtson (1994) formulated four general conclusions regarding the advent of animal skeletons: 1. Biomineralization has an ancient history and was only a prerequisite for the advent of skeletons. 2. Skeletons are constructed using a variety of processes and materials. Minerals are suitable because they give hardness to the composite material, can be produced using exapted pathways, and are physiologically cheap. 3. Whereas the initial choice of shell mineral usually precludes future evolutionary switches to other minerals (because of the intricate systems developed to modify the growth of the mineral), there is no reliable indication of any

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FIGURE 2—Trophic webs in principal Early Cambrian benthic communities according to Zhuravlev and Debrenne (1996; partly based on data from Conway Morris, 1986, and Kruse et al., 1995). 1, Reefal. 2, Level-bottom open-marine. 3, Level-bottom dysaerobic (diagram to the left indicates relative importance of these environments). D—Deposit feeders; S—Suspension feeders; F—Filter feeders; B—Browsers/herbivores. (Note that all of these categories include various grazing predators according to the broader definition of predation used in the present paper, and that the category “predators” corresponds to macrophagous predators on animals.) Arrow width indicates relative biomass. Question marks indicate categories that are not preserved but hypothesized to be present; question marks within parentheses indicate doubtful trophic assignments of taxa.

regularity in the acquisition of skeletal minerals within or between clades. 4. The propellant in the evolution of skeletons was organismal interactions, and a primary factor behind the evolution of tubes, shells, sclerites, and spicules, was selection pressure from predators.

The primary role of ecological selection pressures does not preclude the possibility that physiological (Marin et al., 1996) or geobiochemical (Kirschvink and Hagadorn, 2000) mechanisms involved in skeletal biomineralization have common evolutionary origins. These mechanisms are of course prerequisites for the appearance of biomineralized skeletons, but their use in skeleton formation is likely to be exaptational.

A survey of the skeletal types appearing in the Cambrian biota (Bengtson and Conway Morris, 1992) differentiated between spicules, tubes, conchs, external sclerites, toothlike structures, carapaces, and calcareous reinforcements. All these have defensive/protective potential, though for some of the skeletal types other functions, such as internal support, may be more fundamental than protection.

It is difficult in fossil material to ascertain the best function of a particular structure, and evidence from living organisms underscores that intuitively correct interpretations are not always the best. A case in point is spicules—mineralized structures, often needle-shaped, distributed within the soft tissues of most major groups of the Metazoa (e.g., Rieger and Sterrer, 1975). Many sponges are full of needle-sharp siliceous or calcareous spicules, which might intuitively seem important to deter predators (Wainwright et al., 1976; Hartman, 1981), but there is in fact little evidence in support of a protective function for the spicular skeleton of sponges (Bergquist, 1978, p. 94). Experimental work on modern sponges (McClintock, 1987; Chanas and Pawlik, 1995, 1996; Dunlap and Pawlik, 1998; Waddell and Pawlik, 2000a, 2000b) indicates that predators of various kinds (fish, arthropods, echinoderms) are not influenced in their selection by the presence of spicules in the prey tissues. Whereas such results could partly be an effect of specialized spongivores having evolved mechanisms to diminish the potential harmfulness

of sponge spicules (Oshel and Steele (1985) reported such a case concerning an amphipod predator), even generalist feeders seem undeterred by spicules in the sponge prey (Chanas and Pawlik, 1995, 1996; Dunlap and Pawlik, 1998).

Vreeland and Lasker (1989) found a similar pattern in spiculated gorgonian octocorals preyed on by a polychaete worm: the polychaete's preference for a particular gorgonian species was not correlated with the sclerite density of the latter. On the other hand, a gastropod feeding on gorgonians showed preference for colonies with short sclerites over those with long ones (West, 1998), and gorgonians respond to predator-simulated mechanical damage by generating a stiffer cortex with longer sclerites (West, 1997).

Similar problems of functional interpretation exist with regard to many of the other skeletal types. Reasonable arguments can be made why most of them should have a primary protective function (Vermeij, 1987, 1990; Bengtson, 1994), but even if that is correct the picture may be obscured by multiple other functions. I will give two examples of early skeletal fossils, however, where a primary antipredatory function appears well supported by the evidence.

Tube-dwellers are common among the early skeletal animals, and the varying composition and morphology of the tubes suggest that a number of independently derived lineages are represented (Bengtson and Conway Morris, 1992). One of the earliest known animals producing a mineralized tube, the late Neoproterozoic *Cloudina*, has been found to display boreholes made by a predatory or parasitic organism (Bengtson and Yue, 1992). Predatory boreholes are known from various types of tubes and shells in the Cambrian (Bengtson, 1968; Miller and Sundberg, 1984; Conway Morris and Bengtson, 1994; Streng, 1999), and they constitute one of the most important records for predation throughout the Phanerozoic (Vermeij, 1987; Kelley and Hansen, 1993; Kowalewski et al., 1998). The presence of such borings even among the earliest skeletal animals strongly suggests that protection against predators was a primary function for these tubes.

The other example of an early exoskeleton with a clear antipredatory function is that of the chancelloriids. These sessile, bag-shaped organisms are common from the Early Cambrian to the early Late Cambrian (Walcott, 1920). They had a soft integument beset with composite calcareous sclerites having sharp, radiating spines (Bengtson and Hou 2001). Since the sclerites were external and non-interlocking, they could not have had a supporting function, and since the body was sessile and attached, the sclerites would not have served to increase friction. Thus there seems to be no other conceivable function for the chancelloriid sclerites than antipredatory: Mechanical considerations suggest that they would prevent access to the integument by large (i.e., about the size of the distance between the sclerites or larger) predators, and the corresponding morphology in spiny cacti is known to deter herbivores (Theimer and Bateman, 1992; LeHouérou, 1996).

Various instances of probably predator-inflicted damages to skeletons of Cambrian animals (Pocock, 1974; Conway Morris, 1985; Conway Morris and Jenkins, 1985; Babcock and Robison, 1989; Babcock, 1993; Pratt, 1998; Nedin, 1999) have also been taken as evidence of the protective function of these skeletons.

Behavior.—One of the crucial pieces of evidence for the Cambrian explosion as an all-encompassing biological overhaul (rather than just the invention of skeletons) has been the dramatic diversification of trace fossils across the Precambrian-Cambrian boundary (Seilacher, 1956; Alpert, 1977; Crimes, 1987, 1989, 1992, 1994; Macnaughton and Narbonne, 1999). During this process metazoans expanded their biotopes into the infaunal realm, somewhat earlier in the clastic than in the carbonate environments (Droser and Bottjer, 1988; Droser et al., 1999; McIlroy and Logan, 1999; Droser and Li, 2001). McIlroy and Logan (1999) interpret this in terms of a positive feedback loop begun in deeper waters by the increased downward flux of organic matter through fecal pellets produced by plankton-harvesting metazoan zooplankters (Logan et al., 1995, 1997; cf. Butterfield, 1997, and discussion above); bioturbation by deposit-feeding

metazoans would then gradually drive oxygen, labile organic matter, and nutrients deeper into the sediment, stimulating deeper bioturbation.

Whereas deposit-feeders are to a great extent driven by the availability of organic matter and nutrients, many traces in the Neoproterozoic–Cambrian reflect activities other than deposit-feeding or grazing (Crimes, 1992). Vertical burrows containing a core of trilobite shell fragments have been interpreted as made by sea anemones preying on trilobites (Alpert and Moore, 1975). Deep dwelling traces (*Diplocraterion*, *Rhizocorallium*, *Skolithos*, etc.) appear to represent protective behavior, in effect equivalent to that used by tube-dwelling animals. They may thus have arisen in response to predation pressure.

Predators on infauna may dig their own holes or be “weasel predators” (Woodin, 1983), entering the sediment through the hole made by the prey. In the latter case, no trace-fossil evidence is likely to be preserved. Some evidence for the former type of predation exists among Cambrian ichnocoenoses. Associations of arthropod traces and “worm” burrows have been interpreted as instances of arthropod predation on burrowing infauna (Martinsson, 1965; Bergström, 1973; Jensen, 1990, 1997; Pickerill and Blissett, 1999); however, a recent study of an assemblage with 29 such associations suggested that the “worm” burrows were formed after the arthropod traces and thus that the “worms” more likely were seeking out patches visited by the arthropod (Rydell et al., 2001). The role of infaunal predation in soft sediments during the Cambrian explosion is thus poorly understood, partly because the trace fossil evidence may be difficult to interpret, but also because the effects of predation in corresponding modern environments are very poorly known (Wilson, 1990).

SUMMARY

Steps in the early evolution of predation.—The foregoing discussion has dealt with predators at different levels of organization, and predation at different trophic levels. The perspective has shifted over the time period covered—from the early interaction between prokaryote cells to the late

emergence of macrophagous predators and second-order consumers. Also, the amount and quality of information available from the respective stages has forced a shift in the level of analysis from speculation based on general biological principles, to hypotheses based on indirect evidence in the fossil record, and to hypotheses more firmly based on fossil evidence.

The theme has been escalation in the sense of Vermeij (1987), but brought to bear on the early history of life up into the Cambrian (where Vermeij's story begins). The etymology of "escalation"—from Spanish *escala*, ladder, and Latin *scala*, with the same meaning—suggests stepwise rather than gradual shifts, and Vermeij (1987) stresses the pattern of punctuated equilibria (Eldredge and Gould, 1972) when analyzing the anatomy of escalation. Although not dealing with punctuated equilibria at the species level, I have focused on some important steps (or escalations) in which predation is likely to have played a key role (Fig. 1). They all represent the attainment of a higher level of organization (in the sense of combining previously existing systems to a new whole), and so correspond to some of the major transitions in evolution as discussed by Maynard Smith and Szathmáry (1995).

Step 1.—From prokaryotic to eukaryotic. Predation was in all probability the determining factor in this event, and the resulting organisms combine characters of predators and prey in a way that opens new evolutionary possibilities. The time for this step is poorly constrained to around 2.7 Ga (when geochemical evidence suggests that the host and at least one of the guest symbionts were available).

Step 2.—From unicellular to multicellular. This step was taken many times independently, but as a means of producing bigger organisms it may reflect predatorial pressures from cell-engulfing eukaryotes. At least in some lineages this happened soon after 2 Ga (when the atmospheric oxygen had gone up and the first non-stromatolite macrofossils appear).

Step 3.—The appearance of mobile selective predators on bacteria and protists. This is the most uncertain event of them all, for it may go back as far as 2 Ga or it may be not much older than the

Cambrian explosion. The combined indications from the decline of stromatolites and the diversification of acritarchs suggest that it may have begun around 1 Ga.

Step 4.—From simple, mostly microbial, ecosystems to ones with complex food webs and second- and higher-order consumers. The appearance of macrophagous predators is the telltale sign, and it took place no later than a few million years before the beginning of the Cambrian, or around 550 Ma.

FUTURE RESEARCH DIRECTIONS

The really interesting new research results are always the unexpected ones. Any recipe for future research that I may attempt to write will be one for stale cookies—the unpredictable cannot be predicted. It should be clear from this review of the early history of predation, however, that there are enormous gaps in our knowledge of the ecological interplay between organisms up to about the Precambrian–Cambrian transition (after that the gaps are only huge). The partial filling of some of these gaps is something that one might humbly wish for.

For example: Where did the main organismal interactions take place that led to the Cambrian explosion of animals? The planktic habitat has of old been considered difficult to analyze from fossils, both because planktic organisms tend to be fragile and because in order to be preserved at all they need to be shifted out of their habitat. The discoveries that delicate animal tissues, such as minute arthropod limbs (Müller and Walossek, 1985; Butterfield, 1997) and embryonal blastomeres (Zhang and Pratt, 1994; Bengtson and Yue 1997; Xiao et al., 1998; Yue and Bengtson, 1999; Xiao and Knoll, 2000), may be exquisitely preserved by carbonization or phosphatization in 3-dimensional detail in rocks of this age spell great promise for the investigation of early animals, whether they be planktic or benthic. The extensive phosphorite deposits from the time period still guard many secrets, and a suitable target in these rocks may be fecal pellets, today an important medium of

preservation of planktic prey (Kitchell, 1983).

Geochemical methods are becoming ever more sensitive, and the search for characteristic biomarkers in Proterozoic rocks has started to yield spectacular insights into the occurrence of organisms in sequences where a morphological record is lacking (McCaffrey et al., 1994; Brocks et al., 1999; Summons et al., 1999). The recently realized possibility of analyzing isotopic ratios in individual Proterozoic microfossils (House et al., 2000) may let us characterize fossil organisms physiologically and thereby throw light on their mode of life. The use of lipid ratios in Pleistocene mollusc shells to identify predators vs. suspension feeders (CoBabe and Ptak, 1999) is a particularly fascinating extension of biogeochemical methods with great ecological significance, although the currently available analytical procedures are hardly applicable to the Proterozoic and Cambrian fossil record.

Trace fossils are a direct reflection of behavior, and may represent the currently most profitable avenue for research into early predatory and antipredatory behavior. Whereas Cambrian trace fossils and bioturbation are almost ubiquitous, late

Neoproterozoic examples are comparatively scarce, and reports of trace fossils older than 600 Ma have yet to find general acceptance. Nonetheless, several reports of earlier trace-like fossils (e.g., Faul, 1950; Kauffman and Steidtmann, 1981; Breyer et al., 1995; Seilacher et al., 1998; Rasmussen et al., 2002) have still to be given a better explanation. Rather than being ignored as freakish occurrences, they should be used as search images in a more concerted exploration for evidence of possible early adventures into motile multicellularity and associated behavior.

In the Cambrian, the prospects are quite good for a deepening understanding of the ecological interactions shaping the biota. The main reason for this is that the Cambrian is unusually blessed with fossil preservation lagerstätten. New Cambrian life forms are being reported from these each year, and when the basic morphologic and taxonomic information has been obtained, the foundation is laid for spectacular advances in the synecology and autecology of the Cambrian biota. With that, we will also get a better handle on the ecology of the Cambrian explosion itself.

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