An Ecological Theory for the Sudden Origin of Multicellular Life in the Late Precambrian

(adaptive radiation/Cambrian/evolution/paleontology/predation)

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ABSTRACT   According to modern ecological theory, high diversity at any trophic level of a community is possible only under the influence of cropping. Until herbivores evolved, single-celled algae of the Precambrian were resource-limited, and a small number of species saturated aquatic environments. In the near-absence of vacant niches, life diversified slowly. Because the changes required to produce the first algae-eating heterotrophs were therefore delayed, the entire system was self-limiting. When the "heterotroph barrier" was finally crossed in the late Precambrian, herbivorous and carnivorous protists arose almost simultaneously, for no major biological differences separate the two groups. These events automatically triggered the formation of a series of self-propagating feedback systems of diversification between adjacent trophic levels. Comparable systems arose among multicellular groups, which radiated rapidly from the newly diversifying protist taxa. The sudden proliferation of complex food webs formed by taxa invading previously vacant adaptive zones produced an explosive diversification of life over a period of a few tens of millions of years. The rapid appearance of skeletons in various groups, though of special geological importance, was no more dramatic than other aspects of the radiation. The overall rate of diversification was comparable to rates for less-extensive adaptive radiations of the Phanerozoic.

Students of the history of life have long been troubled by the fact that, after a long Precambrian history of slow unicellular evolution, multicellular organisms arose and radiated suddenly near the beginning of the time interval we have come to call the Cambrian Period. This fundamental radiation forms our basis for division of the geologic time scale into two major parts. Its cause has been widely regarded as the foremost unresolved problem of paleontology (1–3). Two approaches have been emphasized in recent attempts to solve this and other riddles in the history of primitive life. The first is invocation of external physical and chemical controls, such as levels of ultraviolet radiation and atmospheric oxygen (2, 4–6). The second, sometimes intertwined with the first, is recognition of major adaptive breakthroughs, such as the appearance of autotrophy, eukaryotic organization, sexuality, multicellularity, collagen secretion, and shell formation (3, 5–8). Neither approach has produced a generally accepted, unified explanation for the sudden late-Precambrian evolutionary explosion. What has been missing, it seems, is the application of relevant ecological theory.

CHRONOLOGY OF EVOLUTIONARY EVENTS

In a recent authoritative evaluation of existing fossil evidence bearing on the origin of multicellular life, Schopf *et al.* (3) reached the following conclusions:

Eukaryotic organisms arose earlier than 1300 million years ago, and perhaps even earlier than 1700 million years ago, but were probably haploid and asexual at first. The oldest convincing evidence of sexuality comes from spore-like unicells in the 900 million year-old Bitter Springs fossil flora. The advent of sexuality should have greatly increased genetic variability and correspondingly increased rates of evolutionary diversification. It is then puzzling that the Bitter Springs flora and various other fossil assemblages of similar age are impoverished relative to modern eukaryote assemblages. They have yielded only simple spheroidal unicells, none of which exhibits features typical of even moderately advanced thallophytes (e.g., tissues, differentiated sporangia, true branching, or polarity of organization). Although the precise time of origin of metaphytes is unknown, the fossil record shows that green, red, and brown algae appeared before the beginning of the Cambrian, and perhaps slightly before 650 million years ago. The oldest known metazoan assemblages, the Ediacara fauna of Australia and its equivalents, are of similar age. Animal-like protists must have arisen before metazoans, although we have no definite record of their earlier presence. Schopf *et al.* suggested that the proliferation of early metaphytes may have contributed to the initial diversification of metazoans. To explain the gap between the advent of sexuality and the origin of multicellularity, these authors suggested that eukaryotic sexuality was a novel experiment in Bitter Springs time and that its evolutionary impact was somehow delayed at least 250–300 million years (substantially longer if sexuality appeared well before Bitter Springs time). This delay, they suggested, might have been caused by the gradual nature of the trend from a haploid-dominated life cycle to a diploid-dominated cycle of the type that characterizes modern algae.

In fact, the idea that the diploid stage, once present, was somehow suppressed is difficult to justify by the "adaptive innovation" approach to Precambrian evolution. Once the diploid stage arose, this approach would predict its immediate rise to dominance if it was a major innovation. Certainly, however, Schopf *et al.* were correct in stressing a previously ignored fact: that metaphytes and metazoans originated almost simultaneously. The delayed origin of both groups may, I believe, be explained by application of a newly established principle of ecology, which leads to the conclusion that the origin of metazoans brought about the diversification of metaphytes. Further, this approach offers a likely explanation for the sudden radiation of both groups in comparison to the gradual modernization of unicellular autotrophs, which required hundreds of millions of years of Precambrian time.

CROPPING AND DIVERSITY

The relevant ecologic principle, apparently first formulated for multispecific situations by Paine (9), holds that the addition of a trophic level to a given food web tends to promote increased diversity at the next lower trophic level. Increase in diversity at an existing level can have the same effect. This generalization has recently gained strong support from experimental and theoretical studies on the effects of cropping. Field experiments have shown, for example, that removal of the chief natural carnivore of an intertidal community produces a drastic reduction in herbivore diversity by permitting one superior competitor (a mussel) to monopolize space (9). Similarly, introduction of predatory fish to an artificial pond has led to increased zooplankton diversity (10). Lower in the food web the same effect is seen. Removal of grazing sea urchins from multispecific communities of benthic algae has led to dominance by a single algal species (11). There is also evidence that the grazing of diverse herbivores on seeds and seedlings in tropical forests has contributed to the high diversity of trees because many herbivores tend to feed on high-density populations, which naturally occur near parents; increased dispersion and reduced density of populations has then permitted a large variety of tree species to coexist within habitats (12). Even in the deep sea, remarkably intense predation appears to contribute to the characteristically high diversity of benthic life (13).

Phillips (14, 15) has provided a mathematical analysis of the cropping phenomenon. His theory, which applies to simple well-mixed aquatic systems containing plankton, is particularly applicable to Precambrian aquatic communities of unicellular autotrophs. The theory assumes a region of finite volume, with spatially uniform populations that react to variations in nutrient supply at rates that are slow relative to their own rates of reproduction. Under these conditions, it turns out, the number of species at equilibrium must be equal to or less than the number of removable nutrients, and for every species there will be at least one domain of values of removable nutrients in which only this species will grow. Under most conditions the system will be stable. In a stable system, change in rate of supply of certain nutrients will cause a decrease in the number of species surviving. Introduction of herbivores changes the system drastically. With cropping, the competitive exclusion principle fails, and a much greater diversity of producers is possible. Although the exact predictions of this theoretical model must be expected to differ somewhat from events in natural systems, where the assumptions will be violated to varying degrees, the experimental evidence cited above indicates that the cropping principle holds for systems in general in at least a qualitative way. Furthermore, the single-trophic-level systems of the Precambrian would seem to approximate the uncropped system of Phillips far better than present-day natural systems, in which cropping is nearly universal. Polluted, eutrophic systems form perhaps the best modern examples.

THE DELAY OF HETEROTROPHY

The Precambrian trend from simple producer communities to producer–herbivore and producer–herbivore–carnivore communities can be viewed as a long-term natural cropping experiment resembling those performed by living ecologists. The following scenario can be envisioned:

Since we are considering the original adaptive radiation of eukaryotic life, initial diversity was very low. We have good evidence that planktonic eukaryotic autotrophs were well established by 1300 million years ago, and it seems reasonable that similar benthic forms were also present, although they were clearly subordinate to blue-green algae (3, 17). As both habitat groups of autotrophs developed, they must rapidly have attained quite substantial biomasses, for in the absence of cropping, abundances would have been limited only by environmental resources, including light, space, and nutrient supply. Blue-green algae, having evolved first, apparently tended to exclude early eukaryotes from benthic settings (17). The fact that well-preserved floras contain fewer planktonic than benthic species, although the former are largely eukariotic (17), probably reflects the greater uniformity of the pelagic realm. There has been much debate about the relationship between food web complexity and stability (16), but as Phillips (14) has shown mathematically, a simple aquatic producer system of the type just described should have been relatively stable. Not only would within-habitat diversity have been constrained, with relatively few species dominating, but like modern unicellular aquatic forms, most species must have had broad geographic distributions. Even freshwater and marine forms were probably quite closely related, as they are today (18). In short, worldwide diversity must have been extremely low, especially for the dominantly planktonic eukaryotes. We can envision an all-producer Precambrian world that was generally saturated with producers and biologically monotonous. Morphologic diversity must also have been suppressed, for speciation can occur only in the presence of available niches. Rates of speciation must have been very low relative to those that have characterized more modern multitrophic communities. Speciation events may have been confined largely to replacement of lineages terminated by extinction, but low worldwide diversity must have made even these events very rare. Gradual changes may have occurred within species as adaptations for more efficient exploitation of their existing niches, but such changes also could only have produced slow differentiation. Even if metaphytes had somehow appeared before the advent of cropping, their diversification too would have been greatly restricted. Heterotrophs had to appear before resource limitation could be relieved and diversification accelerated. The important point is that the changes required to produce unicellular heterotrophs, to say nothing of metazoans, had to arise slowly because diversification was so slow. The self-limiting nature of this system would seem to account for the impoverished nature of eukaryote floras of Bitter Springs age and for the delay in origin of metaphytes, as well as heterotrophs.

When they finally arose in the late Precambrian (we do not know the exact time), cell-eating heterotrophs may have fed on bacteria. There would seem to have been no distinct barrier to feeding on algae, however, as the ability to ingest larger food particles evolved. The first algae-eaters must have relieved resource limitation of algal growth in certain habitats, although modern animal-like protists cannot ingest some kinds of benthic algal cells, and they are also relatively unsuccessful as zooplankters, even in lakes (18). One might suggest that, in the initial absence of carnivores, the diversification of algae-eaters and rise of carnivores might have been suppressed in a way parallel to the earlier suppression of

autotroph diversification. The difference is that no marked change was required in certain heterotrophic groups to permit them to develop carnivorous habits. Feeding on unicellular heterotrophs differs little from feeding on unicellular autotrophs, and many living protist groups (especially ciliate taxa) do both (19). The Flagellata, generally regarded as the ancestral protists, include a very limited variety of free-living heterotrophs today (20). Presumably the origin of the Ciliata was an important step in diversification.

Thus, the adaptive breakthrough to algal feeding, when it finally came, rapidly led to the addition of successive trophic levels. Not only autotrophs, but also heterotrophs below top carnivore levels were permitted to diversify. A key point is that, in general, diversification at any trophic level promotes diversification, not only of the level below by cropping, but also of the level above by providing more feeding options. Thus, when one trophic level diversifies, a mutual feedback system is set up with both super- and subadjacent trophic levels. In diverse communities this system is damped. When algae-eating protists first arose, however, self-propagating systems of this type, operating in numerous azoic environments, must have produced explosive rates of evolution. Rapid advancement to multicellularity must also have ensued. Whether they arose slightly earlier or slightly later than metaphytes, metazoans must have played a crucial role in permitting metaphytes to differentiate, for protists could not have grazed effectively on metaphytes. Being more efficient algal grazers than animal-like protists, metazoans probably fostered even greater diversification of unicellular algae as well. The earliest metazoans must have been herbivores that fed on unicellular taxa. Like herbivorous protists, however, such creatures intergrade with carnivores. In fact, many extant species of the Coelenterata and Rotifera, which perhaps represent levels of organization not far removed from late-Precambrian metazoans, are difficult to classify unequivocally as suspension feeders or carnivores.

INDEPENDENT EVIDENCE FROM STROMATOLITES

To test the above arguments we can consider what fossil evidence exists, in addition to that already cited, indicating limitation of Precambrian algal growth by resources rather than by cropping. Dominantly planktonic assemblages like the Bitter Springs flora represent unusual preservation conditions and are too rare to provide useful data for this purpose. The most abundantly fossilized Precambrian producer communities are those forming stromatolites (laminated sedimentary structures produced chiefly by blue-green algal mats that trap and bind sediment). Stromatolites were in fact extremely widespread in the Precambrian, living in a wide range of intertidal and subtidal marine environments. Garrett (21) has convincingly argued that their rapid decline at the start of the Phanerozoic was a result of their destruction by grazing and burrowing animals. Taxa with the potential to form stromatolites have persisted, but in greatly reduced biomass. Today they are able to flourish well enough to form stromatolites only in hostile environments, like hypersaline lagoons and some supratidal areas that are largely devoid of metazoans. Garrett found experimentally that persistent mats formed in more hospitable environments only when metazoan grazers and burrowers were excluded. Also where surficial mats were forming naturally, introduction of grazing snails resulted in their destruction. Garrett

concluded that marine blue-green algae grew rampantly in the Precambrian because of the absence of metazoans (most species that form stromatolites, being filamentous and covered by a mucilaginous sheath, are inedible to unicellular herbivores). After the origin of eukaryotic organization, blue-green algae were relegated to an unimportant role in the diversification of plant life. Nonetheless, their abundant growth throughout the Precambrian provides strong evidence that they and other photosynthetic autotrophs saturated aquatic environments until very late in the Precambrian, being limited only by resources, including nutrient supply. In fact, the period during which only prokaryote life existed may have been prolonged by the total absence of cropping, just as eukaryote diversification was later delayed.

DISCUSSION

In summary, the explosive radiation of life in the late Precambrian (giving rise to our distinction between the Precambrian and the Phanerozoic) was produced by a kind of self-propagating mutual feedback system of diversification between trophic levels, which was initiated by the advent of heterotrophy. The nearly simultaneous origin and explosive radiation of heterotrophic protists, metaphytes, and metazoans were inevitable. In contrast, the self-limiting, saturated autotrophic system of the earlier Precambrian had strongly inhibited diversification, to delay crossing of the "heterotroph barrier" for hundreds of millions of years.

The seemingly explosive appearance of skeletons, giving rise to the diverse fossil record of the Cambrian, was no more sudden than the rest of the radiation, which apparently produced most currently recognized multicellular phyla during only a few tens of millions of years. Although earliest appearances of fossil taxa are difficult to delimit precisely because of the limitations of preservation and stratigraphic correlation, it seems that most phyla known from the Cambrian appeared during the first 10 million years or so of the period (22). Some of these may have arisen as soft-bodied taxa in the late Precambrian. Many important phyla and classes did not contribute to the known fossil record until later Cambrian or Ordovician time. Skeleton formation was, in fact, probably in part a response to predation pressure, as Hutchinson and Brooks each suggested (23). Furthermore, the overall rate of diversification, which, after all, was operating during the invasion of previously vacant adaptive zones, was not inordinately high. For comparison, it is worth noting that most major types (i.e., orders) of Cenozoic placental mammals, from bats to whales, arose during a period of only about ten million years (24).

The theory presented above has four attractive features: first, it seems to account for what facts we have about Precambrian life; second, it is simple, rather than complex or contrived, as some earlier explanations have tended to be; third, it is purely biological, avoiding *ad hoc* invocation of external controls; and fourth, it is largely the product of direct deduction from an established ecological principle.

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