

The Cambrian Explosion: macroevolution and biomineralization

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Abstract

Recent advances in our understanding of the Cambrian evolutionary diversification event (Cambrian Explosion) show that although eumetazoan stem taxa were present in the late Proterozoic, a tremendous burst of macroevolutionary change occurred near the beginning of the Cambrian. Explanations relying on paleoecological feedback are insufficient to explain the macroevolutionary patterns observed, particularly those associated with the near-simultaneous appearance of new higher taxa. The diversity of biomineralization types among the small shelly fossils of the early Cambrian Period can be explained if putative ancestral scleritome bearers (found in both Proterozoic Eon and Cambrian Period strata) had, as some new data suggest, intact scleritomes that hosted individual sclerites of varying biomineral composition.

Keywords: *Cambrian Explosion, metazoa, macroevolution, adaptive radiation, arthropoda, Chordata*

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1. Introduction

The Ediacaran–Cambrian eumetazoan diversification event, also known as the Cambrian Explosion (541 Ma), is responsible for the cardinal division in the geological time scale. The event remains one of the key milestones in the history of life. Although commonly viewed as extending out over some tens of millions of years (with the Ordovician Period diversification viewed as an extension of the Cambrian event), both theoretical considerations and the fossil records suggest an abrupt event (no more than 5 million years long) that generated most of the living (and a few now extinct) eumetazoan phyla and classes. An important new development has been the recognition that true eumetazoan representatives, albeit from stem clades rather than from crown groups representing modern phyla, are indeed present in the late Proterozoic Era, and that in fact, some of these ancient taxa had weakly mineralized scleritome exoskeletons.

2. Animal origins

In a mismatch between “rocks and clocks”, the molecular clock age of animal origins has been estimated at Tonian Period or Cryogenian Period age (850–650 Ma), whereas the animalian fossil record begins only at around 580 Ma [1]. A recent reinterpretation of putative keratose sponge fossils and thrombolites from the 890 Ma Little Dal reefs of the Stone Knife Formation, Canada, as metazoan trace fossils [2] implies an origin of animals well before the Sturtian Snowball Earth glaciation of 720–635 Ma [3]. In the Kris and McMenamin [2] interpretation, the microburrows and burrow clotting in

thrombolites are the earliest evidence for eumetazoan animal (and, any animal, for that matter) life. If this interpretation stands [4], then the origin of animals dates back to the time of Rodinia (ca. 890 Ma), which is a closer match to the molecular clock age range (890–850 = 40 Ma) than is the current mismatch on the other end of the interval (650–580 = 70 Ma). Animals, thus, may be very ancient indeed, which begs the question of why it took so long from the origin of animals until the Cambrian Explosion (890–541 = 349 Ma). More than a third of a billion years may have elapsed between the origin of animals and the Cambrian Period diversification event.

3. Biomineralization variations of the scleritome

An important recent development has been the discovery of metazoan scleritomes in Proterozoic strata. Intact scleritomes of two Ediacaran metazoa, the kimberellomorph *Zirabagtaria ovata* and the stem aculiferan *Korifogrammia clementensis*, plus an isolated sclerite from a second stem aculiferan (*Clementechiton sonorensis*), were found in the ca. 580–555 Ma Clemente Biota of the Clemente Formation, Sonora, México [5]. The presence of Proterozoic scleritomes was later confirmed by the reinterpretation of the Ediacaran *Corumbella* as having a cataphract aragonitic skeleton [6]. Osés et al. [6] determined that the original skeletal composition was aragonitic due to elevated Sr content and patches of original aragonite mineralogy. Preliminary analysis of the *Zirabagtaria ovata* holotype shows a

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bilaterally symmetric, U-shaped pattern in the Fe content of the fossil surface (presumed here to reflect the original sclerite composition; **Figure 1**), suggesting that, as is the case for many modern mollusks, the scleritome consisted of both high-Fe and low-Fe content sclerites. The scaly-foot gastropod or volcano snail (*Chrysomallon squamiferum*), with its curious pyrite and greigite sclerites [7], represents a criterion modern example.

Variations in sclerite composition are currently underappreciated in Cambrian scleritomes. These can vary from phosphatic to calcitic [8]. Tommotiids such as *Lapworthella* and *Canadiella* are generally considered to have hydroxyapatitic (i.e., phosphatic) sclerites. However, an unnamed sclerite observed in petrographic

thin section (**Figures 2 and 3**), while resembling *Canadiella filigrana* that occurs in the same strata [9], had a strictly calcareous composition. This calcareous fossil may represent a new genus or even family of tommotiid. This is no surprise, as early brachiopods (presumed descendants of tommotiids) can have either phosphatic or calcareous valve compositions. The interesting possibility exists that the isolated sclerite shown in **Figures 2 and 3** is, in fact, conspecific with the phosphatic sclerites of *Canadiella filigrana*; in other words, the species had both phosphatic (**Figure 4**) and calcareous elements in its scleritome. These fossils have been recovered from the continuous Proterozoic–Cambrian Cerro Rajón stratigraphic sequence of northwestern Sonora, México (**Figure 5**).

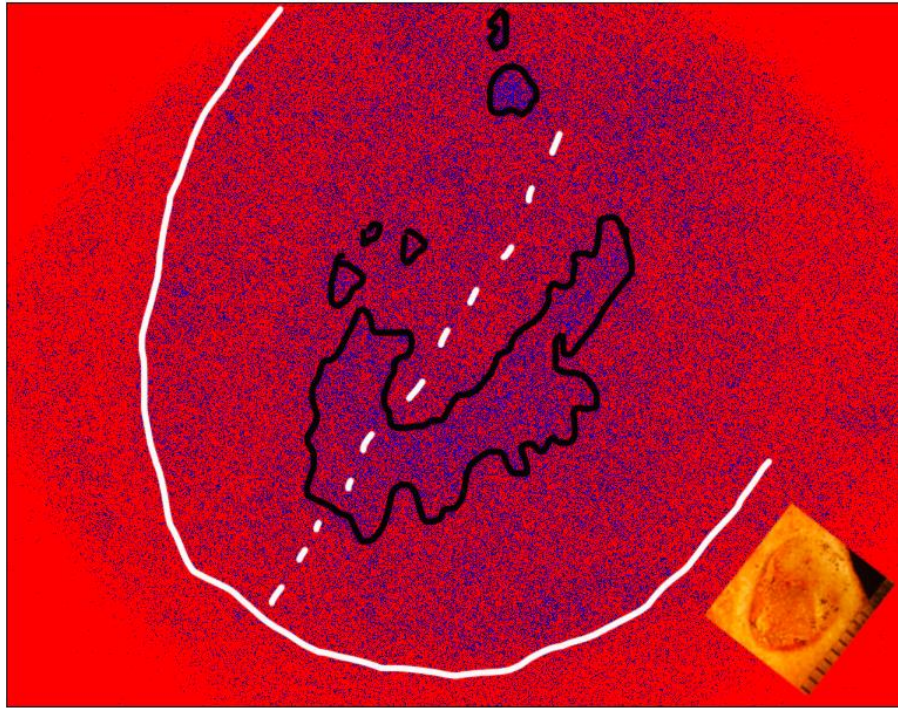


Figure 1 • *Zirabagtaria ovata*. Energy dispersive spectrometer (EDS) element map of the surface of the holotype showing a U-shaped band (outlined here in black) of Fe-enriched sclerites. White line = Outer perimeter (posterior region) of fossil; dashed white line = Axis of bilateral symmetry. Inset shows a reflected light image of holotype (Clemente Formation, field sample 6 of 3/16/95; IGM 4995). Scale bar on inset in millimeters.

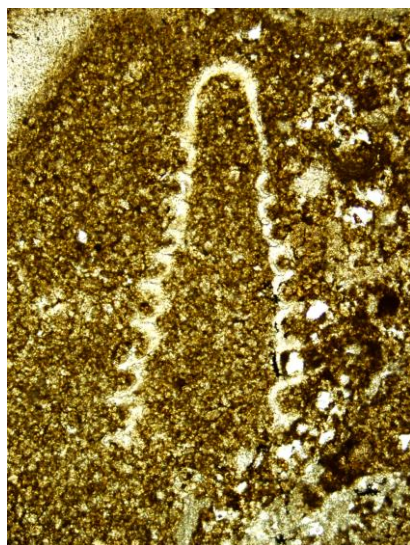


Figure 2 • Unnamed calcareous sclerite in thin section. Type B sclerite. Archaeocyathan–calcimicrobe limestone, field sample MM-82-51a, IGM 7459a, Cerro Rajón, Sonora, México. Preserved length of sclerite is 1.4 mm.

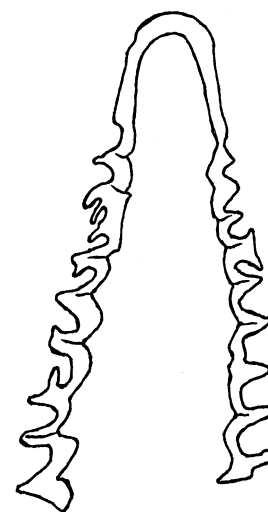


Figure 3 • Sketch of fossil in the previous image. Preserved length of sclerite is 1.4 mm.

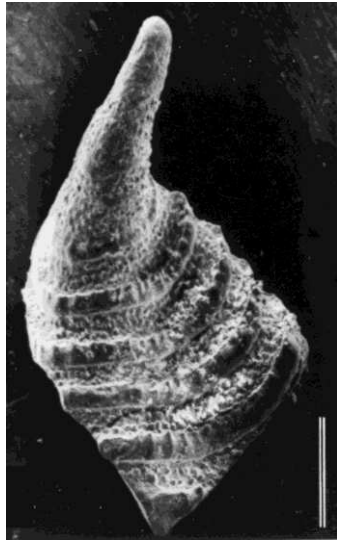


Figure 4 • *Canadiella filigrana*, phosphatic Type B sclerite scanning electron microscope (SEM) photomicrograph showing finger-like apex. Puerto Blanco Formation (unit 3), northwestern Sonora, México, field sample 7c of 12/17/82, IGM 3614(9). Scale bar = 0.25 mm.

4. Review of selected Proterozoic–Cambrian animal groups

4.1. Annelida

One Proterozoic bilateralomorph that may represent an annelid is the tomopterid *Vendamonion truncata* from the Clemente Formation of Sonora, México [5]. The genal spine-like cheek

spines and bifurcated appendages of the modern *Tomopteris* indicate an ancient bauplan that likely predates the basal Cambrian boundary.

4.2. Archaeocyaths

Archaeocyaths are poriferan-grade skeletonized organisms of still uncertain affinities. Although many researchers now place them with the sponges, this may be more conventional than an actual reflection of phylogenetic affinities. Alternate proposals, such as the concept that archaeocyaths occupy an intermediate grade (“archaeozoan” grade; [10]) between poriferan grade and metazoan grade, deserve serious consideration. Archaeocyaths originated on the Siberian platform during the Tommotian Age (Cambrian Stage 2) (525 Ma; [11]) and then underwent the greatest genus-level diversification in the history of life, with hundreds of genera present worldwide by the Atdabanian Age (Cambrian Series 2, Stage 3, ca. 520 Ma). Archaeocyaths experienced a comparably steep decline by the Toyonian Age (516 Ma). The key to understanding the unique archaeocyath body plan (cup-shaped skeleton, conical central cavity, and inner and outer walls with pores and shelves of different types) is to note that they often managed to increase flow through the inner wall by developing large-diameter inner-wall tubes (ethmophyllid archaeocyaths such as *Aulocricus arellani*; [12]) or by double rows of pores in the inner wall, as in *Markocyathus*. Preventing stagnation in the inner cavity was, thus, at a premium. Spinose archaeocyaths such as *Yukonensis* suggest that by the Atdabanian–Botomian time, these sessile filter feeders were already experiencing sufficient macropredation pressure to require protective measures by means of morphological elaboration.

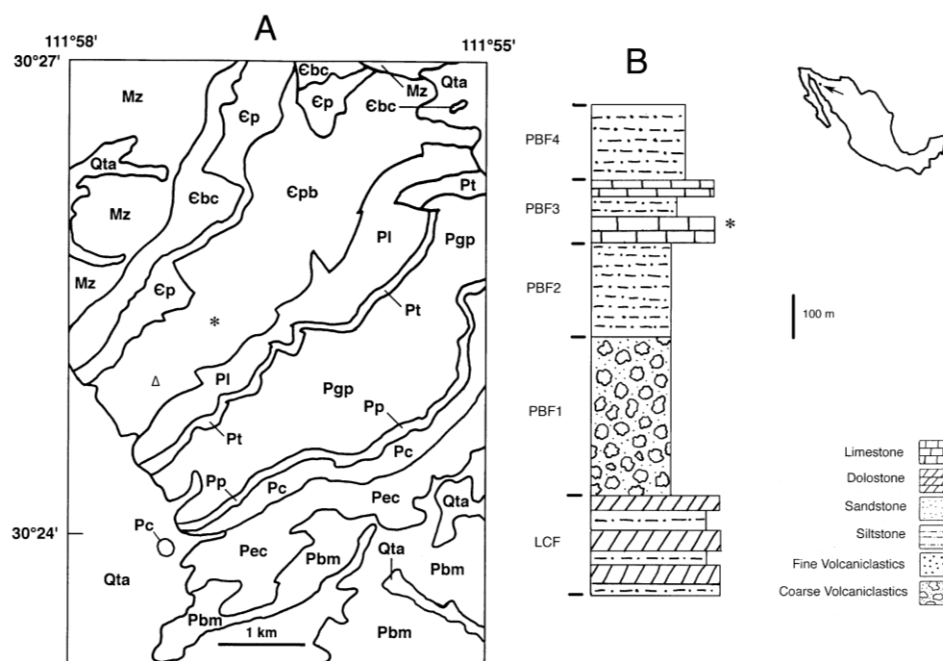


Figure 5 • Geologic map and generalized stratigraphic column for the fossil locality. A. Geologic map showing the southern Cerro Rajón, Sonora. Fossil locality MM-82-51a is shown as a star. Rock units shown on map are as follows: **Pbm**, Precambrian basement and metamorphic rocks; **Pec**, El Arpa and Caborca Formations; **Pc**, Clemente Formation; **Pp**, Pitiquito Quartzite; **Pgp**, Gamuza and Papalote Formations; **Pt**, Tecolote Quartzite; **Pl**, La Ciénega Formation; **Epb**, Puerto Blanco Formation; **Ep**, Proveedora Quartzite; **Ebc**, Buelna and Cerro Prieto Formations; **Mz**, Mesozoic sedimentary, volcanic and igneous rocks; and **Qta**, Quaternary and upper Tertiary alluvial deposits. B. Stratigraphic column of the Proterozoic–Cambrian boundary interval in the southern Cerro Rajón, Sonora. Fossil locality MM-82-51a is indicated with an asterisk. PBF is an abbreviation for Puerto Blanco Formation. Inset map shows the location of the site (arrow) with respect to the map of México.

4.3. Arthropoda

The bilateralomorph that most resembles crown arthropoda is *Palankiras palmeri* from the Proterozoic of Sonora, México [5]. It has a remarkable resemblance (ball-shaped glabella, curved-spike genal spines, and reduced pleural region, sometimes referred to as “fish skeleton” body plan) to cheiruriform trilobites, such as *Deiphon forbesi* from the Silurian of St. Iwan, Bohemia, and to the giant lichid trilobite from the Devonian *Terataspis grandis*. *Terataspis* and *Deiphon* have comparable body forms but are not closely related trilobites, so the resemblance is either due to homoplasy or, more likely in my opinion, shared derivation from a common palankirid ancestor. Parallel evolutionary atavism can, of course, be considered a type of convergent evolution. *Yilingia spiciformis*, although younger (551–539 Ma) than *Palankiras*, is a remarkable trilobate bilaterian that is particularly unique in having a mortichnium associated with its holotype [13]. *Yilingia* shows evidence for directional locomotion. Segment polarity and directional locomotion that would be consistent with interpreting *Yilingia* as a stem arthropod. The earliest trilobites (520 Ma) are ptychopariid bigotinids and redlichiids from Asia [14]. The first trilobites appear in Western North America in Adtabanian Age-equivalent rocks (Cambrian Series 2, Stage 3, ca. 517 Ma) of the Esmeralda Basin of western Nevada, USA [15]. This fauna includes the trilobite genera *Amplifallotaspis*, *Fritzaspis*, and *Repinaella*. Bivalved arthropods of various types and sizes, including *Pseudoarctolepis sharpi* of the House Range, Utah [16] and the rapidly diversifying bradoriids [17], make a prominent entrance during the Cambrian event. The most striking of these is the giant bivalved hymenocarine arthropod *Balhuticaris voltae* from the Burgess Shale [18].

In terms of synecology, radiodonts such as *Anomalocaris* and *Peytoia* are thought to be the keystone predators in the Cambrian marine ecosystem [19]. Discovery of the impressive *Titanokorys gainesi*—a hurdiid radiodont from the middle Cambrian—has added a large (50 cm long) new member to the Burgess Shale fauna [20]. Some of the fossilized damage to prey that had been attributed to radiodonts may, in fact, be due to trilobites (*Redlichia rex*; [21]).

4.4. Bivalvia

Bivalved mollusks make a rapid appearance during the Cambrian Explosion, including presumed stem taxa such as *Anabarella*, *Fordilla*, *Pojetaia*, and *Watsonella*, with four Cambrian genera thought to possibly be members of crown group Bivalvia (*Arhouriella*, *Buluniella*, *Camya*, and *Tuarangia*; [22, 23]). All are presumed to have had originally calcareous valves.

4.5. Bryozoa

Long thought to be the one major Paleozoic marine invertebrate phylum that did not appear during the Cambrian Period, instead appearing later in the first part of the Ordovician Period, bryozoans (or at least stem-group bryozoans) have now been reported from Cambrian strata. *Protomelission gatehousei* is a stem bryozoan from the Cambrian of South China and Australia [24]. The zooids of *Protomelission* look convincingly bryozoan. A second possible Cambrian bryozoan (Harkless Formation, Cambrian Age 4) is claimed to be the oldest fossil of a mineralized (palaeostomate) bryozoan [25],

but the tubes of this putative bryomorph are very thin, and the fossil is thus subject to other interpretations. Brachiopod and mollusk biomineralization is considered to be an evolutionarily conserved process that was lost in the phoronid–bryozoan stem lineage [26].

4.6. Brachiopoda

The oldest brachiopods are from the basal Tommotian (Terreneuvian, Cambrian Stage 2) of Siberia and consist of paterinid brachiopods [27] belonging to the species *Aldanotreta sunnaginensis*. Halkieriids first appear in the Fortunian (Terreneuvian) of the first part of the Cambrian. Related cataphract skeleton bearers such as tommotiids are thought to be ancestral to the brachiopods, rendering a phylogenetically telescoped sequence lasting only about 7 million years from the origins of the halkieriids/tommotiids (535 Ma) to the origin of brachiopods (528 Ma). The derivation of brachiopods from a tommotiid ancestor is a widely held view that involves two main hypotheses. The first hypothesis is known as the brachiopod fold hypothesis (BFH). In this scenario, a halkieriid/tommotiid with enlarged sclerites as head and tail shields folds in half to form the first brachiopod. The *Mickwitzia* stem brachiopod serves as an intermediate step between the two end members of the BFH. An alternate hypothesis, the scleritome tube hypothesis (STH), holds that brachiopods originated from a tube-like tommotiid with a tubular scleritome. The scleritome underwent sclerite reduction to become a bivalved brachiopod.

4.7. Chordata

A remarkable thing about early chordates, and indeed all early deuterostomes, is that not a single unambiguous deuterostome has been reported from rocks older than the base of the Cambrian Period. As such, they provide a unique signature of the Cambrian Explosion and (unlike the total group Animalia) can rightly be thought to have had an evolutionary origin at or near the beginning of the Cambrian. The deuterostome body plan is in stark contrast to many protostomes, with a gut that runs backward (with respect to the protostome condition as traditionally understood), and a body plan that is essentially upside down (with a dorsal as opposed to a ventral nerve chord).

A challenge to Cambrian chordate research is that the most taxonomically significant features (except for the notochord and myomeres) tend to be the ones that decay most rapidly. Key apomorphies thus rot away, resulting in “stemward slippage”, meaning that a particular fossil organism appears more “primitive” than it actually is, because the relevant derived characters are not preserved [28]. Nevertheless, the Cambrian fossil record records cephalochordates, urochordates, and even vertebrates as well as the bizarre vetulicolians [29].

Well represented in the Chengjiang Lagerstätte and other Cambrian deposits, deuterostomes undergo an explosive radiation near the base of the Cambrian, as shown by the appearance of the cambroernids (an extinct clade consisting of *Eldonia*, *Phlogites*, and *Herpetogaster*); hemichordates (acorn worms and graptolites); vetulicolians (the enigmatic group with a tadpole-shaped *baiüplan*), echinoderms, and chordates. Early jawless fishes from the first-half of the Cambrian are represented by *Myllokunmingia* and *Haikouichthys*. *Metaspriggina* and the famous *Pikaia* occur in middle Cambrian strata. *Metaspriggina* was initially mistaken as an

Ediacaran survivor, and hence its genus name has been derived from *Spriggina*. *Metaspriggina* has eyes and nostrils, a notochord, a cranium, pharyngeal bars or gill bars of cartilage, and W-shape myomeres with an additional chevron that allows direct comparisons with modern fish. The gill bars in *Metaspriggina* are a crucial feature that may, in fact, serve to help define the crown craniate–cephalochordate clade. The list of vertebrate features in *Myllokunmingia* is extensive: craniate condition, notochord, distinct head region, pericardial cavity with pharynx, cartilage internal skeleton, myomeres with chevrons, dorsal fin, and a *paired* ventral fin.

Yunnanozoans, represented by soft-bodied fossils from the early Cambrian, have recently been reinterpreted as early vertebrates by Baoyu Jiang and coauthors [30] at Nanjing University. These exquisite bilaterian fossils, abundant in the Chengjiang biota (Cambrian, *ca.* 518 Ma) of China, show characters such as early evidence for a pharyngeal arch skeleton consisting of cellular cartilage. But, in spite of these features that may be precursors to the skull and jaw, yunnanozoans appear to lack a notochord. Myomeres are also absent from the yunnanozoan *baüplan*, placing these creatures in a crucial stem position with regard to the crown craniate–cephalochordate clade. Myomeres have been described from another bilaterian deuterostome from the Chengjiang biota, *Shenzianyloma yunnanense* [29]. *Shenzianyloma* is assigned to the Vetulicolia—a likewise enigmatic group of chordates. Few of these early forms manifest biomineralization, which finally appears in the Chordata with development of dermal armor in Cambro-Ordovician ostracoderms [31].

4.8. Ctenophores

The Chengjiang biota of China (Cambrian Series 2) has yielded five genera of skeletonized comb jellies (scleractenophores) [32]—an interesting case of biomineralization in a diploblastic phylum.

4.9. Echinodermata

Echinoderms, minimally defined as eumetazoan deuterostomes with (strictly calcite in composition) stereom skeleton, are known only from Cambrian Period and later rocks. After chordates, they are the second largest group of deuterostomes. The oldest known echinoderm is the soccer ball-like, globular *Sprincrinus inflatus* from the lower Poleta Formation, White-Inyo Mountains, California (early Cambrian; *Avefallotaspis maria* zone; [33, 34, 10]). A striking feature of Cambrian echinoderms is the appearance of helical plating in forms such as *Helicoplacus*. Interestingly, eocrinoids such as *Guizhoueocrinus yui* may develop a type of crypto-helical plating [35]. The synecological relationships of Cambrian echinoderms are becoming clearer with new discoveries. For example, eocrinoids [36] have been found with their stalks attached to the helens of hyoliths (Kaili Formation, Guizhou, China; [37]).

5. Feeding strategies and paleoecology

The long-standing debate over the feeding strategies of the Ediacaran creatures has recently focused on four possible solutions to the problem: osmotrophy, chemoautotrophy, filter feeding, and mixotrophies (that may have included photosymbiosis). The recent discovery that a diverse Ediacaran assemblage could survive in low oxygen conditions indicates that at least some Ediacarans had a lifestyle that was facultatively

anaerobic [38]. Biogeochemical challenges such as sulfide accumulation in tissue could have been solved in Ediacarans by symbiosis with sulfur-oxidizing bacteria [39].

6. The untenability of the ecological feedback hypothesis

Stromatolites have witnessed the entire history of life on our planet [40, 41]. Stromatolites are not fossils of individual organisms but rather “organosedimentary structures” built by communities of microbes. A variety of different microbes can participate in the construction of a single stromatolite, although communities are usually dominated by a few types of cyanobacteria. The stromatolite-building microbes can be thread like (filamentous) or spheroidal (coccoid) in morphology. These morphologies are best observed in petrographic thin sections of silicified stromatolites, where individual microbes can be observed as well as stacked layers of fossilized biofilms that constituted the upper surface of the stromatolite. Biofilms and biomats have dominated the sea floor for most of the Earth’s history, extending from the origins of life on earth to the present day.

Destruction of the marine biomats by grazing metazoans has frequently been invoked as a causal explanation for the Cambrian Explosion. The basic scenario is as follows: Grazing metazoans such as *Kimberella* and *Dickinsonia* left linear scars (using rudimentary radulas) or digested oval holes, respectively, in the biomat, thus weakening the felt-like film and leaving it vulnerable to shredding by sea floor currents. A byproduct of this effect was the genesis of flat-pebble conglomerates—a sediment type that is best known from marine strata of late Proterozoic to Ordovician age. In a way similar to the way that suspended sediments can become a haven for microbes, flat-pebble conglomerate clasts (with their relatively high surface area) became havens for burrowing and boring organisms. Recent advances now permit the recognition of burrows *versus* borings in flat-pebble conglomerate intraclasts [42].

The resultant clouds of sediments (no longer held down by intact biomat) dispersed through the water column provided dramatically enhanced surface area for the cultivation of microbes such as marine bacteria. This, in turn, led to a massively expanded food source for metazoans, who rushed in to take advantage of the bonanza by means of filter and suspension feeding. Then, this subsequently drove a macroevolutionary diversification that led in short order to the appearance of 40 to as many as 100 (depending on who is counting) eumetazoan phyla, many of which are still with us today.

The problem with this scenario is that even with the putative major expansion in suspended marine food resources, filter feeding was already well established in Proterozoic time (indeed, it, alongside grazing [43], is perhaps the “easiest” trophic strategy in marine waters), and it seems unlikely that even a massive increase in suspended food could, by itself, drive the appearance of dozens of new eumetazoan phyla in such a relatively short interval of geological time. The fossil record shows macroevolution in high gear, complete with phylogenetic telescoping, instead of what might have been expected to be a relatively modest expansion of new taxa (at the taxonomic level of, say, family or order) accruing from an expansion of marine trophic resources in the water column. Thus, the ecological feedback hypothesis (where new predators capitalize on the new, and newly abundant filter feeders)

seems insufficient to explain the outpouring of new higher taxa. Some other factor must be at work.

7. Conclusions

Recent data and new interpretations suggest that the Cambrian Explosion, rather than representing the initial appearance of animals as once thought, occurred hundreds of millions of years after the origin of animals, with origination occurring as far back as 890 Ma. As shown above, advances in our understanding of the Cambrian evolutionary diversification event (Cambrian Explosion) show that although eumetazoan stem taxa were present in the late Proterozoic, a tremendous burst of macroevolutionary change occurred at near the beginning of the Cambrian. Explanations relying on paleoecological feedback may well be insufficient to explain the macroevolutionary patterns observed, particularly regarding those associated with the near-simultaneous appearance of new higher taxa. The diversity of biomineralization types among the shelly fossils of the early Cambrian can be explained if putative ancestral scleritome bearers (found in both Proterozoic and Cambrian strata) had, as some new data suggest, intact cataphract skeletons that held individual sclerites with a variety of biomineral compositions.

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