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Not armour, but biomechanics, ecological opportunity and increased fecundity as keys to the origin and expansion of the mineralized benthic metazoan fauna

BERNARD L. COHEN*

IBLS, Division of Molecular Genetics, University of Glasgow, Pontecorvo Building, 56 Dumbarton Road, Glasgow G11 6NU, Scotland, UK

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This paper offers a new biotic interaction hypothesis for the Cambrian ‘explosion’ of mineralized, benthic, metazoan diversity. It proposes that organic-mineral composite structures (e.g. shells and muscle lever-arms) originated in Proterozoic lineages of primary larva-like, but reproductively competent, pelagic bilaterians because mineralization was both mechanically and energetically favourable, *not* because it provided armour against predation. Increased strength and rigidity of composite structures permitted growth to sizes incompatible with a continued pelagic existence, while the increased density resulting from massive mineralization facilitated settlement into, and stability in, a nutrient-rich, Proterozoic benthic zone that offered new ecological opportunities. Because evolutionary success is recognized by the formation of recoverable fossils, which requires large, enduring populations, successful lineages are those that responded to the new opportunities by achieving broad niche occupancy through the evolution of metamorphosis to larger, mineralized ‘adult’ body forms with more efficient food-collecting apparatus and higher fecundity. Niche modification (e.g. reef and shell-bed formation) by early mineralized benthic settlers may have increased the likelihood of further successful settlement, leading to the appearance of a period of ‘explosive’ increase in benthic, mineralized, metazoan diversity. Predator-prey arms races may then have followed, causing early faunal turnover and possible selection for *improved* armour. © 2005 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2005, **85**, 483–490.

ADDITIONAL KEYWORDS: benthic settlement – Cambrian explosion – metamorphosis – organic-mineral composite.

INTRODUCTION

The rapid growth of massively mineralized, benthic-dwelling, metazoan diversity that appears in the Early Cambrian fossil record presents a problem that continues to excite interest and controversy (reviewed in Budd & Jensen, 2000). This problem resembles a jigsaw puzzle with pieces missing, shapes uncertain, interlocks ill-defined, and no authentic picture on the box. Accordingly, no definitive solution can exist. But any proposed solution that unites many pieces with little strain, while offering new perspectives (Kell & Oliver, 2003), may be an advance. Here, I propose one such solution.

FAUNAL BACKGROUND

The nature of the Proterozoic fauna is indicated by palaeontological and other evidence which strongly suggests that the earliest Proterozoic multicellular metazoans were pelagic heterotrophs, comparable in general form to extant primary larvae but reproductively competent (Jagersten, 1959; Nielsen, 1998) and that, by the Cambrian, much diversification had taken place in the pelagic realm, i.e. that a ‘slow fuse’ of diversification (Cooper & Fortey, 1998) preceded the onset of massive mineralization. This evidence includes the following:

1. Photosynthetic plankton were abundant in Early Proterozoic seas (e.g. Summons, Powell & Boreham, 1988; Brocks *et al.*, 1999).
2. Molecules of eukaryotic origin occur in marine deposits of c. 2700 Mya (Brocks *et al.*, 1999) and are

*E-mail: b.l.cohen@bio.gla.ac.uk

- abundant in the Middle Mesoproterozoic (Summons *et al.*, 1988).
3. The first eukaryotes appeared before 2100 Mya (Han & Runnegar, 1992), with unambiguous evidence of plant multicellularity and sexual reproduction *c.* 1200 Mya (Butterfield, 2000). The commonality of sexual reproduction implies that plant and animal multicellularity evolved roughly in parallel, placing the origin of complex metazoans before *c.* 1200 Mya.
 4. The Late Proterozoic to Early Cambrian fauna comprised protostomes, deuterostomes and multicellular animals of uncertain status (e.g. Cloud & Glaessner, 1982; Conway Morris, 1986; Bengtson & Zhao, 1997; Fedonkin & Waggoner, 1997; Cooper & Fortey, 1998; Jensen, Gehling & Droser, 1998; Xiao, Zhang & Knoll, 1998; Vannier & Chen, 2000; Erwin, 2001; Shu *et al.*, 2001; Zhang *et al.*, 2001; Lieberman, 2002; Xiao, 2002; Zhu, Zhao & Chen, 2002; Chen *et al.*, 2003; Zhang, Hou & Emig, 2003).
 5. In the Middle Cambrian Burgess Shale fauna, most individuals were unmineralized and not benthic (Conway Morris, 1986, 1992; Powell, Johnston & Collom, 2003).
 6. If microphagy of protists and other (by implication, pelagic) metazoans was primitive (Vermeij & Lindberg, 2000), the size of some Early and Middle Cambrian pelagic heterotrophs, e.g. *Isoxys* (Vannier & Chen, 2000), agnostid trilobites, and conodont organisms, implies that pelagic, metazoan prey of appreciable size had by then evolved.
 7. Although all such analyses may be controversial and some may be flawed (Graur & Martin, 2004), at least some careful molecular clock reconstructions place bilaterian diversification well before the time of the palaeontologically visible 'explosion' (e.g. Knoll, 2003; Levinton, Dubb & Wray, 2004). Fossil evidence for bilaterian metazoans ~50 Myr before the Cambrian has recently been presented (Chen, *et al.*, 2004).

While none of these facts individually is conclusive, taken together they support, and nothing excludes, the 'slow fuse' of Precambrian faunal diversification.

BIOMECHANICS, NOT PREDATION, ACCOUNTS FOR THE ORIGIN(S) OF MINERALIZATION

It has been argued that the massive mineralization of shells or other exoskeletal structures evolved as armour in response to predation (e.g. Vermeij, 1990; Bengtson & Conway Morris, 1992; Signor & Lipps, 1992; Bengtson, 1994; Marshall, 2003). But such a response would require expressed genetic variation that includes some predation-resistance due to shell, to mineralization, or to both. Thus, epigenetic path-

ways to mineralized structures would necessarily have preceded predation; at most, predation might have selected for genetic assimilation (Waddington, 1953, 1957) of pre-existing, rarely expressed, traits capable of leading to mineralized armour.

Moreover, it seems implausible that predation pressure could select for the *de novo* formation of so complex and integrated a set of traits as the expression of mineralization pathways and the formation of developmentally organized armour. Because organisms are functionally integrated wholes, the primary role of mineralization should more plausibly have involved some more basic, integrated physiological function(s). Brachiopods, which were among the earliest mineralized animals and are therefore highly relevant, provide evidence for what this may have been. In ontogeny, the earliest reinforcement of the mantle epithelium is by ectodermally secreted organic polymers (Cusack, Williams & Buckman, 1999). Not only do such unmineralized primary mantle 'shells' occur today (Yatsu, 1902), but comparable structures are revealed in Early Palaeozoic fossils by virtue of the surrounding, ontogenetically later, mineralized shell (Williams *et al.*, 1992, 1994, 1998a, b; Williams, 2003).

That the ontogenetically earliest brachiopod shells are and were unmineralized, coupled with the presence of muscle insertions (Williams *et al.*, 1997), identifies two potentially powerful selective forces that could favour *ab initio* mineralization. First, the plasticity of organic mantle reinforcement implies limits to the strength of inserted muscles and the lengths of muscle lever-arms, thus potentially restricting growth and functional morphology. Second, replacement of organic load-bearing structures by organic-mineral composites is both energetically (Palmer, 1992) and mechanically favourable (Currey, 1999), and the more massive the structure, the more important these properties: composite parts are cheaper, more rigid, and more durable.

The advantageous properties of organic-mineral composites can likewise account for the independent origins of massive mineralization in other phyla, e.g. stem-group arthropods, molluscs and echinoderms. They may also underlie the initiation of mineralization as support for extended feeding epithelia and three-dimensional porosity in corals and Proterozoic sponge-like organisms (Wood, Grotzinger & Dickson, 2002), respectively.

A further strong argument against massive mineralization as a protective response to predation applies if, as argued above, most precursors of mineralized lineages were pelagic. For such organisms, mineralization would have been an inappropriate response because other ways to deter or avoid predators (*viz.* distastefulness, aposematic signals, camouflage, invisibility, or active evasion) entail less radical life-history

consequences than the acquisition of high-density structures.

The long Phanerozoic record of drilling predation in brachiopod and other shells (Kowalewski, Dulai & Fürsich, 1998; Bengtson, 2002; Hua, Pratt & Zhang, 2003) is not evidence of selection pressure favouring *ab initio* shell mineralization, because both chemical and mechanical drilling mechanisms in predators imply the pre-existence in prey either of hard structures to be drilled, or of soft-tissue drilling by the same mechanisms (for which there is no evidence). Indeed, the apparently high prevalence of successful drilling in the early mineralized fossil, *Cloudina* (Hua *et al.*, 2003), can be taken as evidence that mineralization was *not* effective armour.

Together, these considerations indicate that massive mineralization originated in diverse lineages of pelagic bilaterians as a way to build larger, cheaper, and/or stronger body parts. Predation was not a primary driving-force for mineralization; armour can at most have been a secondary consequence of it. Further evidence for an early and fundamentally biomechanical role for tissue reinforcement is provided by diverse Lower Cambrian lobopodians (Hou *et al.*, 2004: figs 14.1–14.11), in which isolated sclerites are well positioned to accept limb muscle insertions on the otherwise soft body-wall.

MINERALIZATION, GROWTH AND SETTLEMENT

Unmineralized or lightly mineralized pelagic organisms sink (slowly) unless they possess buoyancy aids or swim upwards (Chia & Rice, 1978; McEdward, 1995; Herring, 2002; Huisman *et al.*, 2002). Mineralization increases sinking speed: a substantial increase has been measured in one case (Pennington & Strathmann, 1990), and a smaller effect (*c.* 10%) has been calculated for another (S. Humphries & C. Lüter, pers. comm.). Although mineralization may not be essential for benthic access, faster sinking may increase the chance of successful settlement through deep, turbulent, or heterogeneous water. Moreover, time to benthic fixation may be critical given limited nutrient stores or competence periods. Thus, a potentially important side-effect of mineralization (especially when so massive as to substantially change density) is to facilitate access of pelagic organisms to the benthic zone.

If strengthening of muscle lever-arms and other functional elements in pelagic organisms permits growth to larger size, it will result in either a trade-off between the cost of density countermeasures and the benefits of increased size, or the attainment of some functional/mechanical limit to the pelagic habit. In both cases continued size increase will be possible only if the pelagic habit is replaced, either by more active

swimming (leading in a direction not relevant to this discussion), or by settlement to the benthos. Once in the benthos, increased density should also provide some stability against turbulent resuspension, although calculations suggest that this effect may be small (S. Humphries, pers. comm.). However, in Late Proterozoic forms with no attachment mechanism, even a small benthic stabilization force could have been critically important over evolutionary time, and in forms that had some ability to adhere or attach to a substrate, stabilization could have been important temporarily to individuals, e.g. during a limited period of attachment competence, or in regions exposed to wave action. In larger, active swimmers (e.g. early arthropod predators), stabilization due to increased density could also have been energetically advantageous if it reduced the effort required to hold position against currents and/or reduced losses of feeding-time caused by turbulent re-suspension.

ECOLOGICAL OPPORTUNITIES ARISING FROM BENTHIC SETTLEMENT

In the Mid and Late Proterozoic, dissolved mineral nutrients and the rain of detritus ('marine snow') appear to have been plentiful (Tucker, 1992), the faecal pellets of increasing numbers of pelagic metazoans sped the descent of organic carbon (Rothman, Hayes & Summons, 2003), and bioturbation was absent or minimal. Thus, the sea floor was nutrient-rich and stable, consolidated by microbial mats and stromatolites (Tucker, 1992; Walter, 1994; Bottjer, Hagadorn & Dornbos, 2000; Noffke, Hazen & Nhelko, 2003). Benthic trace fossils with a metazoan grade of complexity first appeared in the Late Neoproterozoic, and their diversity and complexity increased across the Precambrian–Cambrian boundary, as did bioturbation (Brasier, Dornamjaa & Lindsay, 1996; Crimes, 1992a, b; Jensen, 2003). But the diversity and biomass of trace fossil-makers cannot have been high enough to consume all the available 'snow', much of which would have been suspended in turbulent, epi-benthic water. Suspension- and particle-seizure feeders reaching the sea-floor by settlement would therefore have found food-gathering faster and more reliable than in the upper water column. Moreover, currents bring cost-free food resources to sessile, benthic suspension-feeders.

In these ways, benthic settlement would have been nutritionally advantageous, allowing growth to continue beyond the size limits imposed by the pelagic habit and favouring the development of the larger structures permitted by mineral reinforcement, as well as permitting the evolution of new feeding habits and structures, e.g. the laminar-flow and inhalant/exhalant currents of brachiopods, the tiered filtration fans of pelmatozoans, and various sediment-mining

structures (Ubaghs, 1967; Baumiller, 1997). Evidently, we know only of those lineages of settlers that did encounter and respond to benthic ecological opportunities with changes that led to palaeontologically visible lineages; we know little or nothing of those that met no favourable opportunity or responded in unreserved ways.

EVOLUTIONARY SUCCESS, THE BIPHASIC LIFE CYCLE AND NICHE-BROADENING AS CONSEQUENCES OF BENTHIC SETTLEMENT

Evolutionary success means the persistence of a lineage over time and space in numbers sufficient for fossils to be both formed and recovered. Both are enhanced by broad niche occupancy (e.g. Kammer, Baumiller & Ausich, 1997), which itself reflects fecundity, i.e. the number of zygotes formed by the gametes of individual parents and the success of zygote maturation and dispersal. Because floating or swimming animals of relatively simple morphology must generally be size-limited, with concomitant limits on fecundity, adoption of a benthic habit and increased body size (both resulting from massive mineralization) would have jointly promoted evolutionary success. Increased fecundity would also have resulted in additional genetic diversification, further enhancing broad niche occupation (Van Valen, 1965), buffering against ecological fluctuation and facilitating long-term survival.

The equation of high fecundity with evolutionary success can also account for the origin of the biphasic life-cycle, in which planktonic larvae settle and reproduce only after a metamorphosis in which they develop a secondary body form that permits the formation of more efficient or selective feeding structures, growth to much larger size, and high fecundity. This sequence, in which novel, mineralized 'adult' characters are added to a 'larval' ontogenetic programme, with delay of reproduction to the adult stage, differs only slightly from Nielsen's hypothesis for the origin of metamorphosis (Nielsen, 1998, 2000), and implies that the lack of evidence for indirect development in the Proterozoic results from the small size and fragile construction of unmineralized, premetamorphic forms (Budd, 2004).

A striking feature of the fossil record of mineralized metazoan diversity is that its rapid expansion appears to have been concentrated into a short time-period. One possible prediction of the hypothesis being advanced here is that this is a taphonomic artefact; many sporadically mineralized lineages may have arisen at earlier times but generally left no trace because their census size never became high enough to ensure bulk fossilization (i.e. the deposition of marl or limestone) and recovery. If so, the appearance of a

short-lived Cambrian diversity explosion may be explained by positive feedback between the number of potential attachment-sites (e.g. in shell-beds or reefs) created by the first numerically successful, mineralized, benthic lineages and the probability of subsequent, successful benthic settlement and attachment. The number and complexity of available benthic niches (total niche breadth) may have grown (perhaps for a time autocatalytically) as the number and types of successful settlers increased (Odling-Snee, Laland & Feldman, 2003).

PHYLOGENETICS OF MASSIVE MINERALIZATION

Various lines of evidence indicate that even if the biochemical components of mineralization are plesiomorphies (of Metazoa or some higher clade), massively mineralized skeletons and shells are polyphyletic. For example, stem- and crown-group brachiopods (which probably include phoronids) display at least seven different mineralization styles or fabrics (Conway Morris & Peel, 1995; Williams, 1997, 2003; Williams *et al.*, 1998b; Cohen, 2000; Williams, Lüter & Cusack, 2001; Holmer, Skovsted & Williams, 2002; Williams & Holmer, 2002; Cohen, Holmer & Lüter, 2003) most of which can hardly be derived from one another. Although all involve secretion by an ectodermal epithelium, they presumably reflect the evolutionary recruitment of different cellular and biochemical mineralization pathways in related stem-group lineages. This was probably also true for other phyla: certain lineages would independently and sporadically mineralize (e.g. Brasier, 1982: fig. 4) by initiating the expression of plesiomorphic biochemical mineralization pathways (or less probably by acquiring them *de novo*), for example siliceous and calcareous sponges before the Cambrian, ectoprocts not until the Ordovician, some phyla not yet. Among groups such as arthropods, where mineral reinforcement of the chitinous skeleton is widespread (strengthening muscle insertions and hardening mouthparts, e.g. Fortey & Owens, 1999), its biochemical and phyletic origin may have been more unitary, with differentiation between lineages being mainly in degree. However, Early Palaeozoic arthropod mineralization was not entirely unitary; lineages of trilobites are known with either calcite or apatite secreted as a complete external layer (Briggs, Fortey & Wills, 1992; Fortey, 2001). These and many other examples of localized mineralization (e.g. Lichtenegger, 2002; Warén *et al.*, 2003), provide further evidence for its independent origins.

ARMOUR AGAINST BENTHIC PREDATION

Given the sort of benthic radiation described above, with concentration of macroscopic, mineralized biom-

ass in the benthic zone, new predation opportunities would follow, leading to possible arms races between benthic predators and prey (Willmer, 1990; Bengtson, 1994). Increased predation in the benthos follows from a simple quantitative argument: as long as predators and prey inhabited the three-dimensional water column, encounters would have been relatively rare and selection for predation-resistance, low. However, once a substantial occupation of the benthic zone had been established, prey–predator interactions would have occurred in (nearly) two-dimensional space, with increased predation pressure and stronger selection, although under conditions where *improved* armour could now confer greater protection *without* radical new life-history consequences. Benthic predator–prey co-evolution may therefore have accounted for early benthic faunal turnover, e.g. the extinction of hyoliths and of the scleritomorph halkieriid- and tommotid-like brachiopod stem-groups. Similarly, it may have promoted survival of sessile and infaunal, shelled brachiopods, as well as the further evolution of the various mineralized molluscan classes, and the echinoderm radiation. But for the reasons given above, *ab initio* mineralization must generally have preceded such predation.

DISCUSSION

In the hypothesis advanced here, a range of elements is used to build a new reconstruction of biotic interactions that may underlie the apparent increase of mineralized, benthic metazoan diversity between the Precambrian and Cambrian periods. In short, that mineralization originated because it is mechanically and energetically favourable and that, when massive, it facilitated settlement of bilaterians from the water column into the nutrient-rich, Proterozoic benthic zone. Mineralization and settlement were joint necessary preconditions for the evolution of greater fecundity through the origin of biphasic life cycles, and hence for palaeontologically recorded, evolutionary success. Some elements of this hypothesis have been noted and discussed by previous authors (e.g. Brasier, 1982; Tucker, 1992; Rieger, 1994; Fortey, Briggs & Wills, 1997), but others, including the bio-mechanical basis for mineralization, and the synthesis, appear to be novel applications of established knowledge.

Justification for advancing a new hypothesis lies in the extensive arguments presented elsewhere (Budd & Jensen, 2000) for rejecting existing explanations of Precambrian-Cambrian metazoan evolution, and in the new arguments given here for rejecting predation pressure as an important factor. Several other proposals can also be rejected. For example, that mineralization was prevented (until the Cambrian) by low

ion concentrations in seawater is inconsistent with: (1) the essentially unlimited scope for the evolution of protein–ion association constants (Bogarad & Deem, 1999), (2) the existence of inherited (between-taxon) variation in the effect of carbonate ion concentration on calcification rate (Marubini, Ferrier-Pages & Cuif, 2003), (3) the intracellular, membrane-bound, or periplasmic and homeostatically controlled formation of mineral skeletons (e.g. Al-Horani, Al-Moghrabi & de Beer, 2003), and (4) the quasi-simultaneous origins of apatite, aragonite, calcite and silica mineralization (Brasier, 1982: fig. 4). Likewise, the suggestion that metazoan body size was oxygen-limited ignores the widespread existence of gas transport proteins, circulatory systems, and adaptations to life under anoxic conditions, all of which are components of the ground-plan of metazoan lineages with Precambrian origins (e.g. Kusche, Ruhberg & Burmester, 2002). Explanations that invoke genomic reorganization lack adequate supporting evidence; indeed, gene diversification by duplication appears to have occurred in two bursts, one long before and one after the Cambrian explosion (Miyata & Suga, 2001). As this discussion indicates, no process previously proposed to explain the observed patterns appears satisfactory.

By contrast, the combination and sequence of processes described here (with a broad brush, to avoid excessive lineage-, time- and place-specific detail) appear to provide a biologically and ecologically coherent and plausible explanation for most aspects of the diversification of metazoan lineages with massively mineralized body parts whose remains constitute the conspicuous, early fossils. Other benthic metazoans, such as the complex trace fossil fauna (Crimes, 1992a, b), the Ediacaran fauna (Cloud & Glaessner, 1982; Seilacher, 1989; Jensen *et al.*, 1998) and Cambrian infauna such as sipunculids and priapulids can be understood as descendants of (presumably once pelagic) Proterozoic lineages that followed unmineralized developmental and evolutionary routes to a benthic habit and relatively large size.

By its nature, the puzzle of the Cambrian explosion can never be completely solved. However, the picture drawn here brings together, with little strain, more of the pieces, and appears more completely integrated than any that have been presented hitherto. It should be pasted on the box until a better one is devised.

NOTE ADDED IN PROOF

The diversity of mid water predators in Early Cambrian times has been discussed by J. Vaunier & J. Chen (2005). Early Cambrian food chains: new evidence from fossil aggregates in the Maotian Shau State Biota, SW China. *Palaos* **20**: 3–26.

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One complete review of “Not armour...” for Biol. J. Linn. Soc.

This is an intriguing paper which flies in the face of conventional ideas that armour was the trigger for the increase in metazoan diversity in the Cambrian. The paper is by its nature speculative but this should not prevent publication. The message is deliberately provocative and you may be afraid to publish it, but publish it you should. It is bound to stir the waters and could well lead to new studies designed to test the basic idea.