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10 A Grand Unified Theory of Biomineralization

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10.1 Introduction

The geological record indicates that the major animal phyla began biomineralizing in a relatively short interval of time during the Cambrian evolutionary explosion, about 525 Myr ago. Because these phyla diverged well before this biomineralization event, it was triggered either by an unprecedented lateral genetic transfer, or was the result of parallel exaptation of an ancestral biomineral system in many separate lineages. As magnetite (Fe_3O_4) biomineralization is the most ancient matrix-mediated system, and is present in most animal groups, it may have served as this ancestral template for exaptation. Complete sequencing of the genome of a magnetotactic bacterium, and identifying the magnetite operon, might provide a 'road map' for unraveling the genetics of biomineralization in higher organisms, including humans.

One of the most sobering things a modern biologist can do is to examine the results of a 2-D gel taken from biomineral-forming tissue. The complexity and the number of protein products involved in what looks like a rather simple biological process is daunting. Years of work can go into unraveling the identity and function of a single product, such as the sea-urchin SM50 protein [1].

Perhaps the despair is premature, as the existing complexity observed today had to evolve from a pre-existing, presumably simpler system. One major process by which complex biological systems evolve is by taking an existing genetic pattern that evolved for one function, and then duplicating it, linking it up differently, and adapting it for a new role. The nascent system is then gradually debugged and improved through the process of random mutation and natural selection. This evolutionary pattern has been termed 'exaptation' [2]. If the biomineralization systems present in the major animal phyla today evolved in this fashion, then it makes sense to examine that ancient system first, and to use it to provide an evolutionary road map for the modern processes. The paleontological record of biomineralization supports the idea that many animal groups experienced an evolutionary 'trigger' during the Cambrian Explosion, which, as noted below, is compatible with repeated exaptation of an ancestral processes. Certainly, there does seem to be some funda-mental underlying immunological similarity between the macromolecules involved in hydroxyapatite formation in the vertebrates, and those involved in the aragonite present in molluscan nacre [3, 4]; freshly ground nacre fails to elicit an immune

response in humans, and in fact stimulates bone regeneration. This would be highly unlikely if both biominerals had evolved through separate pathways, and argues for a common ancestor.

10.2 Geological Record of the Cambrian Explosion

The geological record provides an important clue to the origin of biomineralization in the animal phyla, as has been noted by many previous authors [5-12]. Prior to the Cambrian (~ 544 Myr ago), almost the only evidence for animal life was the soft-bodied Ediacaran fauna (Fig. 10.1). Together with related bed-parallel tracks

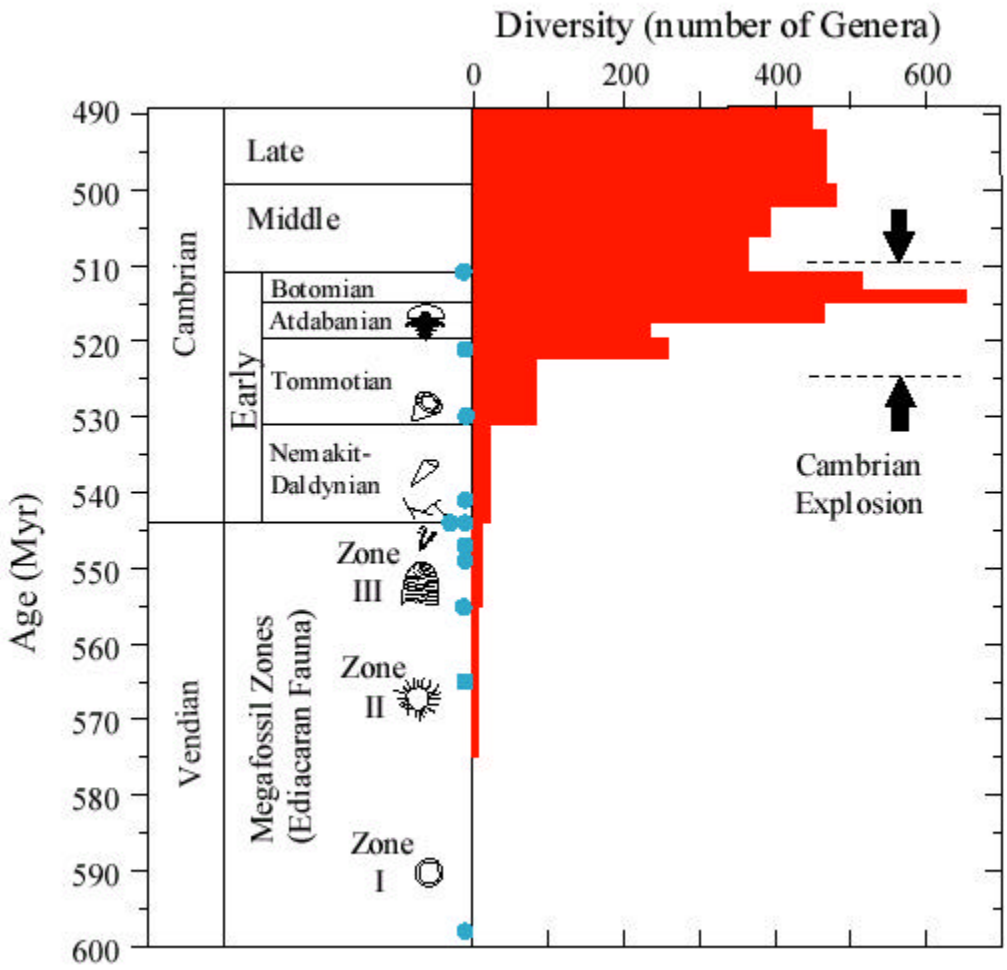

Figure 10.1. Radiometric age constraints and generic diversity for Vendian and Cambrian time. Position of the actual U/Pb constraints are indicated by solid blue dots. Data for the generic diversity have been compiled from Narbonne *et al*. [27] and Sepkoski [28], and are plotted as the number of taxa reported in each reference time interval. The black arrows indicate the approximate time of the Cambrian Explosion / true polar wander event [31]. The original figure was adapted from that of Grotzinger et al. [25].

and trails of this interval, these extraordinarily rare fossils are typically preserved as casts/molds at bed interfaces, and display no evidence of biomineralization. Molecular clock studies of protein divergence times for the major animal phyla have indicated consistently that major phyla separated up to several hundred mil-lion years prior to their first appearance in the fossil record [13-18]. The first clear evidence of matrix-mediated Ca-biomineralization is the latest Precambrian invertebrate *Cloudina* [19] (Fig. 10.2). Extensive work on the numerical calibration of the geological time scale for this interval illustrates that *Cloudina* first appeared about 550 Myr ago, with other mineralized forms appearing during the next 40 Myr [20-26]. However, the largest burst of new biomineralization activity is clearly in the Tommotian/Atdabanian interval, where the diversity of fossil organisms (mostly new biomineralizing groups) increases nearly exponentially over a ~10 Myr interval.

The trigger for this Cambrian Explosion has been a subject of extensive debate in the geological literature. It seems to have been a time of general climatic insta-bility, as reflected by intense oscillations in the stable isotope record of carbon [17, 29, 30], probably driven by tectonic events of global magnitude [31]. Thus, it was a good time for new evolutionary innovations, because the climatic instability pro-vided opportunities for novel forms to become fixed within small populations. But the mineralization drive itself may have been triggered by a separate development: the evolution of an animal predator as suggested by Stanley [5]. Although there is no evidence for animal predation among Ediacaran paleocommunities, some of the earliest trace fossils associated with the Ediacarans appear to be scratch marks made by the hardened radula of an unidentified mollusc [32]. Similarly, the earliest skeletonized fossils (*Cloudina*) contain clear evidence of predatorial borings – borings likely to have been made by the rasping of a mineralized feeding apparatus [12]. It is therefore likely that the adaptive advantages conferred by skeletal and tooth biomineralization were an important factor influencing the intensity of the Cambrian explosion, and they may have been amplified by the co-evolution of predator/prey systems.

The mere presence of a good evolutionary driving force is not enough to com-pletely reinvent a complex biochemical system multiple times within a geologically short interval. Lowenstam and Margulis [6] noted that the vast majority of new biomineral products observed in the Early Cambrian were based on calcium - either some form of $CaCO_3$, or Ca-phosphate minerals as shown on Fig. 10.2. Noting that precise control of intracellular calcium is necessary for the formation of the microtubules needed by all eukaryotic cells, they suggested that these calcium regulation and transport systems provided the evolutionary prerequisites for their eventual use in biomineralization (in effect, exaptation, although the word had not been coined in 1980). Calcium, carbonate, and phosphate ions are abundant in the world oceans, and hence would be favored for use in skeletons over much rarer materials like Fe, Sr, Mn, etc.

However, gathering the components is only a small part of the biologically controlled mineralization process. They need to be brought together in a confined volume, in a controlled fashion, and induced to crystallize. The growing crystallites need to be properly tended, fed, and confined to the desired size, shape, and crys-tallographic orientation. Hence, it seems that another biochemical/genetic system,

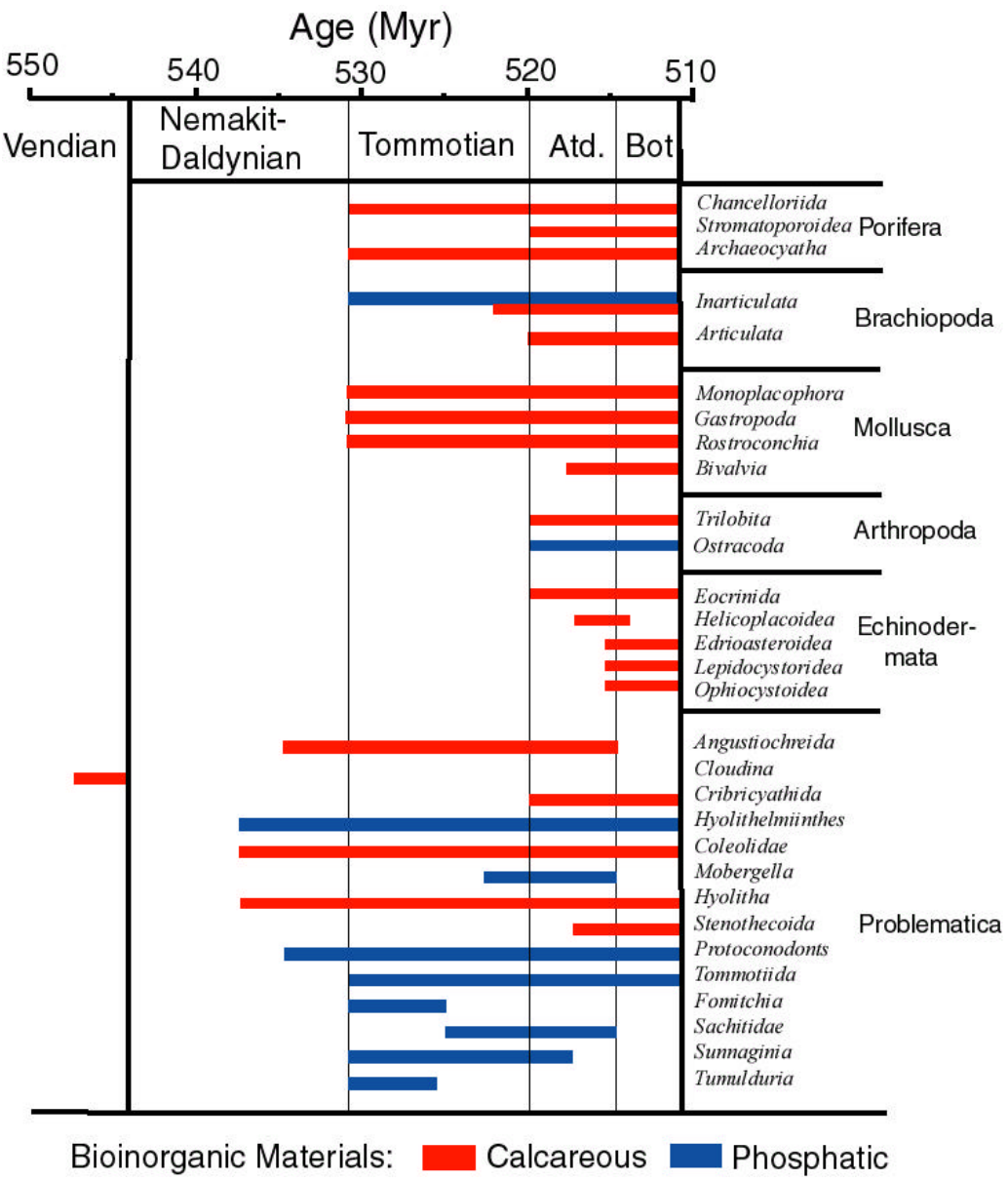

Figure 10.2. Stratigraphic ranges and first appearances of major fossil taxa that employ calcareous and phosphatic biomineralization. Not all families and problematic taxa are listed, nor are silica biomineralizing groups; for summaries of the stratigraphic range of these groups, see Bengtson [11]. Note that the mineralogy of *Cloudina* is poorly constrained; Grant [19] inferred a primary mineralogy of high-magnesian calcite based on preferential dolomitization of shell layers. Data from Lowenstam & Margolis [6] and Bengtson [11].

in addition to the ion transport system was involved in this exaptation which led to widespread biomineralization in the Early Cambrian. In all of these respects, the magnetite (Fe_3O_4) biomineralization system present in extant magnetotactic bacteria seems to fit as this missing link. As noted below, it is ancient, appears to be present in most of the animal phyla, and has all of the essential aspects of biologically controlled mineralization processes present in higher organisms. With apologies to physicists, it seems appropriate to dub this concept the "Grand Unified Theory of Biomineralization". Unlike some physical 'GUT' theories, this one can be tested easily.

10.3 Magnetite Biomineralization

Heinz A. Lowenstam of the California Institute of Technology first discovered biochemically-precipitated magnetite as a capping material in the radula (tongue plate) teeth of chitons (marine mollusks of the class ***Polyplacophora*** [33]). He and his students were able to demonstrate the biological origin of this material through a variety of radioisotope tracing studies and by detailed examination of the tooth ultrastructure [34-36]. Prior to this discovery, magnetite was thought to form only in igneous or metamorphic rocks under high temperatures and pressures. In the chitons, the magnetite serves to harden the tooth caps, enabling the chitons to extract and eat endolithic algae from within the outer few millimeters of rock sub-strates. Nesson and Lowenstam [36] reported the results of detailed histological and ultrastructural examinations of magnetite formation within the radula, and noted that the process begins with an initial transport of metabolic iron to the posterior end of the radula sac. This iron is deposited as the mineral ferrihydrite within a pre-formed proteinaceous mesh [34], forming one or two distinct rows of reddish teeth. This ferrihydrite is converted rapidly to magnetite via an unknown process.

Magnetotactic bacteria were the second organisms found to contain biogenic magnetite [37, 38], a typical example of which is shown in Fig. 10.3. They precipitate individual sub-micron sized magnetite crystals within an intracellular phospholipid membrane vacuole, forming structures called "magnetosomes" [39. 40]. Chains of these magnetosomes act as simple compass needles which passively torque the bacterial cells into alignment with the earth's magnetic field, and allow them to seek the microaerophilic zone at the mud/water interface of most natural aqueous environments. These bacteria swim to the magnetic north in the northern Hemisphere [37], to the magnetic south in the southern hemisphere [41, 42], and both ways on the geomagnetic equator [43, 44]. Magnetite-bearing magnetosomes have also been found in eukaryotic magnetotactic algae, with each cell containing several thousand crystals [45]. The magnetite formation process in bacteria has an overall similarity to that in chiton teeth, as both involve deposition of a ferri-hydrite-like mineral precursor prior to magnetite formation [35, 46].

Magnetite crystals formed within these magnetosome vesicles have five main features that distinguish them from magnetites formed through geological pro-

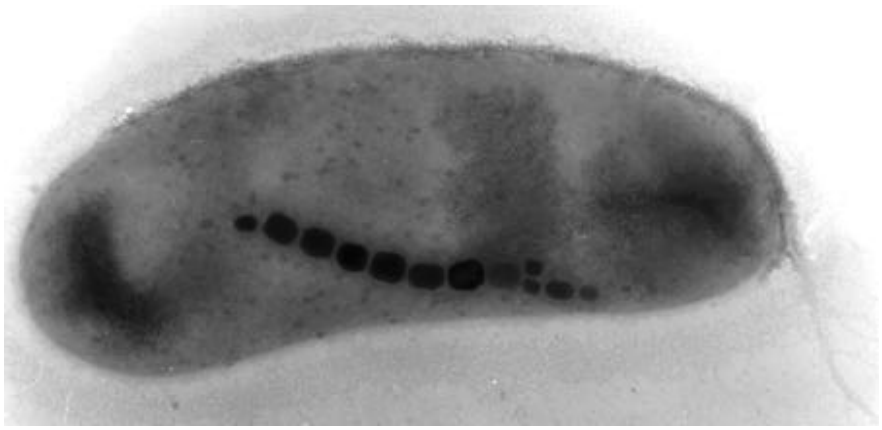

Figure 10.3. TEM image of a typical magnetotactic bacterium. The bacterium is 3 μm in size, with typical magnetite crystals on the order of 30-50 nm in length.

cesses: (1) High-resolution TEM studies reveal that bacterial magnetites are almost perfect crystals, which (2) often violate the cubic crystal symmetry of magnetite. They (3) are usually elongate in the [111] direction [40, 47-49], (4) are chemically quite pure Fe_3O_4, and (5) are restricted in size and shape so as to be uniformly magnetized (single-magnetic-domains). Inorganic magnetites are usually small octahedral crystals, often with lattice dislocations, chemical impurities, and other crystal defects. The elongation of biogenic crystals in the [111] direction serves to stabilize the magnetic moment of the particle, and presumably is the result of nat-ural selection for their magnetic properties [40, 50]. Bacterial magnetite crystals are restricted to a size range from 35-500 nm, with shapes that confine them to the single-domain magnetic stability field [51, 52]. Inorganic magnetites tend to have log-normal size distributions that often extend up into the multi-domain size region. Bacterial magnetites tend to be rather pure iron oxide, with no detectable titanium, chromium or aluminum, which are often present in geologically-produced magnetite. An additional feature is the alignment of the crystals into linear chains, which can be preserved in the fossil record [53, 54]. These characteristic features have enabled bacterially-precipitated magnetites to be identified in Earth sediments up to 2 billion years old [44], and possibly in 4-billion year old carbonate inclusions in the ALH84001 meteorite from Mars [55, 56].

As shown in Figures 10.4 and 10.5, many of these same features are shared by the magnetite crystals extracted from salmon [57] and from the human brain [58, 59]. The simplest interpretation of these results is that many higher organisms, including humans, possess the biochemical ability to form magnetite.

In higher animals, an obvious function for magnetite biomineralization is its role in magnetoreception [61-63]. Magnetoreception is now well established in virtually all major groups of animals [64], and specialized cells containing single-domain chains of magnetite are the best candidates for the receptor cells [60, 65]. In the brown trout, Walker *et al*. [60] have shown elegantly that magnetically-sensitive nerves in the ophthalmic branch of the trigeminal nerve connect to specialized, tri-lobed cells in the olfactory laminae which contain magnetite crystals. Similarly, behavioral work with honeybees and birds has shown that brief magnetic pulses are

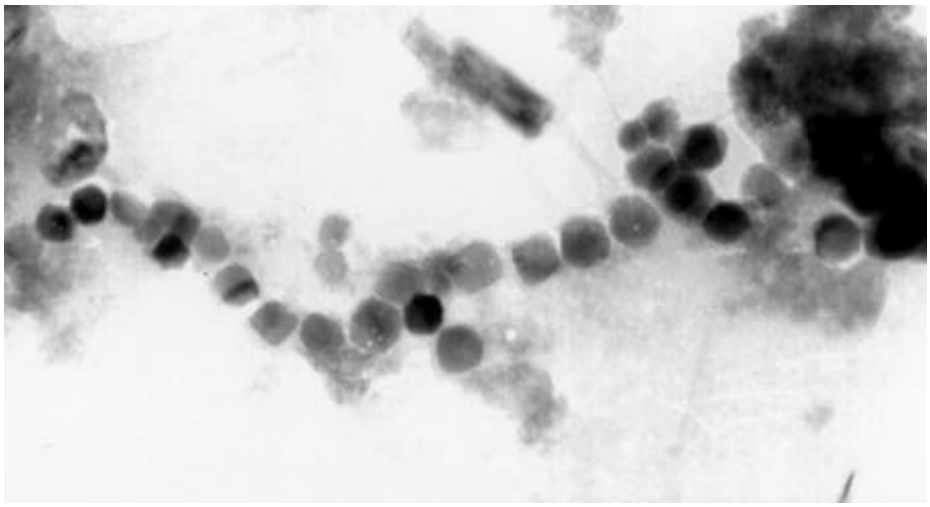

Figure 10.4. Single-domain magnetite crystals extracted from the frontal tissues of the sockeye salmon [57]. These particles are structurally nearly identical to those present in magnetotactic bacteria. Recent studies have shown that these are indeed present in the magnetosensory cells in fish [60].

able to alter the magnetic responses, confirming that a ferromagnetic material like magnetite is indeed part of the magnetic sensory system [66-72].

From an evolutionary perspective, it now seems clear that magnetite-based magnetoreception, and hence magnetite biomineralization, date back at least to the last common ancestor of Chordata, Mollusca, and Arthropoda (~600 to 900 Myr ago). The existence of magnetotactic protists argues that this genetic ability for magnetite biomineralization may go back even further to the evolution of the first eukaryotes nearly two billion years ago. Indeed, Vali & Kirschvink [40] argue that the ancestral eukaryotes probably inherited the ability to make magnetite from magnetotactic bacteria during the endosymbiotic events which formed this cell type. Therefore, the magnetite system must have been present in most of the animal phyla in the massive biomineralization episode during the Cambrian Explosion, and hence available for exaptation to form other biomineral systems. This may account for the apparent lack of a human immune response to molluscan nacre noted earlier. The fact that two of the most primitive molluscan groups, the *Archaeogastropods* and the *Polyplacophorans*, both use iron minerals to harden their radular teeth (goethite and magnetite, respectively [33, 73]) indicates that they adapted this from a preexisting iron biomineral system. Hence, magnetite biomineralization is a prime candidate for this missing “evolutionary precursor”.

10.4 Discussion

The magnetotactic bacteria are the most primitive organisms known which use a vacuole-based system to form their biomineral products. In mammals, much of the

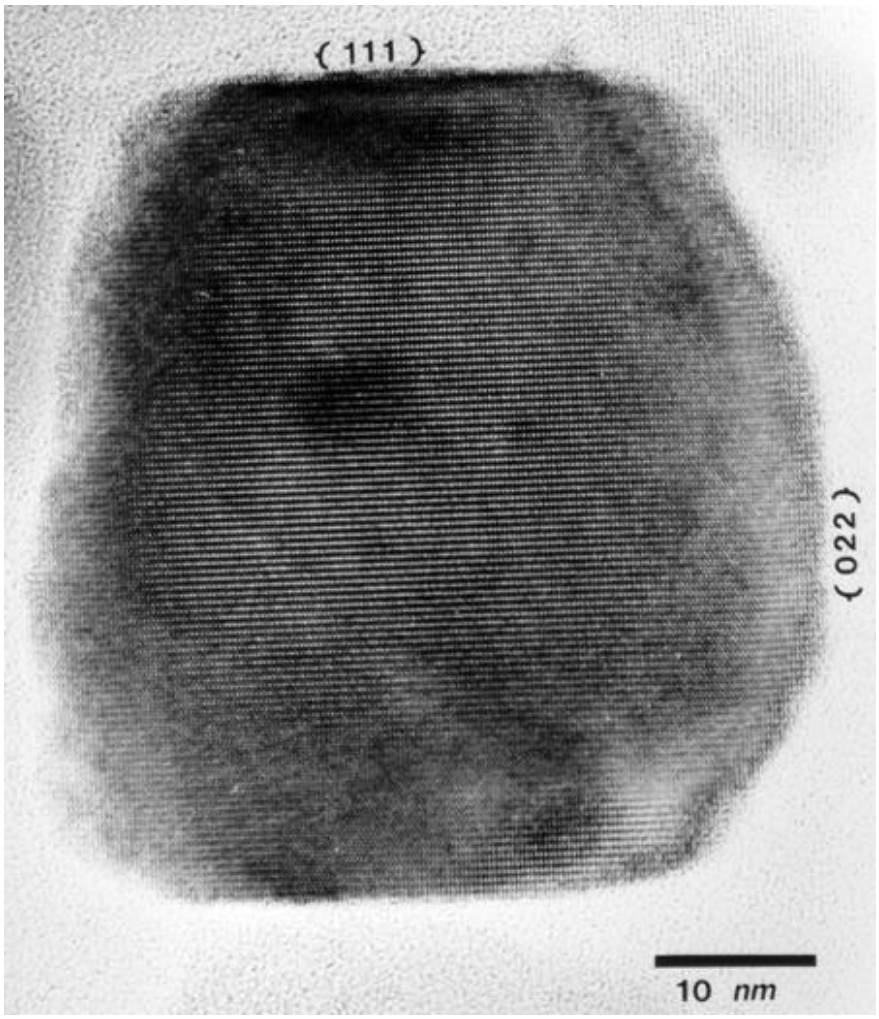

Figure 10.5. Magnetite crystal extracted from tissues of the human brain [58].

hydroxyapatite in bone and teeth is formed via a similar process, in which the chemical precursors are transported first to a vacuole storage system, and then dis-crete peptides are added to nucleate the desired crystal forms [9]. Understanding how this process evolved in bacteria ought to provide insights for understanding how the more complex biomineralization systems in eukaryotes operate.

Most of the published genetic analyses of magnetotactic bacteria to date have focused in using 16s RNA to infer phylogenetic relationships [74-77]. As of this writing, only one protein directly involved in the magnetite biomineralization process has been found using transposon mutagenesis [78], in an as-yet unnamed magnetotactic bacterium dubbed AMB-1. The protein coded by this open reading frame (termed MagA) is known to reside both in the cell membrane and in the magnetosome membrane [79], and is involved in transporting and accumulating iron within the magnetosomes [80]. It demonstrates strong homology with known Ca^{2+} trans-membrane transport proteins in other bacteria.

In an attempt to attack the magnetosome problem from the standpoint of the iron mediating enzymes, Bertani *et al*. [81] focused on the gene coding for bacter-ioferritin (bfr) in *Magnetospirillum magnetotacticum*. In contrast to *E. coli*, which has only one bfr gene, *M. magnetotacticum* has two genes, bfr1 and bfr2, which are strongly homologous to bacterioferritins. The subunit encoded by bfr1 is more similar to *E. coli* bacterioferritin than it is to the subunit encoded by bfr2. These genes are strange in two other ways: First, the open reading frames overlap by one base pair, with the last base pair of the stop codon of the first gene serving as the first codon of the second protein. Second, the amino acid residues of the region in the putative bfr2 subunit, which is thought to be involved in the binding and nucleating of the iron oxide mineral at the core of the ferritin protein (the mineral ferrihydrite), are completely different from the other bacterioferritins, which are otherwise highly conserved. This characteristic indicates that the proteins are *not* acting to nucleate ferrihydrite deposition, and Bertani *et al*. [81] speculate that this peculiar feature may have something to do with the mineralization process.

In summary, the genetic basis of biomineralization – for all mineral systems – is still a mystery. The "Grand Unified Theory of Biomineralization" presented here suggests that an understanding of magnetite biomineralization in the magnetotactic bacteria might provide a template for unraveling, or at least understanding, por-tions of vacuolar-based biomineral systems in higher animals, including humans. The first major step for understanding the bacterial system would be, of course, determining the complete genome sequence for a magnetotactic bacterium.

It is fitting to close this article with the first stanza of Rudyard Kipling's famous poem, *Cold Iron:*

> Gold is for the mistress – silver for the maid –
> Copper for the craftsman cunning at his trade.
> "Good!" said the Baron, sitting in his hall,
> "But Iron – Cold Iron – is master of them all."

Acknowledgments

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