# EARLY SKELETAL FOSSILS

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ABSTRACT—The Precambrian-Cambrian transition saw the burgeoning of diverse skeletal organisms ("small shelly fossils"), represented in the fossil record by spicules, tubes, tests, conchs, shells, and a variety of sclerites and ossicles. Whereas calcareous biomineralization as such may have been facilitated by changes in ocean chemistry at this time, the utilization of biominerals in mineralized skeletons is a different process. The massive appearance of skeletons is most likely an epiphenomenon of the general radiation of body plans and tissues. The "choice" of biominerals (mainly calcium carbonates, calcium phosphates, and silica) may reflect the environmental conditions under which the particular skeleton first evolved.

THE TERM "small shelly fossils" was used in the title of a seminal review paper by Crosbie Matthews and Vladimir Missarzhevsky in 1975 and has plagued the world ever since. Regardless of the clever derivations ("small silly fossils", "small smellies", etc.), the term seems triply inappropriate to denote fossils of the earliest skeletal animals: they are not always small, they are commonly not shelly - and the term might equally well apply to Pleistocene periwinkles. Not everyone may agree with Gould's (1990) assessment that the term is "a catchall name that spells frustration"; in fact, answering to a certain need for sloppy terms, this one has become immensely popular and even seems to defy translation, as exemplified by the (mostly) French title of a recent article (Steiner et al., 2004) in the journal *Geobios*: "Small shelly fossils du Cambrien inférieur...".

Terminological gripes aside, the Matthews & Missarzhevsky paper did much to draw the non-Russian-reading world's attention to the remarkable fossil biotas that Soviet palaeontologists had discovered in beds underlying those containing those classical Cambrian fossils, the trilobites (e.g., Fonin and Smirnova, 1967; Rozanov and Missarzhevsky, 1966; Rozanov et al., 1969). They were, in fact, the earliest fossils of hard skeletons, and their discovery did much to throw light on the larger evolutionary event they reflected, the Cambrian explosion. They included spicules, tubes, shells, and various disarticulated sclerites belonging to unknown animals. Taken together, they indicated much higher diversity and disparity of the earliest Cambrian faunas than had been previously recognized. To wit, elements and even rich faunas of this type had been previously reported from early Cambrian beds (e.g., Billings, 1872; Cobbold, 1921; Cobbold, 1935; Poulsen, 1967; Shaler and Foerste, 1888), but these early reports had failed to bring home the message that the early faunas contained a diverse world of animals apart from the traditionally recognized trilobites, archaeocyathans, etc. Soviet palaeontologists now established a Siberian stage called the Tommotian, and proposed that this stage correlated with pre-trilobitic beds worldwide (Rozanov et al., 1969).

At the time of the "rediscovery" of these early skeletal fossils, the notion of a long, hidden Proterozoic history of the animal kingdom had strong proponents (e.g., Durham, 1971; Glaessner, 1972), although the contrary, "explosive", view pioneered by Preston Cloud (1948; 1968) was gaining acceptance under the influence of developing concepts of major events in evolution taking place as rapid bursts (Eldredge and Gould, 1972; Simpson, 1953). The issue was not in itself resolved by the revelation of high diversity of the early Cambrian faunas, but the systematically ambivalent nature of many of the early skeletal fossils inspired a view that they represented a high initial disparity representing a more bushy
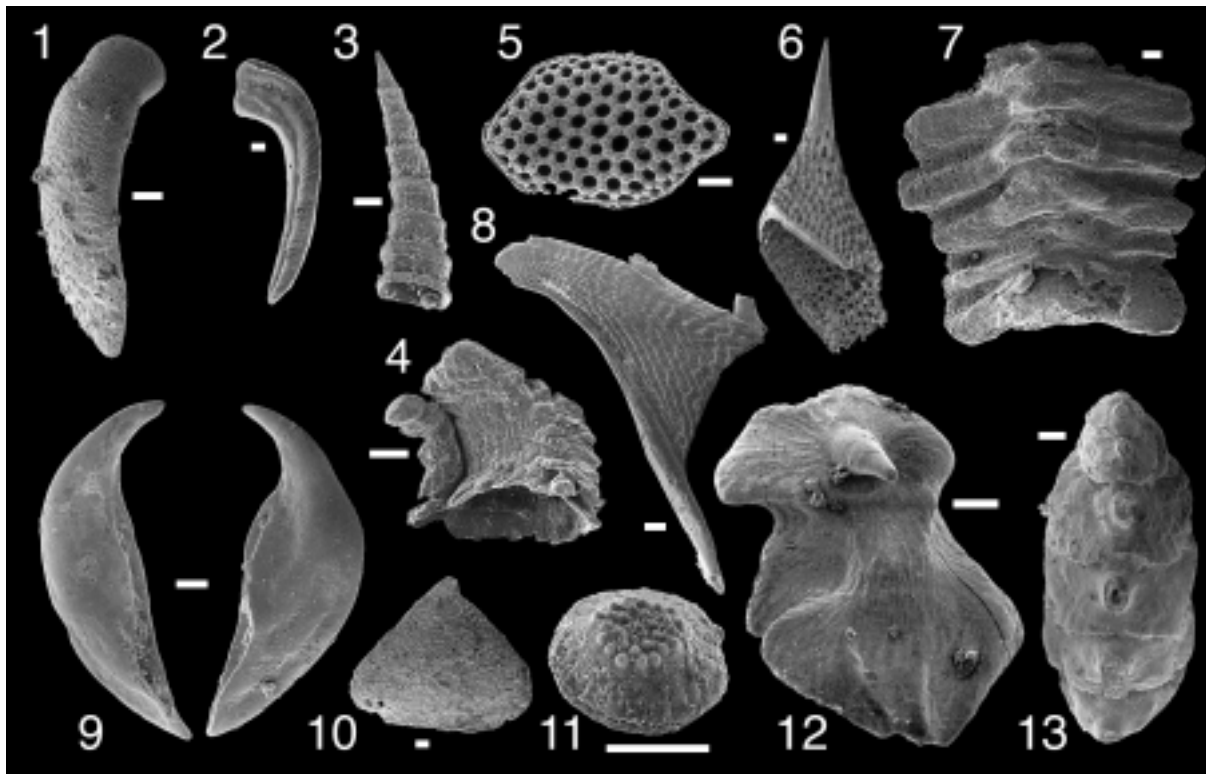
FIGURE 1— Early Cambrian sclerite-bearing animals. 1, *Siphogonuchites* and 2, *Hippopharangites*, coeloscleritophorans represented by loose sclerites. 3, Sclerite of *Lapworthella*, a tommotiid. 4, Sclerite of *Eccentrotheca*, another tommotiid. 5, 6, Sclerites of *Microdictyon*, a lobopod. 7, *Tumulduria*, possibly related to brachiopods. 8, Sclerite of *Scoponodus*, of unknown affinity. 9, Jaw-like elements of *Cyrtochites*. 10, Sclerite of *Porcauricula*, possibly a tommotiid. 11, Dermal element of *Hadimopanella*, a palaeoscolecid. 12, Sclerite of *Cambroclavus*, and 13, sclerite of *Paracarinachites*, animals of unknown affinity. Scale bars 0.1 mm.

beginning of the tree represented by surviving phyla. In the words of Stanley (1976): "the variety of problematical forms ... would seem to document 'experimentation' in animal evolution not merely at the level of order or class but, for the only time in geological history, at the level of phylum." (see also Bengtson, 1977; Bengtson, 1986.)

In the following decades there was a flood of publications reporting "small shelly fossils" from Proterozoic-Cambrian transitional beds in various parts of the world. Particularly rich biotas have been described from China (Luo et al., 1982; Qian and Bengtson, 1989; Yin et al., 1980), Mongolia (Esakova and Zhegallo, 1996; Missarzhevsky, 1977; Voronin et al., 1982), Kazakhstan (Missarzhevsky and Mambetov, 1981), Australia (Bengtson et al., 1990; Bischoff, 1976; Brock and Cooper, 1993; Gravestock et al., 2001; Laurie, 1986) and Antarctica (Evans and Rowell, 1990; Wrona, 2003; Wrona, 2004). Biotas of some diversity have also been reported from India (Azmi, 1983; Bhatt et al., 1985; M. D. Brasier and Singh, 1987), Pakistan (Mostler, 1980), Iran (Hamdi, 1989; Hamdi et al., 1989), Europe (M. D. Brasier, 1984; Hinz, 1987; Kerber, 1988), and North America (Bengtson and Fletcher, 1983; Conway Morris and Fritz, 1980; Landing, 1988; Landing and Bartowski, 1996; Landing et al., 1989; Signor

FIGURE 2— Early tube-dwelling animals. 1, *Cloudina*, one of the earliest animals with a mineralized skeleton reinforced with calcite (late Neoproterozoic). 2, *Aculeochrea*, an anabaritid with an aragonite-reinforced tube showing the three-rayed symmetry typical of the group (Precambrian-Cambrian boundary beds). 3, *Hyolithellus*, an animal reinforcing its tube with calcium phosphate (early Cambrian). 4, *Olivooides*, possibly a thecate scyphozoan polyp. 5, Pre-hatching embryo of *Olivooides*. Scale bars 0.1 mm.

et al., 1987). These occurrences are not restricted to "pre-trilobite beds", and the global biostratigraphic relevance of "pre-trilobite beds" has come under question. Indeed, the enthusiasm for using "small shelly fossils" in interbasinal correlation has somewhat cooled down, although they retain some usefulness as part of more broadly based methods of correlation.

The idea that the high initial disparity of the early skeletal fossil reflected an early abundance of short-lived taxa comparable to the ones that survived to found the traditional phyla of animals (Bengtson, 1977; Bengtson, 1986; Stanley, 1976) was used by Stephen J. Gould in his acclaimed book on the Burgess Shale, "*Wonderful Life*" (Gould, 1989). As Gould somewhat ungenerously remarked in this book, the "Tommotian" biota is represented by "tiny caps and covers that tell us nearly nothing about the creatures underneath". Gould depicted the "weird wonders" of the Burgess Shale as reflecting an evolutionary tree "more like a Christmas tree". Ironically, this was at the same time that some of the more enigmatic of the early skeletal fossils began to couple up with discoveries in Burgess Shale-type deposits elsewhere , and the combined information then helped to formulate phylogenetic hypotheses describing the relationships of these animals with known phyla. This was the case with the halkieriids, the scale-like sclerites of which had been interpreted as covering a slug-like animal (Bengtson and Conway Morris, 1984), and which was now shown to have a more complex scleritome (Conway Morris and Peel, 1990) suggesting it to fit near or within the crown-group molluscs (Bengtson, 1992) or to represent stem-group lophophorates (Conway Morris and Peel, 1995). Even more significantly, Gould's prime example of early "weird wonders", *Hallucigenia* as well as the enigmatic sclerites of *Microdictyon* (Fig. 1.5, 1.6) turned out to be lobopodians comparable to living onychophorans (Ramsköld, 1992; Ramsköld and Hou 1991) (Chen et al., 1995).

## Functions of Hard Skeletons

Hard skeletons may serve an array of functions, such as protection, support, attachment, friction against substrate, muscle leverage, food handling, formation of filtration chambers, and storage of essential substances. The original function(s) may be defined as the one(s) that provided the selective advantages stimulating the evolutionary appearance of the hard skeleton in the first place. Secondary functions are those that arose as
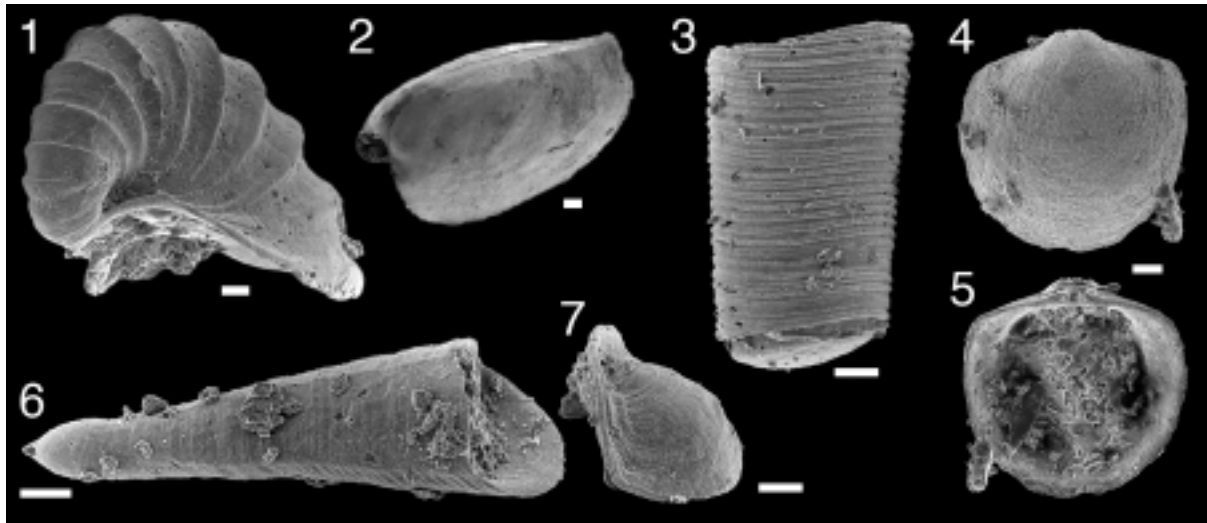
FIGURE 3—Early Cambrian shell-bearing animals. 1, *Archaeospira*, a possible gastropod. 2, *Watsonella*, a mollusc possibly representing an ancestral lineage to rostroconchs and bivalves. 3, *Cupitheca*, an animal decollating its conch during growth. 4, 5, Pit valve of *Aroonia*, a probable stem-group brachiopod. 6, 7, Conch and operculum (image reversed to fit that of conch) of *Parkula*, a hyolith. Scale bars 0.1 mm.

corollaries of the existence of a skeleton. In many cases a secondary function is easy to recognize as such (for example, the use of the valves for swimming in pectinids), but identifying an original function unequivocally is much more difficult, particularly as it may not be retained in later phylogenetic stages.

Most of the functions listed initially in the preceding paragraph might conceivably be original in specific instances. In such a perspective, the origins of hard skeletons may be seen as an epiphenomenon of the general radiation of body plans and tissues: the appearance is no more and no less significant than the appearance of other tissue types. Nonetheless, there are certain patterns in the appearance of the early skeletal fossils that indicate more general processes behind the origins of skeletons. These concern the distribution of skeletal types, the composition of the skeletons, and the parallel evolution of skeletons in unicellular protists.

## Types of Hard Skeletons

The scarce skeletal faunas in the late Neoproterozoic are represented by mineralized and non-mineralized tubes (Fig. 2.1) (Grant, 1990; Ivantsov, 1990), basal supportive skeletons (Wood et al., 2002), spicules and spicular frameworks (M. Brasier et al., 1997; Gehling and Rigby, 1996), as well as stalked tests (Grotzinger et al., 2000). The more diverse assemblages appearing later, in the early Cambrian, also include univalved and bivalved shells (Fig. 3), tooth-like structures (Fig. 1.9), arthropod-type exoskeletons, echinoderm ossicles, and - most characteristically - dermal sclerites of various description (Figs 1 and 4) (e.g., Bengtson et al., 1990; Qian and Bengtson, 1989; Rozanov et al., 1969). Tubes (Fig. 2.2-2.4) and spicules (Fig. 5) also expand their diversity and disparity to make up significant proportions of the early skeletal assemblages.

The tubular fossils are commonly not very informative with regard to the identity of their inhabitants; different tubes have been variously
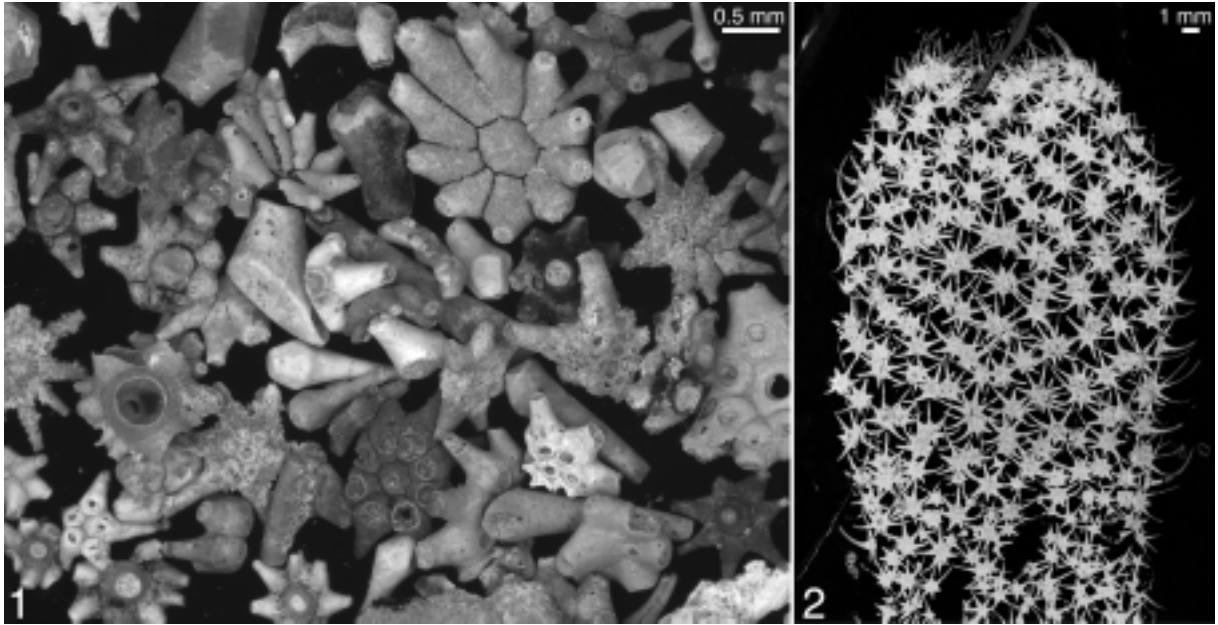
FIGURE 4—*Chancelloria*, a coeloscleritophoran. 1, Disarticulated sclerites from a microfossil preparation (Early Cambrian). 2, Upper part of cactus-like body (Middle Cambrian).

identified as belonging to foraminiferans, cnidarians, polychaete and pogonophoran annelids, sipunculids and others. They are clearly a heterogenous group, as their wall composition and structure are very diverse, and the distinction between tubes and conchs (as, for example, in hyoliths) is somewhat arbitrary. Although spicular fossils might be expected to be equally difficult to assign phylogenetically because of the lack of anatomical information, some forms appear sufficiently characteristic to allow a referral to a known group of organisms. This is particularly true of hexactinellid sponges (Fig. 5.1), and the identification of Cambrian sponge spicules is commonly facilitated by the not uncommon presence of whole-body preserved sponges (Rigby, 1978; Rigby, 1986; Rigby and Collins, 2004).

Dermal sclerites are elements belonging to composite exoskeletons, scleritomes. In many cases, the body shape of the bearer and the distribution of sclerites on the body are not known, but finds of complete scleritomes or even bodies in shale deposits give occasional and crucial insights (e.g., Chen et al., 1995; Conway Morris and Peel, 1995). Thus the star-shaped composite sclerites of the chancelloriids (Fig. 4) are known to belong to a cactus-like animal that in its organization seems closest to sponges: sedentary, sac-shaped bodies with an apical orifice and no evidence of internal organs (Bengtson and Hou 2001; Walcott, 1920). The sclerites belong to a type called coelosclerites, consisting of a mineralized envelope around a space originally filled with organic tissue and showing no evidence of accretionary growth (Bengtson and Missarzhevsky, 1981). The halkieriids and siphogonuchitids (Fig. 1.1, 1.2) are characterized by scale- or spine-shaped coelosclerites, and finds of complete specimens of halkieriids show the animal to have been slug-shaped, with two large anterior and posterior shell plates in addition to the sclerites (Conway Morris and Peel, 1990; Conway Morris and Peel, 1995). It is not clear whether coelosclerites are a convergent feature, independently evolved in several groups, or whether they were inherited from a common ancestor of the various groups of
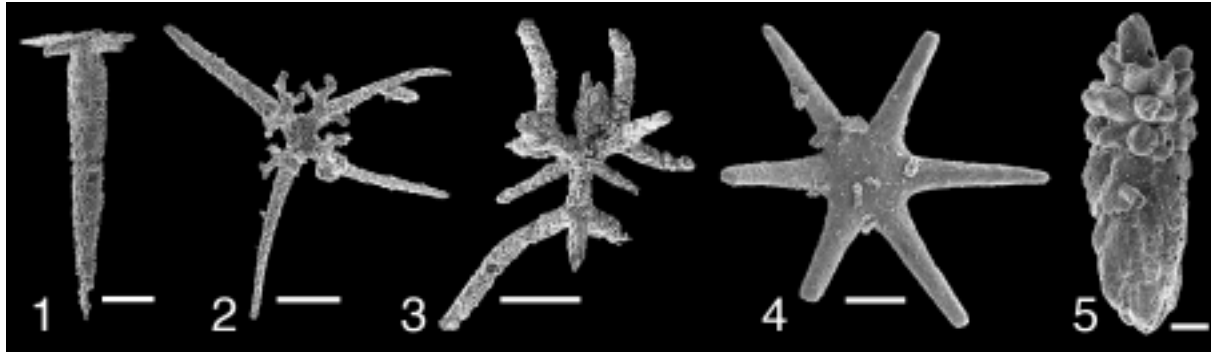
FIGURE 5—Early Cambrian spicules. 1, Hexact of hexactinellid sponge. 2, *Taraxaculum*(?), a probable demosponge. 3, *Dodecaactinella* and 4, *Eiffelia*, calcareous sponges. 5, *Microcoryne*, a possible octocoral.

coeloscleritophorans (Bengtson et al., 1990).

Other sclerites were growing by stepwise accretion and often used calcium phosphate rather than calcium carbonate as shell mineral. The most widespread group of such phosphatic sclerite-bearers are the tommotiids (Fig. 1.3, 1.4), of which so far no complete skeletons have been found (Bengtson, 1970; Bischoff, 1976; Evans and Rowell, 1990; Fonin and Smirnova, 1967; Landing, 1984). Tommotiids show a variety of sclerite shapes and ultrastructures and may in fact represent a polyphyletic assemblage of lineages that independently acquired a phosphatic scleritome. Other phosphatic sclerites include tooth- or hook-shaped objects as well as a variety of plate-like types, most of which are of unknown origin (e.g., Qian and Bengtson, 1989). Some of the more outlandish and enigmatic ones (including the *Microdictyon* of Fig. 1.5, 1.6 and the *Hadimopanella* of Fig. 1.11) are now known to represent external platelets of worm-shaped animals (Brock and Cooper, 1993; Chen et al., 1995; Ivantsov and Wrona, 2004; Müller and Hinz-Schallreuter, 1993).

It is important to note that a number of more-or-less hard skeletons appearing in the Cambrian explosion do not incorporate biominerals: there are many purely organic skeletons (e.g., tubes and arthropod-type cuticles) and many that are only weakly mineralized (e.g., "chitinophosphatic" brachiopod shells and scyphozoan-like thecae, Fig. 2.4). Some tube-dwelling animals incorporate extraneous grains into their walls (e.g., the mica-clad *Onuphionella*; Mens, 2003).

Thomas et al. (2000) applied the concept of "skeleton space" (Thomas and Reif, 1993) to an analysis of Cambrian faunas. The "skeleton space" is an array of general characters and character states of animal skeletons, nearly all of which appears to have been filled by animals at one time or another. Thomas et al. found that in the earliest Cambrian (Tommotian Stage of the Lena River) about half and in the Middle Cambrian (Burgess Shale, British Columbia) more than 80% of this "skeleton space" had been utilized. Although the results are flavored by the ecological and taxonomic structure of the particular faunas, a general conclusion drawn by Thomas et al. is that the skeletal structures that predominate in the Cambrian faunas are such that are related to the simplest possible strategies for increasing body size. This conclusion was reached even though the two faunas investigated are not particularly rich in scleritome-bearing animals, otherwise prime examples of simple strategies to cover a large body with a protective exoskeleton. Such forms appear to have been more diverse in other regions of the early Cambrian world, in particular south China (Qian and Bengtson, 1989) and Australia (Bengtson et al., 1990).

## Mineralizing a Skeleton

Skeletization serves the purpose of making the tissue stiffer (less prone to deformation), tougher (less prone to tearing), or harder (less susceptible to abrasion). Stiffness and hardness can be attained in organic skeletons without mineralization, for example by protein tanning (as in insect cuticles) or the incorporation of metals, or by the agglutination of foreign particles (as in sabellid worms). The strongest skeletons, however, are those that incorporate biominerals to some degree. The biominerals are typically stiff and hard but at the same time brittle. The latter deficiency is overcome by combining the minerals with structural organic matter (mostly proteins and polysaccharides) into composite materials.

The common minerals used are calcium carbonates [$CaCO_3$, mostly calcite, magnesian calcite, and aragonite], calcium phosphates [mostly apatites, particularly carbonate hydroxyapatite (dahllite, $Ca_5(PO_4, CO_3)_3(OH)$)], and opal [a hydrated gel of silica, $SiO_2$]. These are just a small subset of the more than 60 minerals known to be produced by organisms (Lowenstam and Weiner, 1989) - most biominerals are not used in skeletons. The mechanical properties of the skeletal tissue are not greatly dependent on the type of mineral used, but rather on how the mineral is incorporated into the tissue. The physiological cost of producing the mineral is generally small in comparison to that of producing the organic matrix (Bengtson, 1994).

There have been proposals to interpret the appearance of mineralized animal skeletons as a biomineralization event in response to increasing levels of Ca2+ in the ocean water (Brennan et al., 2004; Degens, 1979; Degens et al., 1985; Kaźmierczak et al., 1985; Kempe et al., 1989; Kempe and Kaźmierczak, 1994). Such a relationship is not unlikely with regard to biologically induced calcification (i.e. calcification as a byproduct of an organism's metabolic activity, including detoxification). The massive appearance of cyanobacterial calcification around the Precambrian-Cambrian boundary may well be explained by changes in ocean chemistry (Arp et al., 2001; Riding, 1982; Riding, 2000; Riding and Voronova, 1982). As a general explanation of why animal skeletonization happened around that time it appears insufficient, however. Whereas increased ambient Ca2+ levels may have stimulated biocalcification in animals, the incorporation of the resulting minerals into composite skeletal material does not follow as a necessary consequence. Also, the "Cambrian explosion" involved not only skeletons impregnated with calcium salts, but also spicules constructed of silica (in hexactinellids and demosponges), agglutinating tubes, and purely organic skeletons.

A clue to how skeletal biominerals are selected for may be gathered from a recently discovered scleritome-bearing gastropod living near black smokers at a deep-sea hydrothermal vent (Warén et al., 2003). The sides of the foot of this animal are covered with imbricating scales. The scleritome resembles that seen in certain animals of the Cambrian explosion, but phylogenetic analysis demonstrates that it is a recent acquisition. Although the conch retains the normal gastropod shell mineral, aragonite, the sclerites are instead mineralized with the iron sulfides pyrite and greigite, otherwise unknown as skeletal minerals in the Metazoa (Lowenstam and Weiner, 1989). The main advantage with the iron sulfides in this context does not seem to be their mechanical or magnetic properties, but that they are physiologically cheap to make in this particular environment laden with dissolved sulfide and metal ions. The fact that some Cambrian animals (e.g., tommotiids) made their sclerites with calcium phosphate, others (e.g., halkieriids) with calcium carbonate may thus primarily reflect the availability of carbonate and phosphate ions, respectively, in the environment where they first evolved.

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