

PALEONTOLOGY

Variation and Early Evolution

Gene Hunt

Variation is often said to be the raw material for evolution. In the absence of heritable variation, no mechanism—natural selection included—can cause evolutionary change within populations. That variation is necessary for evolution is uncontroversial, but scientists have long wondered if abundant variation might play a more active role in facilitating or channeling evolutionary change (1, 2). Any evolutionary influence of variation would presumably operate continually, but there have been some indications that during the Early Cambrian (542 to 513 million years ago), the link between variation and evolutionary divergence may have been especially strong.

At roughly the same time as the greatest known burst of biological innovation, the Cambrian Explosion of animal body plans, it appears that species may have been unusually variable in their morphology. Although intriguing, the evidence for this increased Cambrian variability has been somewhat equivocal. However, on page 499 of this issue, Webster (3) presents the results of a novel analysis of trilobite variability that puts this pattern on much firmer empirical footing. He reports that during the heyday of innovation in the Cambrian, trilobite species were in fact unusually variable, more so than at any other time in their history.

Previous suggestions of elevated Cambrian variability involve a variety of taxa, but special emphasis has been placed on trilobites (4, 5), which have by far the richest fossil record during this interval. One commonly cited example is the number of body segments in the thorax of adult trilobites. Within some Cambrian species, this feature is variable, whereas in post-Cambrian trilobites, the number of segments is almost always fixed within species, and often within higher taxonomic levels such as genera and families (6). As interesting as this example is, it applies to only one trait and a small number of trilobite species. More convincing evidence for enhanced variation would require a broader and more systematic survey of characters and traits, but there are formidable obstacles to measuring variation in a meaningful way

across very different traits and taxa.

Webster gets around these difficulties by cleverly exploiting a large set of expert observations already in existence. Since the advent of cladistic methods in systematics, specialists generally represent their morphological obser-

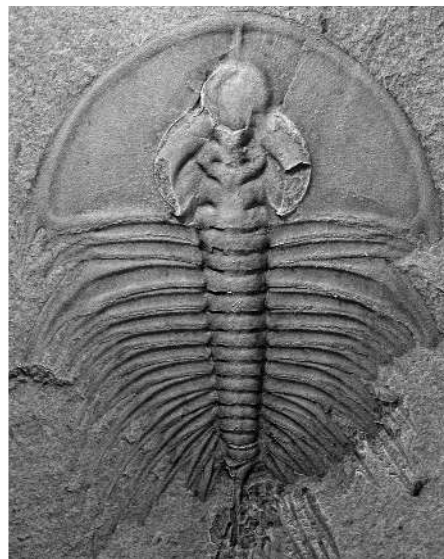
Trilobite fossils provide evidence for elevated morphological variation during the Cambrian Period.

vations as explicitly defined characters with discretely coded character states. For example, a character might reflect the number of ridges in a defined region of the trilobite head, and there would be different character states corresponding to the presence of one ridge, two ridges, and so on. Systematists not only record the character state attributed to each species in a study but also usually indicate for each character which species were variable. Such coding of species represented by individuals with two or more different character states is called “polymorphic” by systematists.

By tracking the preponderance of polymorphic versus invariant characters over time, Webster was able to document a dramatic pattern: In the early intervals of trilobite evolution (the Early and Middle Cambrian), polymorphism was much more common than in any subsequent period of trilobite history. Because the elevated polymorphism was not limited to any particular kinds of traits, trilobite species during these early intervals were very likely to have been exceptionally variable in their overall morphology. Moreover, this period of elevated polymorphism occurs at the same time that trilobites were diversifying taxonomically and morphologically, suggesting to Webster that elevated variation may have promoted the radiation of trilobites. Although this large data set of observations is not a random sample of trilobite lineages or traits, a variety of sensitivity analyses suggest that whatever its biases, they do not appear to change markedly over time.

This study, in establishing the reality of increased Cambrian variability for trilobites, implies that evolutionary processes in the distant past may have acted differently, or in a different balance than in more recent periods of time. The cause or causes for these differences likely relate to the proposed explanations for the extravagant evolutionary inventiveness of this period. These explanations fall into two broad categories: genetic and ecological (7, 8). The former suggest that Cambrian genomes were less constrained, or otherwise less apt to generate profoundly novel morphologies, whereas the latter invoke the relative sparseness of early animal ecosystems in allowing large evolutionary jumps to become successfully established.

As Webster notes, either or both of these



Before and after. (Top) An early Cambrian trilobite from an order (Redlichiida) with highly variable species. (Bottom) An Ordovician trilobite from an order (Phacopida) with less variable species.

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explanations may account for the greater variability of Cambrian trilobites; more loosely organized genomes might be expected to produce a greater range of morphologies, and less occupied adaptive landscapes might be more permissive of the broad production of variants. Nevertheless, this work highlights the uniqueness of the early Cambrian interval in

the evolution of animals and thereby the importance of placing broad evolutionary patterns in a historical and paleontological context.

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MATERIALS SCIENCE

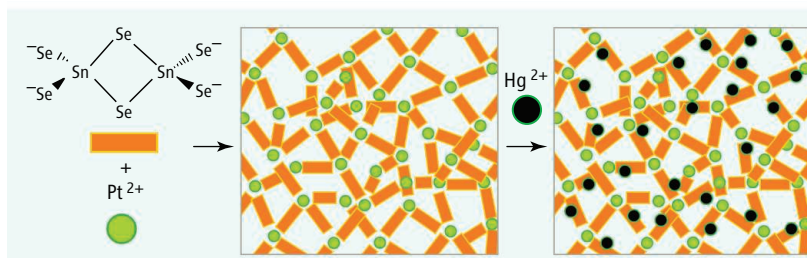
Filling a Void

Stephanie L. Brock

Porous inorganic materials are widely used as filters and catalysts—applications that involve the transport of molecules or ions to reactive surfaces. Such materials include zeolites and mesoporous solids (both of which have ordered pore structures), as well as dried gel structures such as aerogels (with a disordered pore structure). The materials vary in the number, size, and distribution of pores, but with few exceptions, they are oxides. This “chemical exclusivity” has severely limited their potential applications. Thus, zeolites efficiently absorb calcium and magnesium ions and are therefore effective water-softening agents, but they are largely ineffective for remediation of heavy metal ions, such as mercury or lead.

The problem with oxides is that they prefer to form bonds with small metal ions such as magnesium and zinc. Heavy metals are large and polarizable and cannot be effectively bound by porous oxides. One way to get around this problem involves modifying the surface of the oxide so that it presents a larger, more polarizable binding atom, such as a sulfur group, permitting selective adsorption of heavy metal ions (1). On page 490 of this issue, Bag *et al.* report another approach (2): They use a sol-gel reaction to construct porous solids that are analogous to oxides but contain the heavier chalcogenides (such as sulfides or selenides) instead of oxide. The resulting chalcogenide aerogels selectively bind heavy metals without requiring modification.

A few methods for making porous chalcogenide



Chalcogel formation and mercury absorption. Bag *et al.* show that chalcogenide molecular ions or clusters such as $\text{Sn}_2\text{Se}_6^{4-}$ (orange bar) can react with Pt^{2+} (green sphere) in water to form a polymeric cross-linked network. This network can absorb up to ~650 mg of mercury per gram of chalcogel from contaminated solutions.

genide aerogels have previously been reported. These methods used either thiolysis chemistry, in which molecular metal precursors are reacted with hydrogen sulfide (3), or the oxidative condensation of preformed metal chalcogenide nanoparticles (4). The method reported by Bag *et al.* promises additional flexibility because it starts from molecular ions or small clusters of semiconducting metal chalcogenides and uses metal ions as linkers. Both the cluster and the metal ion can be varied to adjust the properties of the resulting material.

This general approach—the linking of chalcogenide clusters with metal ions—has been previously used to prepare mesostructured chalcogenides (5–8). In these studies, surfactants served as templates, organizing the metal chalcogenide component around the micellar structures, analogous to the synthesis of mesoporous aluminosilicate materials (9). However, in contrast to mesoporous aluminosilicates, attempts to remove the surfactant by washing or heating resulted in collapse of the pore structure. The present surfactant-free strategy is simpler, eschewing order completely, yet generating stable porous structures.

Bag *et al.* use a metathesis (or partner-switching) reaction between a metal chalcogenide salt and tetrachloroplatinate in aqueous solution to obtain a solvent-swollen

Random gel networks formed from chalcogenide clusters and metal ions can selectively remove heavy metal ions from water.

chalcogenide polymer. Wringing out this “sponge” without collapsing the structure can be achieved by drying from a supercritical solvent, producing an aerogel [a term that refers to the fact that the pore solvent has been replaced by air (10)].

The chalcogenide aerogels prepared by

Bag *et al.* have high surface areas and can be molded into solid monoliths with densities less than 5% that of a corresponding fully dense material. Like any sponge, they are highly absorbent, but because they are composed from polarizable binding groups, they are particularly effective sponges for heavy metal ions. To test this, Bag *et al.* placed the chalcogenide aerogels in a solution consisting of commonly found (and nontoxic) metal ions with low to moderate polarizability, like zinc, along with rarer (but extremely toxic) highly polarizable ions like mercury. The aerogels preferentially adsorbed the heavy ions, removing 99.9% of the mercury but just 40% of the zinc.

The differences between porous chalcogenides and oxides also extend to their optoelectronic properties. Chalcogenide semiconductors tend to be more covalent than oxides, leading to smaller band gaps (the threshold energy for photon absorption) that can be tuned from the ultraviolet to the infrared. In contrast, most oxide semiconductors absorb in the ultraviolet (think of titanium, a white paint pigment). Thus, the absorption properties of chalcogenides are better matched to the solar spectrum than those of oxides, making them useful for applications such as photocatalysis (11). In the present case, the effective band gap of the

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