A Lopsided Look at Evolution

An analysis of the fossil record reveals some unexpected patterns in the origin of major evolutionary innovations, patterns that presumably reflect the operation of different mechanisms

THE BURGESS SHALE, which was deposited some half billion years ago in what is now British Columbia, offers a window onto an extraordinary period in Earth history. This was a time when evolutionary innovation appears to have been in high gear, generating a wide range of marine organisms where previously there had been few: forms familiar and unfamiliar are entombed in layer upon layer of hardened mud that constitute the shale. Characterized as the Cambrian explosion, this ancient event has long fascinated biologists interested in uncovering the evolutionary processes underlying the paleontological patterns that constitute the record of multicellular life on Earth.

Described recently as "the most important evolutionary event during the entire history of the Metazoa," the Cambrian explosion established virtually all the major animal body forms—Baupläne or phyla—that would exist thereafter, including many that were quickly "weeded out" and became extinct. Compared with the 30 or so extant phyla, some people estimate that the Cambrian explosion may have generated as many as 100. The evolutionary innovation of the Precambrian/Cambrian boundary had clearly been extremely broad: "unprecedented and unsurpassed," as James Valentine of the University of California, Santa Barbara, recently put it.

It is easy to explain why the Cambrian explosion was unprecedented in producing a great array of novel body forms: it was close to the origin of multicellular organisms, and so there could have been little previous opportunity. (The rate at which it happened is, however, impressive.) But why has this burst of evolutionary invention never again been equaled? Why, in subsequent periods of great evolutionary activity when countless species, genera, and families arose, have there been no new animal body plans produced, no new phyla?

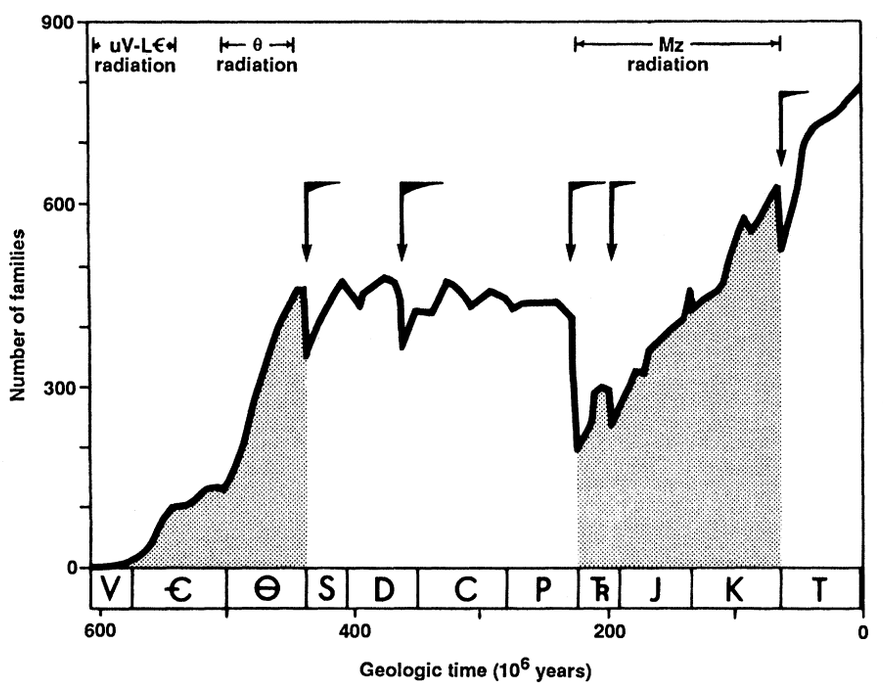
This strikingly asymmetric pattern demands explanation, not only in itself but also in what it might imply about the origin of major evolutionary innovation in general. This is especially important because, as David Jablonski, of the University of Chicago, and David Bottjer, of the University of Southern California, recently observed: "The most dramatic kinds of evolutionary novelty, major innovations, are among the least understood components of the evolutionary process." Valentine and Jablonski and Bottjer have recently been addressing this issue: Valentine using the temporal asymmetry of the Cambrian explosion, and Jablonski and Bottjer the spatial asymmetry of later evolutionary events in the marine realm.

"A widely held view has been that higher taxa, and therefore Baupläne, are created by the same processes of microevolution which are responsible for [the origin of new species], but acting over long periods of time to produce great morphological divergence," says Valentine. From their separate but convergent perspectives, Valentine and Jablonski and Bottjer reject this view. "Different patterns imply different processes," say Jablonski and Bottjer, succinctly stating their conclusion that evolution operates in different ways at different levels in the genealogical hierarchy (species at the bottom, phyla at the top).

The fact that all existing (and many extinct) phyla arose during that burst of evolutionary activity at the Precambrian/Cambrian boundary is striking enough. And it could be explained in part, perhaps, by arguing that never again would there be another similar opportunity: specifically, to fill an otherwise biologically empty world. Except, of course, that it is not true.

Valentine, in company with Douglas Erwin of Michigan State University and John Sepkoski of the University of Chicago, compared the Cambrian explosion with events that followed the great Permian extinction some 200 million years ago, which pushed upwards of 96% of species to extinction. The post-Permian world was therefore about as biologically empty as the Precambrian world.

"In each case, a strong diversification ensued," note Erwin and his colleagues. "Phanerozoic diversity trends are best known at the family level, where the pace of these two diversifications appears rather similar. At still higher taxonomic levels, however, the diversifications were significantly different: large numbers of phyla and



Two bursts of diversification, *300 million years apart, were quantitatively but not qualitatively comparable.* [*D. H. Erwin* et al., Evolution ***41***, *1177 (1988)*]

classes burst upon the scene during the early Paleozoic, while none are known to have originated immediately following the Late Permian mass extinction."

In other words, there appeared to have been the opportunity in the wake of the Permian extinction to replay quantitatively and qualitatively the events of the Cambrian explosion. But it did not happen. Both bursts of diversification generated about 450 new families, making the two periods quantitatively similar. However, as one goes up the genealogical hierarchy—from orders to classes to phyla—there is a rapidly increasing bias toward origination in the first of the two great diversifications. Clearly, the two periods were distinctly different qualitatively: the first produced many new themes, the second variations upon established themes.

Several possible patterns exist for the establishment of higher taxa, the two most obvious ones of which are the bottom-up and the top-down approaches. In the first, evolutionary novelties could emerge bit by bit, eventually creating sufficient morphological distance between the first and the last species to merit order, class, or phylum distinction. Or, a punctuational shift might occur, rapidly establishing a new higher taxon and from which incremental variants at lower levels would develop. The Cambrian explosion appears to conform to the second pattern, the top-down effect.

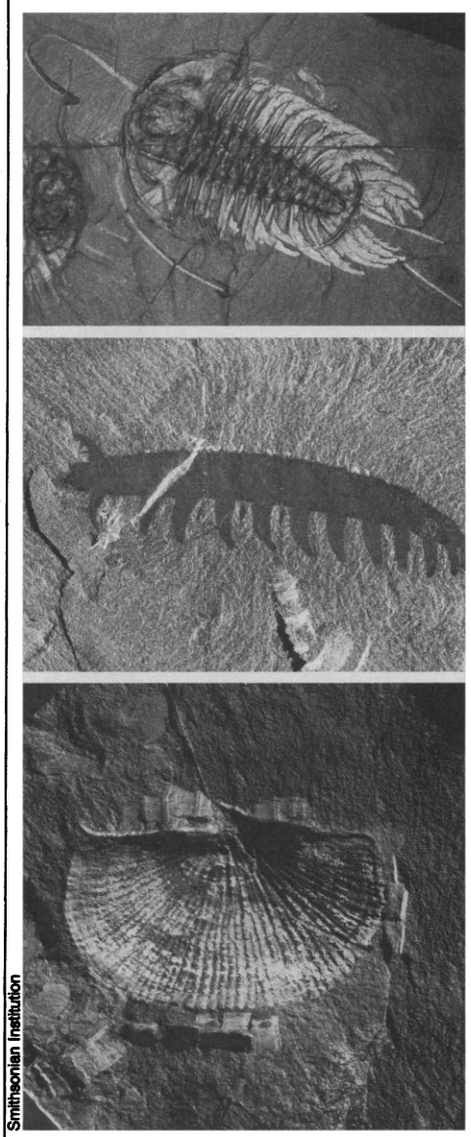
"The fossil record suggests that the major pulses of diversification of phyla occurs before that of classes, classes before that of orders, and orders before that of families," say Erwin and his colleagues. "This is not to say that higher taxa originated before species (each phylum, class, or order contained at least one species, genus, family, etc. upon appearance), but the higher taxa do not seem to have diverged through an accumulation of lower taxa."

Looking at the overall pattern of major evolutionary innovation, the question remains of why it should be concentrated in the earlier period, around the Precambrian/Cambrian transition. Two principal hypotheses have been offered over the years, the ecological hypothesis and the genomic hypothesis.

"The ecological hypothesis holds that the low-diversity marine faunas of the early Paleozoic afforded an ecological setting of greater opportunity for the establishment of divergent morphologies than did later times," explain Jablonski and Bottjer. The idea here is that evolutionary innovation is in fact rather constant, but that new forms become established only when there is sufficient "adaptive space" to accommodate them. Even poorly adapted innovations might have survived initially, because of the limited level of competition in early Cambrian times.

However, as competition got tougher, some of the forms would be lost, thus perhaps explaining in part the reduction of phyla from as many as 100 to the current 30 or so. "Thus, the long-term taxonomic patterns reflect the restriction of ecological opportunities as the biosphere becomes increasingly densely occupied," suggest Jablonski and Bottjer.

The genomic hypothesis holds that in early Metazoan history genomes were less tightly canalized, so that mutations could more readily generate major shifts in developmental programs. As a result, major morphological variants could more readily become established. Later in Earth history, when genomes had become more canalized, such major shifts became difficult if not impossible. "Thus, there is a real temporal bias in the generation of major innovations, dictated by evolution in genome organization," say Jablonski and Bottjer.



Ghosts from the Cambrian, *the first glimpse of the complex world of multicellular organisms. (Top)* Olenoides serratus. *(Middle)* Ayshesia pedunculata. *(Bottom)* Nisusia burgessensis.

Of the two hypotheses, the ecological model has traditionally attracted most support, and Erwin and his colleagues lean in this direction in their latest analysis. They argue that, although the Precambrian and post-Permian worlds were equally biologically empty, there was an important difference. In spite of sparsity of species in the post-Permian world, the species present effectively covered a wide range of biological adaptations: the "adaptive space" was full, thus preempting evolutionary innovation. By contrast, the Precambrian world had few species and few Baupläne: its adaptive space was therefore virtually empty, allowing widespread "experimentation."

Erwin and his colleagues conclude that the data from these two great diversifications "are consistent with the hypothesis that it is the extent and pattern of occupation of adaptive space (and the extent of evolutionary opportunity which results therefrom) that was the primary factor in the rise of major evolutionary novelties among metazoans."

This argument undoubtedly is correct, but, as Jablonski and Bottjer point out, these data are also consistent with the genomic hypothesis: there is no exclusive test for either model. And indeed the two models may not be mutually exclusive. Moreover, it is likely that evolutionary innovation in the later periods of Earth history was to some extent shackled by various forms of historical constraint: having become specialized in various ways, later body plans may simply have fewer morphological options to explore. Erwin and his colleagues acknowledge this issue, but still plump for external—ecological—rather than internal constraints.

The ecological model is, however, attracting less support than it once did. "I don't like the empty niche idea," says Elisabeth Vrba of Yale University. "Invoking the notion of adaptive space is a knee-jerk reaction. I think we should be looking for internal constraints." One notion that Vrba and an increasing number of biologists favor has to do with the evolution of individuality, a hypothesis proposed recently by Leo Buss of Yale University.

"The central theme is the inherent conflict between selection at the level of cell lineages and selection at the level of the individual organism," says Buss. "What we see in the fossil record of the Phanerozoic is a resolution of that conflict."

Very simply, the argument runs as follows. The evolutionary interests of single cells are to vary and proliferate as much as possible, and this is fine as long as they are single-celled organisms. But once cells are part of a multicellular organism, unbounded variation and proliferation become inimical to the individual. The resolution has been progressively to isolate germline cells and embryological development from the individual, a tactic that has not only rescued the individual from danger but also has constrained variation. "I think this reduced variation is part of the explanation of the lack of phylum-level evolution in the post-Permian," says Buss.

The issue of differences in evolutionary innovation at different levels of the genealogical hierarchy arises not just in temporal comparisons, like that between the Cambrian and Permian, but also in spatial comparisons. For instance, Jablonski and Bottjer analyzed evolutionary innovation in benthic marine organisms and discovered a distinct—and unexpected—pattern. Higher taxa—orders—preferentially arise in shallow-water, onshore environments. "Expectations might have put originations in more stable environments offshore," they noted recently. "Or, if successful innovation is largely a matter of the chance combination of novelty and opportunity, in a bathymetrically random distribution."

Moreover, taxa below orders in the hierarchy—families and genera—arise preferentially in offshore environments. "We could not have predicted the pattern at the ordinal level from the pattern shown by genera and families." Jablonski and Bottjer were able to show that the pattern is not an artifact of preservation: it is real and therefore must be saying something about evolutionary mechanisms. The most obvious message is that a simple extrapolation from one level to another is an unlikely explanation of evolutionary innovation at the different levels.

Currently there is a multitude of possible explanations for this pattern, none of which is more compelling than any other. For now, however, the major point is as Jablonski and Bottjer state: "In terms of the ecology of their evolutionary origins, higher taxa seem to have properties all of their own." In fact, higher taxa may have several properties all of their own, and evolutionary theory must strive to accommodate this.

■ ROGER LEWIN

ADDITIONAL READING

L. W. Buss, *The Evolution of Individuality*. (Princeton Univ. Press, Princeton, NJ, 1987).

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Eye Cancer Gene Linked to New Malignancies

Retinoblastoma gene loss may contribute to the development of breast cancer and small cell lung cancer in addition to the relatively rare retinoblastomas

A FEW YEARS AGO, researchers learned that retinoblastomas, highly malignant tumors that arise in the retina of the eye, are caused by the loss or inactivation of a particular gene, known as the retinoblastoma (RB) gene. More recent research suggests that RB gene inactivation may also contribute to the development of two additional types of cancer, namely breast cancer and small cell lung cancer, that occur much more frequently than the uncommon retinoblastomas.

"This gene, and others like it, may have a fundamental role in the genesis of many tumors, not just the rare eye tumor," says J. William Harbour a medical student who is a Howard Hughes Medical Institute Scholar at the Navy Medical Oncology Branch of the National Cancer Institute (NCI) in Bethesda, Maryland. Retinoblastoma afflicts only about 1,000 patients every year in the United States, whereas some 130,000 individuals develop breast cancer and another 30,000 get small cell lung cancer annually.

The new results may eventually have implications for treating breast cancer and small cell lung cancer, and also for predicting who will get the malignancies. Moreover, the RB gene studies are providing a better understanding not just of carcinogenesis, but of normal cell growth as well.

In particular, they lend further credence to the view that growth inhibitory forces may be just as important to the life of the cell as growth stimulatory forces. The assumption is that the protein encoded by the RB gene normally suppresses cell division. Its loss then causes retinal cells to grow out of control and become cancerous.

One reason why cancer researchers find the RB gene so interesting is that its inactivation may be an early, perhaps even an initiating, event in carcinogenesis. This appears to be the case for retinoblastoma at least.

About half of retinoblastoma patients have an inheritable form of the tumor in which they acquired one bad or deleted copy of the RB gene from their mother's egg or father's sperm. This almost guarantees that retinoblastoma will develop. Some 90% of these individuals get the eye cancer at an early age, usually before they are 3 years old. Another mutation to knock out the second copy of the gene in retinal cells is also required, but this is apparently a frequent event.

Researchers began looking at the RB gene in breast cancer cells partly because of observations about the inheritance patterns of the malignancy. Over the past several years, improved therapies have greatly increased the survival rate of the retinoblastoma patients, and clinicians began to find that children who had been successfully treated for the inheritable form of the disease developed other types of cancer, especially sarcomas such as osteosarcoma (a bone cancer), at higher than expected rates.

Moreover, clinicians are seeing more cases of breast cancer in the survivors of inheritable retinoblastoma, although it is too early to tell whether this represents a true increase in the incidence of the disease in the group. The mothers of children with osteosarcoma do have an increased risk of developing breast cancer, however.

These observations suggested that the same RB gene defect that confers susceptibility to retinoblastoma might increase susceptibilities to the other cancers as well. This was soon confirmed for osteosarcoma. In retinoblastoma cells, both copies of the RB gene are either deleted or so badly rearranged that they cannot be functional. The same thing was happening to the gene in osteosarcoma cells.

Two groups have now shown that comparable RB gene abnormalities occur in breast cancer cells. In a report published in the 8 July issue of *Science* (p. 218), Eva Lee, Wen-Hwa Lee, and their colleagues at the University of California School of Medicine at San Diego describe results showing that two of nine lines of breast cancer cells have the abnormalities and also fail to make detectable RB protein. In addition, Yuen-Kai Fung of the University of Southern California School of Medicine and his colleagues have found RB gene deletions or other abnormalities in 5 of 16 lines of