

EVOLUTION

Life's Winners Keep Their Poise in Tough Times

More than a century ago, paleontologists discerned three great waves of animals in the fossil record. First came the trilobites, the clamlike stalked brachiopods, and other "old life" of the Paleozoic era; next was the "middle life" of the Mesozoic, including reptiles and marine ammonites; and last was the "new life" of the Cenozoic, when mammals, clams, snails, ray-finned fish, and others rose to dominance. But what caused these great tides in evolutionary history, and what gave later organisms the edge over their predecessors? Now, a pair of paleontologists say they have identified a trait that may have helped decide winners in the fight for evolutionary dominance: the ability to buffer the body from environmental insults.

At the annual meeting of the Geological Society of America last month in Salt Lake City, paleontologists Richard Bambach of the Virginia Polytechnic Institute and State University in Blacksburg and Andrew Knoll of Harvard University reported that at least in the sea, what they call "buffered physiology" played a central role in determining evolutionary winners and losers during the past half-billion years. Organisms that could buffer their internal organs from changes in ocean chemistry were less likely to be wiped out and more likely to rebound after a mass extinction than were their more sensitive neighbors, these researchers found. "I think they're onto something," paleontologist David Bottjer of the University of Southern California in Los Angeles says of the team's work. "Why does the last 550 million years conveniently break out into three long intervals? Maybe Bambach and Knoll have the solution."

If Bambach and Knoll have even the beginnings of an explanation for the history of life, it's because they had already tried to explain one brief

chapter of it: the greatest of all the mass extinctions, which ended the Paleozoic 250 million years ago between the Permian and Triassic periods (*Science*, 7 November, p. 1017). They and their colleagues proposed that a stagnant deep sea belched a massive slug of toxic carbon

dioxide into shallow waters, wiping out 90% of all the animal species in the ocean (*Science*, 1 December 1995, p. 1441). To support that contention, they sorted animals by their inferred sensitivity to high carbon dioxide levels. They found that sensitive animals suffered greatly, while those more tolerant of carbon dioxide suffered far less.

Bambach and Knoll have now generalized this notion of physiological sensitivity to the past 550 million years. Using a database of all known marine genera prepared by John Sepkoski of the University of Chicago, the team sorted animals according to whether they have some control over the flow of gases and ions between their tissues and seawater; that ability might determine an animal's sensitivity to environmental stresses such as high carbon dioxide, low oxygen, toxic metals, or high acidity. For example, organisms with closed circulation systems, special gas-exchange organs like gills, or both—such as most mollusks, worms, and arthropods—tended to be buffered from the vagaries of seawater chemistry. But animals whose tissues were chemically open to the sea, such as most sponges, sea urchins, corals, brachiopods, and the flowerlike crinoids, lacked this physiological advantage.

Plotted through time, the buffered and unbuffered animal genera behaved quite differently. Early in the Paleozoic, the unbuffered creatures quickly diversified to about 750 genera, twice as many as the buffered, although Bambach can't say exactly why this group was the early winner. After 200 million years of dominance by unbuffered animals, things changed at the Permo-Triassic extinction.

Both groups suffered greatly, but the unbuffered organisms were hit harder, losing 90% of their genera versus 50% for the buffered. Then, although both groups recovered, the buffered group overtook the unbuffered, eventually attaining the level of diversity the

unbuffered had enjoyed in the Paleozoic. The rules of the game changed again 65 million years ago at the Cretaceous-Tertiary mass extinction. Once again, the unbuffered suffered more, but this time the buffered animals diversified rapidly enough after the extinction to quickly gain a 2:1 edge in diversity; their continued dominance can be seen in the seas today.

The long ascendancy of unbuffered animals in the Paleozoic, says David Jablonski of the University of Chicago, is "yet another validation of the idea that incumbency is important." A species occupying a particular ecological niche may be no better adapted to it than a newcomer species, but the incumbent, which already has a lock on the available resources, usually wins out. "Paleozoic diversity was stuck," says Bambach, with the unbuffered dominating the presumably more capable buffered animals, until the Permo-Triassic extinction broke down the system and allowed the buffered genera to proliferate into the emptied niches.

This new perspective on the history of life also elevates the Cretaceous-Tertiary extinction to the status of a megaevent in the oceans as well as on land. When gauged solely by the number of species lost, the Permo-Triassic extinction towers over the Cretaceous-Tertiary and three other mass extinctions, at least among sea creatures. But the buffered-unbuffered distinction makes the transforming role of the Cretaceous-Tertiary clear. "The two era-ending extinction events are involved in altering the diversity of life in the oceans so completely that ecosystems had to reorganize the way they work," says Bambach.

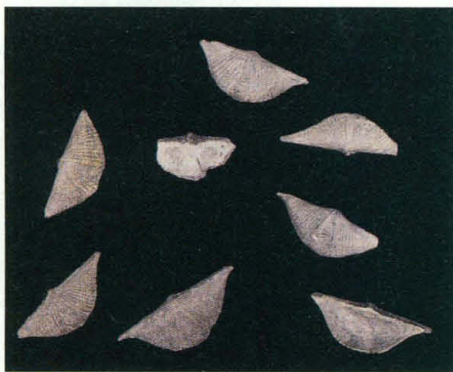
Paleontologists who heard Bambach describe the work at the meeting are impressed. "The physiological explanation is a very seductive one," says Jablonski. "It's going to be really worth digging into. My only hesitation is that correlation is not necessarily causation. It may not be physiology that actually determines the pattern," but some other trait that happens to accompany it.

Bambach and Knoll are open to the idea that something else may be the real cause of the pattern they see. Bambach notes one candidate: Buffered animals are typically also more ecologically and anatomically plastic, capable of taking up new modes of life when given the opportunity. "A coral will never have teeth or swim," as he puts it. He and Knoll are seeking to identify such traits, says Bambach: "This is the beginning of the study, not the end."

—Richard A. Kerr



A winner. Mollusks' robust physiology may have helped them survive.



Losers. Most brachiopods vanished in the Permo-Triassic extinction.