Sizing Up Evolutionary Radiations

By gauging life's diversity from differences in body size and shape rather than numbers of species, paleontologists are gleaning surprising new insights about adaptive radiations

Imagine the world just after a mass extinction. The slate of species has been wiped nearly clean, and those that are left are vying with one another to expand into a relatively empty environment. Some organisms will blossom into a wealth of new forms while others remain locked in their old ways of life—but which ones, and why?

For years, paleontologists have sought to discern the rules in life's long-running game of diversity by charting the species, genera, and families that flourished in evolutionary radiations. But a growing number of researchers have become discontented with that traditional method, charging that taxonomic divisions can create a false flurry of diversity or mask a true flowering of form. On pages 1489 and 1492, two independent papers offer a new way of studying such radiations, by analyzing the physical traits of the fossils themselves—and largely ignoring their classification.

This new method is bringing about what paleobiologist Douglas H. Erwin of the National Museum of Natural History calls a "quiet revolution" in paleontology: a shift from qualitative descriptions of species and higher taxa to quantitative measurements of more universal traits such as tooth shape. "These new quantitative methods will illuminate the fossil record and help us get at the causes of diversity in ways that you never could using the purely descriptive taxonomic approach," explains James W. Valentine, a paleobiologist at the University of California, Berkeley, and himself a pioneer in the older style of diversity analyses.

Indeed, the new studies show that changes in morphology—the size and shape of an organism—often capture broad evolutionary trends that may be missed if only the taxa are tallied. For example, the paper by Mike Foote, a paleobiologist at the University of Chicago, examines the changes in the morphology of crinoids (mainly stalked, sedentary animals that flourished in ancient oceans) during two radiations—and finds more diversity in the second expansion than the taxonomical count suggests. Similarly, Jukka Jernvall, an evolutionary biologist at the University of Helsinki in Finland, and colleagues show that the evolutionary ups and downs of ungulates (hoofed mammals, such as horses), as measured by key features in their molars, don't always track their taxonomic diversity. "That's what's so great" about these papers, says Christine Janis, a mammalian paleobiologist at Brown University. "They've found an innovative way to look at morphology that is independent of taxonomy."

And in decoupling morphology from taxonomy, she and others note, these studies allow researchers to probe more deeply into the ecological forces thought to influence adaptive radiations. For example, by showing that the crinoids rapidly radiated into a similarly diverse spectrum of forms in two ecologically different periods, Foote's work raises the heretical notion that competition from other organisms may not impede evolutionary expansion. And Jernvall's work, by identifying a common adaptation in the molar teeth of ungulates during one radiation, documents a link between ungulate diversification and a shift in climate. "There are questions in evolutionary radiations that are fundamentally ecological," says Foote. "The best way to address those is by measuring the diversity of morphology in organisms, because that is likely to reflect the diversity of their ecology."

When sea lilies flowered. The crinoids radiated into many forms in ancient seas, as in this ocean scene about 330 million years ago.

Crinoid comebacks

Studies of the diversity of past life took off in the early 1980s, as researchers began to test a model presented by Valentine that estimates how fast new taxa appear in relatively empty environments. Later studies sought the rules behind evolutionary radiations by comparing the numbers of taxa that appeared in different events, but the results were sometimes confusing. For example, Erwin and colleagues compared diversification among all marine animal families during life's initial burst of innovation starting 600 million years ago in the early Paleozoic, and about 225 million years later after the worst extinction in history, the Permo-Triassic event.

This catastrophe wiped out many of the orders, classes, and phyla that had made their first appearance in the early Paleozoic. "That left a lot of empty ecological space," says Erwin, "so we thought we'd see that same kind of innovation [and many originations of higher taxa] in the early Mesozoic." Instead, although some new orders appeared, no new classes or phyla arose; most of the expansion occurred at the family level. "There should have been a lot of [morphological] experimentation going on," says Erwin, "but we couldn't find it" in the taxonomic data.

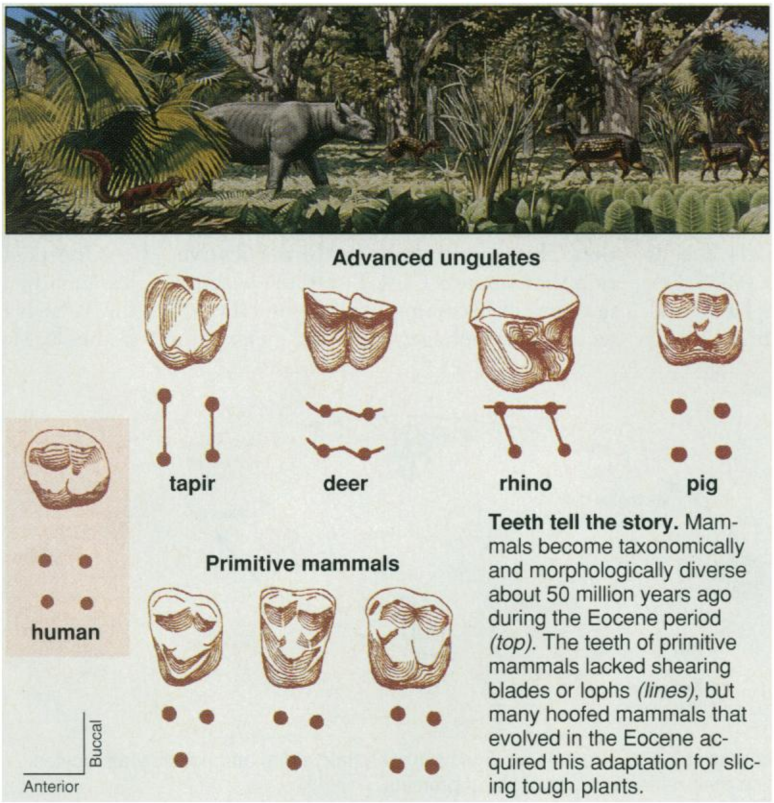
Critics suggested that the classification of the fossils may have biased their results: What is called a family in the Triassic might be recognized as an order in the Cambrian, as taxonomists gave higher rank to new forms earlier in the history of life. If so, comparing Cambrian and Triassic families was like comparing apples and oranges. "That's always the problem when you use taxa as a proxy for morphology," says Erwin.

To avoid this problem, Foote and others pioneered methods to assess evolutionary radiations strictly by measuring the amount of morphological change in organisms. Paleontologists also use morphology to define taxa, but the focus is different: In taxonomic studies, researchers look for details that separate organisms from one another, while Foote and Jernvall sought a subset of traits to use as a "universal ruler" to measure trends in a broad group of organisms. For example, in his current paper, Foote assesses the fate of all the crinoids during a 450-million-year period, from their first appearance about 500 million years ago and subsequent rapid diversification, to their catastrophic extinction in the Permo-Triassic event—when only one lineage survived—and phoenixlike radiation once again in the Triassic.

He focused on 69 discrete features of these invertebrates, including body symmetry, the length of the stalk supporting the body, and the number and density of their feathery feeding arms, all of which are well preserved in the fossil record because of the crinoids' calcium carbonate skeleton. He measured how 355 species differed from one another in each of these 69 characteristics during the two radiations. And he found that in both of them, crinoids achieved a roughly similar range of anatomical design, and in about the same time frame—30 million to 40 million years. In other words, for the Triassic radiation, he discovered Erwin's missing morphological experiments. "The experimentation is there in the morphology," says Erwin of Foote's work.

The extent of the experimentation surprises some paleontologists, however, because even after the extinction, the Triassic marine world was more crowded and competitive than the wide-open oceans of the early Paleozoic. "That's what makes it such an interesting radiation," says Foote. "They get a second chance to diversify, but in different ecological circumstances." Yet the new ecology seems to have had little effect on the crinoid radiation.

That's a remarkable result, says Brian Farrell, an evolutionary biologist at Harvard University: "One of the principles of ecology is that whoever is the incumbent has the advantage. But in this case, even with the cards stacked against them, the crinoids still took off like crazy." This success in the face of competition raises the radical notion that "such radiations are not really dependent on the availability of open niches," adds Michael Sanderson, a phylogenetic systematist at the University of California, Davis. But Sanderson and Foote caution that this pattern has not yet been quantitatively shown in other groups, and that there could be other explanations for the data. "What this emphasizes is our need to know more about the nature of recoveries after mass extinctions," says Erwin.



Teeth tell the story. Mammals become taxonomically and morphologically diverse about 50 million years ago during the Eocene period *(top)*. The teeth of primitive mammals lacked shearing blades or lophs *(lines)*, but many hoofed mammals that evolved in the Eocene acquired this adaptation for slicing tough plants.

TEETH ILLUSTRATION: J. JERNVALL PAINTING: ROBERT J. BARBER/AMERICAN MUSEUM OF NATURAL HISTORY

Tracing mammals by their teeth

The next great extinction, at the Cretaceous-Tertiary boundary, didn't decimate the crinoids, but it did obliterate the dinosaurs and pave the way for rapid diversification in the mammals. Many taxonomic analyses have shown a burst of new mammalian species in the early Eocene about 50 million years ago, including many new ungulates. Jernvall's team studied this radiation by analyzing changes in the ungulates' upper second molars, choosing teeth because they can be linked to diet and thus to the animal's ecology. "We developed criteria to divide teeth into discrete crown types," explains Jernvall, "so then we could look at the ungulates like you do cars on the road: Some are very similar, and some are very different."

For example, a modern deer's molar has two pairs of cusps, joined longitudinally by parallel shearing blades called lophs, while a modern pig's molar shows only four cusps and no lophs (see diagram). Those shapes reflect the animals' diets: The herbivorous deer needs the shearing action of the lophs to slice through tough foliage, but the fruit- and nut-eating pig doesn't.

Jernvall's team then applied its crown criteria to the ungulates' radiation in the Eocene, about 50 million years ago. These animals reached a peak in taxonomic diversity in the late Eocene, and their teeth reflect this diversity peak, says Jernvall. "The Eocene was the time when the ungulates had the most ways of making a living, as we showed by using the crown types as a measure of their ecological niches." For instance, some primitive ungulates may have been partially carnivorous and so lacked the foliage-cutting lophs, while others were developing them.

In the Oligocene, ungulate genera crashed to pre-Eocene levels, and many of the animals with molars in between these extremes went extinct. But like the crinoids, the ungulate taxa staged a comeback, expanding in the Miocene, some 25 million years ago. Yet this radiation was different from the first, says Jernvall, because although the animals once again became taxonomically diverse, the morphological diversity of their teeth was lower. "A simple-minded view might hold that as lineages become diverse, so does morphology," says Sanderson. "But that's not always the case, as their study shows. And because the morphology can be decoupled from the taxonomy, you get a better idea of what was behind the animals' radiation."

For the Miocene ungulates, it was apparently the shearing-blade lophs that enabled them to spread, says Jernvall. "Those with lophs had an evolutionary edge. They were the ones that diversified." That advantage can be clearly seen in the Miocene ungulates of North America, Europe, and Asia. On average, the ungulates from these separate regions evolved nearly the same number of lophs on their molars, although the details of tooth shape differed. "That was a great surprise," says Jernvall. "It meant that the loph number was picking up something shared by those three regions."

That something was the environment, specifically, a global cooling that led to an increase of forest clearings in the Miocene, explains John P. Hunter, a co-author on the paper and a paleobiologist at the New York College of Osteopathic Medicine: "And that change in the ungulate's world—in what there is to eat—is reflected in their teeth."

The molars can thus be used to distinguish between two types of radiation, the authors say. The ungulates' Eocene radiation was a generalized expansion into many different niches, but their second radiation produced new species adapted to a specific way of life: browsing and grazing. "What's intriguing is that they've tied the ungulates' radiation to a mechanism: climate change," says Farrell. "It's a great demonstration of how ecology can drive this whole radiation," adds Erwin.

While both papers cast more light on the nature of adaptive radiations, they also raise questions. Indeed, the next step for both studies, says Erwin, is to bring the taxonomy back in, to see how the changes in morphology relate to the organisms' phylogeny. Still, he and others say that the papers convincingly demonstrate the advantages of decoupling morphology and taxonomy. Brown's Janis, for one, expects that new revelations will appear as the method spreads. Both groups have "made real breakthroughs in detecting important patterns in paleobiology," she adds. "I hope people use them as a model."

–Virginia Morell