PROFILE

Profile of David Jablonski

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Human activities are creating major environmental changes on the planet, contributing to habitat loss, climate change, pollution, and consumption of natural resources. Such changes place enormous pressures on biodiversity, disrupting long-standing evolutionary processes. David Jablonski, a paleontologist at the University of Chicago and a recently elected member of the National Academy of Sciences, integrates studies of past originations and extinctions of species and higher taxa with data on the distributions and evolutionary relationships of living species to provide a multidimensional picture of how biodiversity has worked over geological timescales. Jablonski's research has focused primarily on the extraordinarily abundant and well-preserved fossils of marine bivalves, such as scallops, cockles, oysters, and mussels, and has helped to reveal how these organisms and their spatial distributions have evolved over space and time. His findings could shed light on the origins of global variations in diversity, how evolutionary lineages collapse or rebound from mass extinctions, and how evolutionary processes might operate at several levels at once. These findings may even provide lessons for the future preservation of biodiversity.

Nights at the Museum

By the time he was five years old, Jablonski knew he wanted to be a paleontologist. Born in New York City, Jablonski grew up near the American Museum of Natural History, his self-described "home away from home," where he became fascinated with the museum's dinosaur fossils from a very early age. His parents, both writers, encouraged what Jablonski calls an "intellectually freewheeling existence," and gave him the freedom to follow his passion.

As an undergraduate at Columbia University in the early 1970s, Jablonski made regular visits to the museum, but did so in a city-wide work-study program called the Urban Corps. "It was one of the great thrills of my life," Jablonski says. "One day I was wandering the halls of the museum and the next day I was behind the scenes working for people there." At the museum, the prominent invertebrate paleontologists Roger Batten, Norman Newell, and Niles Eldredge taught Jablonski to look at fossils as objects of serious scientific study and allowed him to sit in on their lively graduate seminars. "That's when I began to get a much better sense of paleontology as a profession and as a science," he says.

Then, in 1973, Jablonski says he had an epiphany after reading the book *Evolutionary Paleoecology of the Marine Biosphere*, by James W. Valentine (1), realizing that he could potentially use the marine fossil record to answer some of the big, open questions in the fields of evolution and ecology, such as the environmental factors that govern the emergence of new species and the impacts of mass extinctions on evolutionary patterns. "This book changed my life. It was so ambitious and so creative that I realized that this was what I wanted to do," Jablonski says. Also, thanks to Valentine's book, Jablonski decided that he wanted to be both a biologist and a geologist. "I even conned the Dean of Students at Columbia into letting me do a double major in biology and geology, which was relatively unusual at the time," he recalls.

Paleobiological Revolution

During this time, Jablonski witnessed a revolution in the field of paleobiology as it moved away from an emphasis on using fossils for environmental information and relative age-determination, and as confirmatory support for existing evolutionary ideas. The field was morphing into a theoretical discipline that expanded the range of evolutionary mechanisms that operated over long timescales (2), beginning with Stephen Jay Gould's and Niles Eldredge's landmark argument for punctuated equilibrium (3), which held that species are relatively stable over long time intervals and show "punctuated" evolutionary changes concentrated in sudden, isolated episodes.

Jablonski found the punctuated equilibrium model particularly fascinating, because he had already been pondering the problem of how to extrapolate from short-term continuous, gradual changes in observable populations to the long-term, large-scale shifts seen in the geologic record. "As an undergraduate, I'd taken courses in evolutionary biology and ecology, and they were very stubbornly fine-scale; the way that you studied evolution or ecology was that you simply extrapolated from the year or two years or three years of a study to millions of years," Jablonski says. "I wanted to know if you really could do that." He began thinking about how he could convert largely theoretical and somewhat abstract ideas into hypotheses that could be tested with data from the geological record.

David Jablonski in one of his favorite field areas, the Smithsonian collections. Image courtesy of Susan M. Kidwell.

As Jablonski neared the completion of his undergraduate degree, Rhodes Fairbridge, a geology professor at Columbia University, recruited him to coedit *The Encyclopedia of Paleontology*. By the time Jablonski started graduate school at Yale University in the mid-1970s, he had contacted more than 100 prominent paleontologists and had begun editing their contributed articles. More importantly, Jablonski had established working relationships with some of the field's heavyweights, including James Valentine, Thomas Schopf, Steven Stanley, and David Raup. "I had a reason to walk up to them at meetings, which is sort of hard to

This is a Profile of a recently elected member of the National Academy of Sciences to accompany the member's Inaugural Article on page 10487.

do when you're a starting graduate student," Jablonski says.

Jablonski's graduate research grew out of his undergraduate work on fossilized shells from the Late Cretaceous Period, roughly 65–80 million years ago, shortly before the mass extinction that wiped out the dinosaurs. "Thanks to Norman Newell, I worked up some fossil samples from some Late Cretaceous localities that were just amazingly well preserved," Jablonski recalls. "It was as if you picked them up off a beach today." The beauty of the fossils captured his imagination and opened doors for new directions of study.

A Rocky Start

Jablonski knew that if he wanted to work on Late Cretaceous fossils, he would need to gain experience in the rocks of that age, so he went to Yale to work with Karl Waage, a paleontologist who specialized in that time interval. While at Yale, Jablonski interacted with Rudolf Scheltema at the Woods Hole Oceanographic Institution in Massachusetts, who had recently written a paper about larval ecology and evolutionary rates in snails (4). Scheltema held that methods for inferring modes of larval development in living species could be applied to fossil shells if they were sufficiently well-preserved. "That was fantastic," Jablonski recalls. "Here was a way of looking at the life history strategies of species that were extinct for 75 million years." That insight helped Jablonski shape an idea for a research project: he would examine his Late Cretaceous fossils to explore how biotic factors, like modes of larval development, influenced origination and extinction rates and the dynamics of lineages in the fossil record.

Jablonski's thesis plan met with some skepticism in his department, however. "I don't think they quite saw how exciting a set of questions these were, how feasible it would be to answer those questions, and how powerful an evolutionary laboratory the Late Cretaceous could be if you did it right," Jablonski says. About halfway through his graduate career, he wrote a letter to Gould at Harvard University. "He wrote back a remarkable letter. It's probably the most important letter I've gotten in my career, in which he basically said, 'you're doing interesting stuff, you're on the right track, stick with it.'" With that sort of encouragement, Jablonski persevered. Norman Sohl of the United States Geological Survey was also a supporter. "He helped me begin to get my eye for identifying these fossils, which was especially valuable because I was looking at the early growth stages of these shells, and those can be very difficult to identify," Jablonski recalls.

Jablonski soon set off on a fossil-collecting spree from New Jersey to Texas, and also examined collections of Late Cretaceous fossils housed in various museums, keeping detailed notes and drawings of each specimen on a series of index cards, one for each species in the region. He analyzed the many hundreds of species recorded in a period of nearly 16 million years of the Cretaceous Period, and some interesting patterns began to emerge. "I found that I could see rules of extinction and survival according to life habits and geographic range sizes. I could even predict the species durations based on the mode of development, which I got from the fossil larval shells," Jablonski says. This work also allowed him to directly test the idea that species could act as units of selection, a controversial extension of the punctuated equilibrium idea. Starting with the premise that geographic range is a species-level property and not one of individual organisms, Jablonski showed that the classic Darwinian criteria for natural selection applied to his Late Cretaceous mollusks at the species level. Specifically, he found that the species varied in their geographic range size, that their survival or duration in the geologic record varied with geographic range, and that this variation in geographic range was "heritable": that is, closely related species were more similar in range size than expected by chance (5). Jablonski recently revisited these analyses using model-selection methods that could serve as a general approach to identifying the operation of such emergent, species-level traits (6–8). "Every species has a geographic range," he says, "so there's a lot of scope for species selection in this strict sense. And of course, every comparative analysis linking differential diversification to organismic or species-level traits is a potential case of species selection in the broad sense."

Jablonski wondered whether these principles would apply more generally to the biotas of other time periods, and wrote a grant with James Valentine, at the University of California at Santa Barbara, to explore this topic. When the grant was funded in 1979, Jablonski filled a midnight blue Cadillac Fleetwood limousine—a drive-away vehicle that needed to be transported across the country—with burlap bags of his Cretaceous fossils and drove from New Haven to California to begin postdoctoral research on modern bivalves of the eastern Pacific.

Out of the Shallows, Out of the Tropics

Within two years Jablonski was awarded a Miller Fellowship to continue postdoctoral work at the University of California at Berkeley, where he immersed himself in evolutionary biology and, while keeping an interest in the present-day mollusks, began to think in detail about the diversity dynamics he saw in the Late Cretaceous fossil record of the Gulf and Atlantic coasts. However, Jablonski wasn't the only one studying fossils from this region: David Bottjer, a paleontologist at the University of Southern California at Los Angeles, was also working there on rocks of the same age. Jablonski focused mainly on species that had lived near the shoreline, whereas Bottjer focused on those from environments further off-shore. When the two compared notes, it became clear that the off-shore communities looked relatively archaic and the on-shore communities looked relatively modern. "There was this weird temporal disconnect in the Late Cretaceous," Jablonski says. Their friend Jack Sepkoski, then at the University of Chicago, was finding similar onshore-offshore contrasts in Paleozoic ecosystems, and this prompted the trio to write a synthesis paper describing nearly 500 million years of ecological history (9).

After several years documenting that the observed pattern was genuine and biological and not an artifact of preservation or sampling, it became clear that the onshore-offshore ecological pattern was produced by a tendency for major groups, such as sand dollars and stony corals, to originate near the coastline, and then expand across the continental shelf over millions of years (10), a pattern that has held up to extensive revision as the metazoan phylogeny has been elucidated by accumulating molecular data (11). Furthermore, Jablonski subsequently found that these major groups preferentially originated in tropical seas, with some lineages later expanding toward the poles over geologic time but almost always retaining their presence in the tropics (12). This finding led to a major attack on the dynamics underlying the latitudinal diversity gradient, the pervasive trend of decreasing diversity from the tropics to the poles. All of the fossil patterns indicated that the tropics both generate and accumulate biodiversity, helping to explain why the tropics are biologically extraordinarily rich compared with higher latitudes (13). "We still don't really understand exactly why that happens," Jablonski acknowledges with apparent relish, calling the nonrandom distribution of evolutionary novelties one of the great puzzles in evolutionary biology. In his Inaugural Article, Jablonski explores how lineages expand out of the tropics, and shows that many of the most widespread species are widespread not because they tolerate a broad variety of conditions, but because they are specialized for habitats that are particularly widespread (14). "That's a surprising result that's going to have really interesting implications for how robust species are going to be both to perturbations in the geologic past and to the pressures that are gathering today, much of it from human activities," Jablonski says.

Extinction Rules

Jablonski also realized that his work on Late Cretaceous fossils, detailing 16 million years of normal, background rates of species origination and extinction, directly abutted the spectacular end-Cretaceous mass extinction, leaving him poised to evaluate differential extinction and survival across this key geologic boundary and, more generally, the evolutionary role of mass extinctions, work he began as an assistant professor in the Department of Ecology and Evolutionary Biology at the University of Arizona in 1982 and continued at the University of Chicago starting in 1985. This evaluation required a shift from working on the Gulf and Atlantic Coast to the global scale, typifying his recent work. "My field areas became the museum collections of the world in cities like Washington, DC, London, Copenhagen, Barcelona, Berlin, Brussels, and Warsaw," he says. "It was quite a change." Jablonski discovered that mass extinctions did not simply increase the intensity of background extinctions, as was generally assumed, nor did they appear to eliminate species randomly (15). "It wasn't simply an intensification of extinction, it was a change in the rules of extinction," Jablonski explains.

More recently, Jablonski has focused on recoveries from mass extinction events that appear to play as important an evolutionary role as the extinctions themselves. Like previous researchers, he saw large spikes in the diversification rates following extinction events, as the surviving organisms expanded to fill vacant niches. However, with his higher-resolution data on bivalves, Jablonski found that background rates settled down to a different level following each mass extinction (16, 17). "So mass extinctions do more than just extinguish some lineages and allow others to radiate; they set the pace of evolution for tens of millions of years afterward," Jablonski says. However, he also found that lineages that survive a mass extinction don't always participate in the subsequent diversification (18). "There are many lineages that drop by the wayside, even though they survived the mass extinction itself," Jablonski says. "If we're going to try to preserve biodiversity and perhaps nurse it back to health in the long run to promote recovery, then this is a crucial question we need to understand."

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