Old Bones Aren't So Bad After All

A synthesis of 16 "studies of the grave" provides good news for paleontologists worried about the fossil record

FOR OLD BONES—AND FOR THEIR MARINE equivalent, old shells—death is not the end. Bones and shells then face a long, tortuous road from death to fossilization, and only a select few make it. Scavengers can crunch the bones of smaller animals, water can dissolve chemically susceptible shells, and herds of beasts can pulverize even the toughest carcass remains. So just how good can the fossil record be, paleontologists have asked themselves, if these and other selective processes have eliminated the weak and unlucky?

If the fossil record were heavily biased, how could paleontologists ever hope to sort out some of the fundamental questions, such as: Is evolution punctuated by sudden jumps? Are mass extinctions gradual or catastrophic events? No wonder researchers have fretted over the faithfulness of the fossil record for years. But now comes some relief in a recent reanalysis of 16 taphonomic studies—literally, studies of the grave. Taphonomists Susan Kidwell of the University of Chicago and Daniel Bosence of the University of London in Egham have found an encouraging consistency in the fossil record and optimism for its use. Once they had sorted through the old data, it became clear that at least the recently deceased mollusk species rather faithfully represent the species that once lived in that same place. "I was delighted we could say something so positive," says Kidwell.

So is paleontologist David Jablonski of the University of Chicago. "Wow, the fossil record is pretty good!" he said after perusing the reanalysis, which is being published as a chapter in a volume on taphonomy. "It looks as if you can actually use relative abundances [of species] in the fossil record to tell you what was living there. All that information we have in the record may actually be telling us how communities lived."

Of course, paleontologists have been using the fossil record all along to sort out how members of a long-dead community lived and interacted with one another, but this new perspective can give confidence to its interpretation. "It fits into what a lot of paleontologists have thought but were reluctant to express, because the taphonomic literature was so confusing," says Kidwell. "But now we can put real numbers on these things."

The confusion in the literature had become a considerable obstacle to paleontologists. "To some degree, the taphonomic literature could be interpreted in whatever way would support your prejudices," says Jablonski. The problem was the difficulties of comparing one narrow and seemingly conflicting study with another. Typically, researchers wanting to know how reliably living species ended up being represented among the dead went to, say, a tidal flat, shoveled up some mud, washed out both living animals and shell debris, counted the species represented by both, and one way or another quantified the differences between the living and the recently dead. Many of these live/dead studies suggested reasonably good correlation between living animals and those entering the fossil record, says Kidwell, but others were more discouraging. From the literature alone, no one could sort out where the truth lay.

Faced with delivering a review chapter on the formation of shell beds, Kidwell and Bosence had a go at making sense of live/dead studies. "Taphonomists have always been the wet blankets," says Kidwell, "the ones who tell people what they can't do. The editors probably expected a chapter on what can go wrong" during fossilization. To find out just how much does go wrong, Kidwell and Bosence ran down the raw data behind the 16 live/dead comparisons of the past 25 years, getting the data from the original researchers or culling them from dissertations. "I found it heartbreaking how much quantitative data was out there and being treated at best qualitatively," says Kidwell. Then, for the first time, all such data were analyzed in the same way, study by study and habitat by habitat from the intertidal zone down to the deep sea.

The reanalysis revealed that, by study area, 83% to 95% of the mollusk species found living at a given site were also found dead in the same place—an encouraging degree of fidelity. But then there was the discouraging way of looking at the same data. Only 33% to 54% of the dead species could be found among the living. Does that mean that the death assemblage, and therefore the fossil record that it becomes, is usually contaminated with species that temporarily lived outside their usual habitats or whose shells were washed in from distant habitats? Should paleontologists even try to figure out who lived where, how they lived, or why they died out?

When Kidwell and Bosence looked more closely at the surveys of living species used in the studies, they found the cause for the discrepancy. Typically, the studies that tended to produce the discouragingly low fidelities between dead and live species depended on a single season's field work, or a single year's. But the longer the duration of the live survey, the higher the fidelity. Once a live survey had lasted long enough to encompass the variability due to storm-shifted sediments, disease, and climatic influences, the proportion of dead represented in the living population rose from 45% to a more satisfying 75%.

Just how long a live survey should be will

S. M. Kidwell

Who were the living? *Studies of living and recently dead mollusks suggest that ancient shell beds like these can be representative of the species that lived millions of years ago.*

Taphonomic Down and Dirty

The fossil record may be reasonably reliable (see main story), but taphonomists still puzzle over the details of what happens to bones and shells between death and the grave. If they could tease more information out of a sea urchin fossil, for example, they might discover how it died, or why that particular sea urchin made it into the fossil record rather than being pulverized by predators. Or they might even learn what the seafloor conditions were at the time that sea urchin died. To that end, taphonomists are adding increasingly quantitative laboratory experiments to their ongoing field work. The result has been greater insight into fossilization—and some pretty smelly labs.

In a recent example, taphonomists Susan Kidwell and Tomasz Baumiller of the University of Chicago decided to test the idea that well-preserved sea urchin fossils were laid down under anoxic—oxygen free—conditions or were suddenly buried by sediment. Otherwise, the assumption went, rapid decay would have rotted the ligaments holding the urchin's body plates together, and it would have fallen into a heap within a few days.


S.M. Kidwell and T. Baumiller

The science of rot. *As the temperature rises* (left to right), *preservation declines.*

Many such taphonomic assumptions have evolved from a type of field work that one researcher describes as "walking beaches and looking at how dead beasts fall apart." But Kidwell and Baumiller were after greater experimental rigor. Reflecting perhaps the immature state of experimental taphonomy, they jury-rigged a testing system: deli mayo jars to hold the urchins in seawater, surplus typewriter platens on which to roll the jars, and an ancient rebuilt motor to drive the rollers. They varied the temperature, oxygen content, and duration of decay (the smelly part of the science), then tumbled the jarred urchins on the rollers to see how quickly they would fall apart.

Contrary to what most taphonomists had presumed, Kidwell and Baumiller found that, in the lab, anoxia had little to do with how well preserved old sea urchins were. Anoxia-loving bacteria could eat up the binding ligaments as fast as any oxygen-lovers. Instead, low temperatures kept urchins intact for at least 5 to 10 weeks. The taphonomists' conclusion: The well-preserved fossil specimens paleontologists find were probably deposited in deeper, colder waters or at higher latitudes than the dismembered ones—information taphonomists can use to reconstruct the urchin's original habitat.

This lab work casts doubt on some other taphonomic rules of thumb. It had been assumed that if the urchin body plates in the fossil record were broken, the living urchin had probably been preyed upon by some plate-crushing animal. If true, that would offer some insight into how urchins died in the past. But Kidwell and Baumiller found that cold seawater preserved dead urchins so long that their plates had a chance to break because of tumbling alone. All of which points to a promising future for the fledgling field of taphonomic lab work.

■ R.A.K.

ADDITIONAL READING

S. M. Kidwell and T. Baumiller, "Experimental disintegration of regular echinoids: roles of temperature, oxygen, and decay thresholds," *Paleobiol.* **16**, 247 (1990).

vary with the animal and the habitat, says Kidwell. A census taken over a few years seems to suffice in a lagoon, she finds, but many decades might be required on the continental shelf. Generally, the duration of a live survey should equal the lifespan of the longest lived species, be it a snail or an elephant.

But longer live surveys still don't solve the problem of shells of the dead with no representatives among the living. Paleontologists should be leery of some of these species, Kidwell and Bosence advise. One particularly untrustworthy type of shell is that of the rare species. Distinguishing between two fossil communities on the basis of rare species, as is sometimes advocated, is dangerous, notes Kidwell, because they are among those least likely to have been faithfully recorded in the record. The smallest shells—on the order of a few millimeters in size—can also be unreliable. They are the most likely to have been carried in from another habitat after death.

Still, there is a leap from Kidwell's work on the recently dead—mollusks that died, say, 1000 years ago—to any conclusions about the fossil record of animals that perished millions of years ago. Paleontologist James Valentine of the University of California, Berkeley, has looked back toward older fossils. He compared the fossil clams and snails preserved along the southern California and northern Baja California coasts during the past million years to those living there now. He found that 77% of the living species are represented in the fossil record, and he estimates that a doubling of the search effort in the fossil record would push the proportion to at least 85%.

"I didn't think [the proportion] was going to turn out to be as good as it was," says Valentine. "I agree with Susan Kidwell that the fossil record isn't all that bad." To Valentine, serious problems with the fossil record come not when shells collect in the mud or when the mud turns to rock, but when over millions of years crustal contortions and erosion destroy the rock and its fossils.

Reading the fossil record gets trickier for another reason as older and older fossils are examined. A few hundred million years ago, it was the brachiopods that dominated the oceans, not the mollusks. Instead of burrowing into the mud, these animals, which look like scallops, stood just above the bottom on short stalks. Did the brachiopods enter the fossil record as faithfully as the mollusks have more recently? Live/dead studies might be done in a brachiopod refuge, such as the one near New Zealand, notes Kidwell. That would be a start, but as paleontologist Karl Flessa of the University of Arizona told an audience a couple of years ago, "We have a long way to go to see the fossil record for what it is rather than what we hope it is."

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ADDITIONAL READING

S. M. Kidwell and D. W. J. Bosence, "Taphonomy and time-averaging of marine shelly faunas," in *Taphonomy, Releasing Information from the Fossil Record*, D. E. G. Briggs and P. A. Allison, Eds. (Plenum Press, New York, in press).

J. W. Valentine, "How good was the fossil record? Clues from the Californian Pleistocene," *Paleobiol.* **15**, 83 (1989).