

PERSPECTIVES: PALEOECOLOGY

Measuring Past Biodiversity

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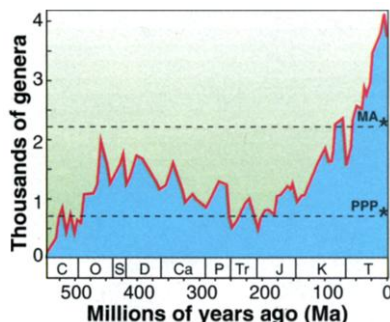
The diversity of animal life on Earth increased from near zero at the beginning of the Cambrian [~540 million years ago (Ma)] to the 4 to 6 million species alive today (1). What was the trajectory of this increase? And can we measure it empirically with the fossil record?

Most attempts to answer these questions have been based on shell-forming marine macroinvertebrates, the animals with the most extensive and well-preserved fossil record (2–4). About 300,000 living species of marine macroinvertebrates have been described, but estimates that account for inadequate sampling range from ~0.5 to 5 million (5). Only one-third contain hard parts likely to be preserved as fossils (6). Furthermore, fossil species are often unnamed. Most compilations are therefore based on genera or families to increase taxonomic consistency (4). Assuming 1 million living species and less than five species per genus on average (7–9), about 67,000 genera of living marine macroinvertebrates would be preserved as fossils.

How many such genera have ever lived? Fossil marine invertebrate genera survive on average about 28 million years (10). If the increase in diversity during the Phanerozoic (~540 Ma to today) was logistic, with a maximum of about 67,000 genera as today (3), then the total number of fossilizable marine macroinvertebrate genera that ever lived would be about 1 million. If Phanerozoic diversity increased exponentially, with most of the increase in

the Cenozoic (65 Ma to today) (2), then the total might be only 200,000 genera.

The five major mass extinctions probably decrease these numbers by no more than 10% (11), whereas earlier peaks in diversity above recent values might increase the totals by an unknown amount (3). Regardless, it is sobering to note that the largest available database of Phanerozoic diversity contains little more than 31,000 genera of marine macroinvertebrates (11), just 3 to 16% of the total based on the calculations above.



Global number of marine invertebrate genera during the Phanerozoic. Adapted from (34). C, Cambrian; O, Ordovician; S, Silurian; D, Devonian; Ca, Carboniferous; P, Permian; Tr, Triassic; J, Jurassic; K, Cretaceous; T, Tertiary. The lower horizontal line indicates the number of genera of scleractinian corals, cheilostome and cyclostome bryozoans, shelled mollusks, crustaceans, and echinoderms recovered from 344 Pliocene samples by the PPP. On the basis of the ratio of extant diversity between the Indo-West Pacific and the Caribbean, we would expect to discover about 2205 genera of these groups in a project similar in scope in the Malay Archipelago (MA, upper horizontal line).

resulting plots of Phanerozoic marine family and generic biodiversity (see the first figure) were widely seen as the first rigorous assessment of the history of the diversity of life.

Sepkoski's paleobiodiversity curves led to many important paleontological advances, including the realization that mass extinctions are important creative factors in the history of life (12) and the critical reevaluation of evolutionary trends (13). Potential biases in the compilation, arising for example from variations in geographic extent, outcrop area, volume, preservation of rocks, and sampling locations (mostly North America and Western Europe), were also evaluated widely (3).

These biases cannot actually be evaluated, however, because the data are not based on ecological sampling. Standard statistical evaluation is thus inappropriate. The situa-

tion is analogous to a human census based on attempts to count every citizen instead of estimating population numbers from samples that can be evaluated statistically (14). The problem with total counts is particularly vexing if we lack confidence in some census takers, who may have got lost trying to find certain neighborhoods, were afraid to enter them, or ran out of time. Such problems turn up easily on a standardized data sheet of samples but not in a final total number.

Similar problems affect existing compilations of paleobiodiversity. We do not know how many places were sampled and how many samples were obtained from each age interval, nor do we know their quality and geographic distribution. The Phanerozoic Marine Diversity Working Group (11) has begun to address these problems by compiling the data based on individual collections that can be treated as samples. This ambitious and important project will allow statistical analysis based on randomized subsampling of the data.

Nevertheless, there is still extreme variability in the size and quality of collections in the database and in the taxa and stratigraphic intervals that are included, the sampling intervals are coarse, and the paleobiogeographic sampling of the data is extremely limited. These problems cannot be addressed effectively without new data.

The Panama Paleontology Project

Our own sampling of one small corner of the world has produced a surprisingly large proportion of the supposed global biodiversity for one of the stratigraphic intervals in the Sepkoski analysis.

The Panama Paleontology Project (PPP) aimed to examine the consequences of the rise of the Isthmus of Panama and global climate change on the composition and diversity of tropical American marine biota over the past 15 million years (15–17). Occurrences of macrofaunal invertebrates from about half of the Caribbean PPP macrofossil collections were summarized recently for scleractinian corals (8), cheilostome bryozoans (9), and bivalve and gastropod mollusks (17, 18). We found 673 genera of these four groups in 344 collections of Pliocene age (5.3 to 1.7 Ma) (19) and more than 735 Pliocene genera of invertebrate macrofossils overall (20).

The latest version of the Sepkoski database contains 4138 Pliocene genera of marine macroinvertebrates worldwide (21). As for all time intervals, this number includes an indeterminate but large number of taxa that range through but do not actually occur in Pliocene collections. Despite the fact that such taxa are not included in our data, our 344 Pliocene collections of macrofossils produced about 18% of the to-

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tal Pliocene diversity in the global database (see the first figure) (19). Yet the area of Pliocene deposition in Panama and Costa Rica is less than 0.1% of the 7 million km² of Pliocene marine sediments worldwide (22). The comparison is even more striking for specific, well-studied taxa. We found 31% of the number of scleractinian coral genera in the global database, 29% of the number of cheilostomes, 22% of the number of bivalves, and 22% of the number of gastropods.

We also compared the PPP data with the Phanerozoic Working Group compilation, which considers diversity within 10-Ma intervals (11). The duration of each interval is similar to the time covered by the entire PPP database. The latter includes 847 genera of scleractinian corals, cheilostomes, bivalves, and gastropods from 689 collections (19). Only one of the intervals from the new global database contains as many genera (11).

The Problem of Uneven Sampling

Why are the global data so obviously incomplete for the Pliocene? The answer is so simple that it is commonly overlooked in studies of biases in the fossil record, which emphasize factors like outcrop area, taxonomic effort, and the poor preservation of fossils in older rocks (3, 6, 23). There are pitifully few modern, extensive monographic studies of tropical Cenozoic (much less Pliocene) corals, cheilostome bryozoans, bivalves, or gastropods because Europe and North America (the sources of almost all collections in the global database) had largely moved out of the tropics by Cenozoic time (24). Yet the tropics contain the great majority of marine biodiversity today, and as far as we know, this was true throughout the Phanerozoic (24).

Estimates without tropical data are doomed to underestimate global diversity severalfold. Contrary to suggestions that diversity was constant throughout the Phanerozoic (3, 11), we conclude that Cenozoic diversity was much higher than Sepkoski observed and more in line with an exponential increase (2, 25). The lack of tropical data also explains why so little is known about the diversification of Cenozoic reef corals in the Pacific (26) and why no one has been able to rigorously test Vermeij's (27) ideas about evolution and escalation of antipredator morphologies in the Indo-Pacific.

How many other periods in the Phanerozoic are as badly sampled as the Cenozoic? The Phanerozoic Marine Diversity Working Group will identify well and poorly sampled intervals, geographic regions, and taxa. Some intervals may be well sampled, such as the tropical shallow seas of the Ordovician and Silurian of the North American Midwest and Europe (28). Moreover, the once controversial impact hypothesis to explain the mass

extinction at the end of the Cretaceous stimulated an enormous collection effort, as have attempts to understand the greatest mass extinction of all at the end of the Permian (29). But recent studies in China show (30) that we have barely scratched the surface of Phanerozoic biodiversity for many critical regions and time intervals in Earth history.

These new data may allow us to evaluate how well each stratigraphic interval or biogeographic province has been sampled—if paleontologists standardize their collection methods to keep track of individual samples and specimen abundances. Only then will we be able to compare sampling efforts using plots of cumulative taxonomic richness and diversity (17, 18). The results in the second figure suggest that good estimates of diversity can be obtained with a practical amount of effort. However, comparable analyses have not been widely applied elsewhere and could probably not be generally attempted because of inappropriately collected data.

We Need New Data

Ever more complete and detailed compilations of old data collected for different purposes, by different methods, with different taxonomic standards, and without abundance data cannot resolve the problem of inadequate and inconsistent sampling. Existing museum collections suffer from the same sampling problems (18), despite their great value for systematics. We propose instead an international program of detailed and intensive sampling of critical intervals and regions designed to address fundamental questions in Earth history, much like the highly successful Ocean Drilling Program.

To find out whether marine biodiversity increased during the Phanerozoic (11), we need about 20 studies comparable in scope to the Panama Paleontology Project, scattered judiciously in time and location. Depending on location and logistics, each study would cost roughly \$3 to 5 million. At 5 to 10 years per project, done simultaneously, we could have the answer in 10 years at a cost of \$10 million per year—a bargain compared with the costs of ongoing surveys of living marine biodiversity.

In each project, a team of geologists, stratigraphers, and paleontologists would study many groups of fossils at the same time. Be-

sides developing new paleontological collections with standard protocols, the projects would require varying amounts of new mapping, stratigraphy, age dating, and reconstruction of paleoenvironments, depending on the information already available. Such an integrated approach is essential to ensure the reliability and utility of the newly collected data.

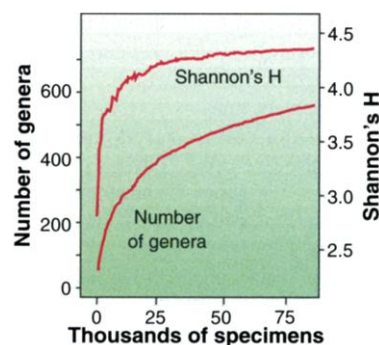
Each study would provide only a few sampling points toward answering the question of how paleobiodiversity evolved through time. But each study would also represent an extraordinary opportunity to gain other new paleontological insights. In the course of the PPP, we discovered that molluscan diversity in the Caribbean was roughly constant over the past 10 million years because mass extinction at the end of the Pliocene was counterbalanced by comparable origination in mollusks (17), although not in reef corals (8, 17), and that the pace of bryozoan speciation was highly punctuated throughout the region (31).

The proposed program would also revitalize the education and training of taxonomists, stratigraphers, and field geologists. Few experts worldwide study many

major fossil taxa, taxonomists and biostratigraphers are retiring, and there is a widely acknowledged crisis in training their replacements (32). In addition, many new Ph.D. paleontologists have done little fieldwork because of an increased emphasis on working from the published literature. Our proposal would require new taxonomy and fieldwork on a large scale and could support the training of a new generation of practitioners of these endangered professions. Because of the need for geographic replication, the program would have

to be truly international and may thus help to break down the barriers in stratigraphic practice and taxonomy that still confound global compilations.

No science can grow without new data. The Ocean Drilling Program and polar ice cores have revolutionized our understanding of Earth's climatic history. In this regard, paleontology is at a critical juncture. We have achieved great synthesis on the basis of Sepkoski's work and the studies it spawned, but our data are inadequate for testing whether diversity has been stable or increased substantially over the past 500 million years and for identifying the underlying processes.



Cumulative diversity curves for Pliocene molluscan genera from the PPP project. The curves show how diversity estimates change as more samples are added. Each curve represents the median of 100 iterations with random input of collections. Shannon's H is a measure of ecological diversity that incorporates both the number and proportional abundance of taxa in an assemblage.

Extensive efforts are under way to document the earliest animals in the fossil record (33) and test alternative hypotheses about the big mass extinctions (29). We must extend these efforts in an organized fashion throughout Earth history if we are to make genuine progress in refining the hypotheses about Phanerozoic paleobiodiversity that Sepkoski laid out for us so brilliantly.

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PERSPECTIVES: CELL BIOLOGY

Life Without Caveolae

Robert G. Parton

Discovered by electron microscopists in the 1950s, caveolae—small surface pits in the plasma membrane—remain one of the most abundant yet puzzling features of many mammalian cells. The principal components of caveolae are proteins called caveolins. If caveolin-1, the isoform found in nonmuscle cells, is produced by cells normally lacking caveolae, then caveolae are formed (1); if cells that normally produce caveolin-1 become deficient in this protein they lose their caveolae (2). On page 2449 of this issue, Drab et al. (3) provide a thorough characterization of mice deficient in caveolin-1 that apparently have no caveolae.

An electron microscopist scanning the surface of a fat cell (adipocyte) that is covered in caveolae could hardly imagine life without these structures. Yet we do not know exactly what they do or how their characteristic shape is related to their cellular tasks (see the figure). It has been proposed that caveolae are important in signal transduction, forming a platform on which different signaling components can congregate (4, 5). In some cases, signaling components in the caveolae may remain inactive, held in check by caveolins until their activation and release by the appropriate external stimulus. The number of caveolae and amount of caveolin decrease dramatically in immortalized (transformed) cultured cells,

hinting that caveolae are important for inhibiting certain signaling pathways that regulate cellular proliferation (4). However, it is becoming increasingly apparent that surface microdomains termed “lipid rafts,” of which caveolae are a subtype, could account for local concentrations of molecules required for efficient signaling (6). In fact, few signaling proteins are exclusively localized to caveolae, although notable exceptions include several putative calcium regulatory proteins (7). Also,

certain cells with very complex signaling pathways such as lymphocytes and some neurons manage fine without caveolae. Even if these cells have proteins that can take the place of caveolins, they do not seem to need caveolae per se for signaling. Besides signaling, caveolae have been linked to cholesterol regulation: Caveolin binds to cholesterol, its production is controlled by cholesterol, and cells with mutations in caveolin exhibit perturbations in their cholesterol-rich lipid-raft domains (2). Again, although definitive evidence is lacking, these studies suggest that caveolae and caveolins may be involved in the regulation of intracellular and surface cholesterol.

Given the variety of possible tasks at-

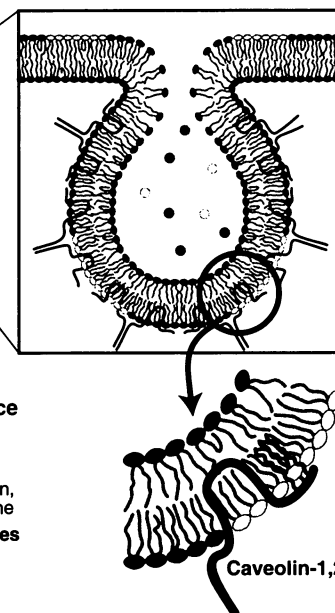


Proposed functions

- **Endothelial transcytosis**
- **Signaling**
Ras, EGF, trimeric G proteins, PDGF, NOS, PLD, Raf, Mek, insulin
Tumor suppression
Calcium transport/regulation
- **Lipid regulation**
Cholesterol transport/regulation

Caveolin-deficient mice

- **Lack of caveolae**
- **Cardiovascular defects**
Aberrant arterial relaxation, contractility, myogenic tone
- **Nitric oxide abnormalities**
- **Lung pathology and physical weakness**



Caveolae and caveolins. (Left) An electron micrograph of small (65 nm) flask-shaped pits called caveolae in the plasma membrane of a human fibroblast. (Right) Caveolae are formed from caveolins, oligomeric integral membrane proteins. Caveolins are thought to have both their carboxyl and amino termini facing the cytoplasm and have palmitoyl groups (red squiggles) attached to carboxyl-terminus amino acids.

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