

## Selected Research Contributions of Steven M. Stanley, by Topic

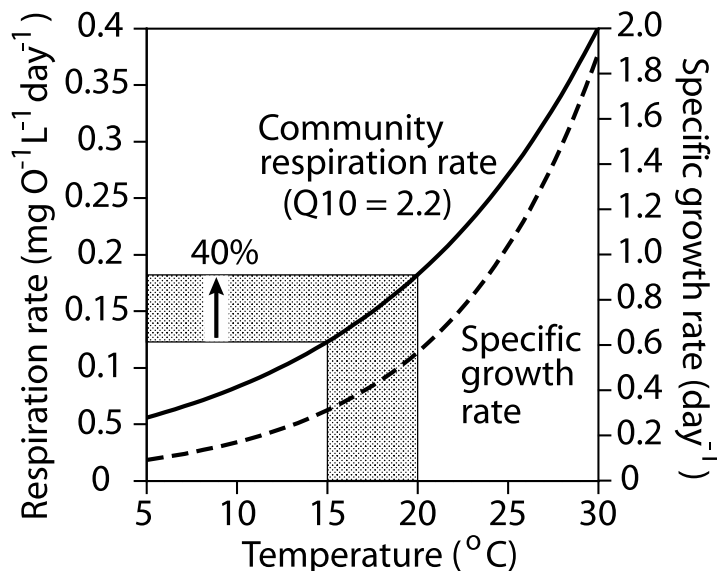
(These descriptions are provided to compensate for the fact the lists in a curriculum vitae do not adequately describe contributions. Publications are not in chronological order here, and some appear under more than one heading.)

### Carbon isotopic excursions in marine sediments

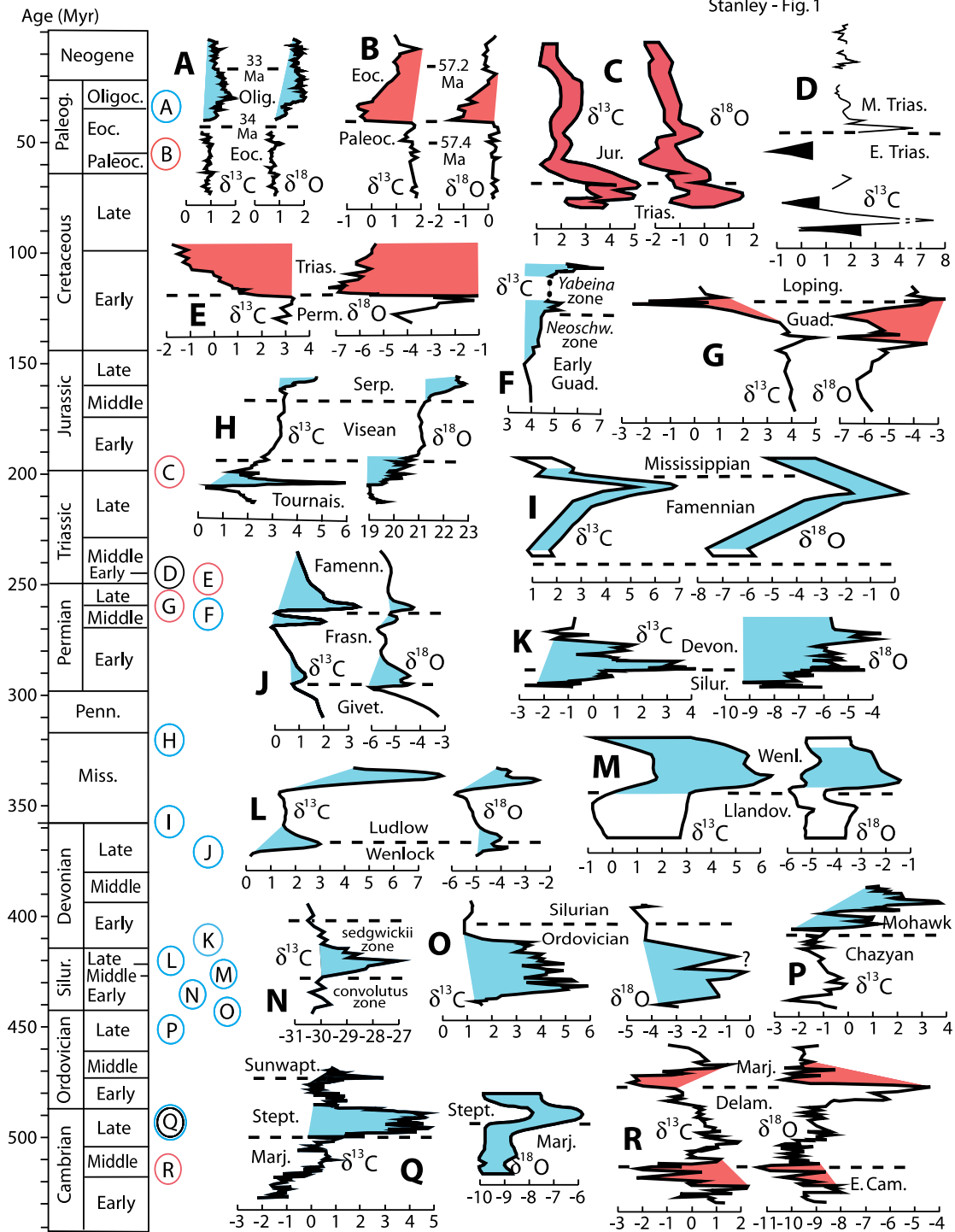
A wide variety of *ad hoc* interpretations have been offered for stable carbon isotope excursions in the sedimentary record associated with mass extinctions. Here I provided a new interpretation of these excursions, offering a unifying explanation for them.

Stanley, S. M., 2010, Relation of Phanerozoic stable isotope excursions to climate, bacterial metabolism, and mass extinctions. *Proceedings of the National Academy of Sciences* 107:19158-19189.

Many *ad hoc* explanations have been offered to explain carbon isotopic excursions in sedimentary sequences that are associated with major extinctions. This paper showed, for the first time, that nearly all of these excursions have coincided with oxygen isotopic excursions, which reflect climate change. This implies that global climate change must have been implicated in the mass extinctions and also in the carbon isotope excursions. A key factor for the latter is that bacterial respiration rates increase exponentially with an increase in temperature, and this relationship must have a profound effect along continental shelves, where 90% of carbon burial in the ocean occurs: the rate of release of isotopically light organic carbon to the ocean by bacterial respiration is inversely related to temperature. Other contributing factors are the inverse relationship between global temperature and phytoplankton productivity, the melting of methane hydrates as global temperature increases, change in the rate or respiration of terrestrial fungi with temperature, and the change in carbon isotope fractionation at temperatures below about 15°C.



Exponential increase for bacterial respiration rates in freshwater and marine sediments.



Parallel positive and negative oxygen and carbon isotope excursions for marine waters coinciding with all major global Phanerozoic mass extinctions. Positive excursions represent global cooling (blue) and negative excursions, global warming (red).

## **The effects of secular changes in the magnesium-calcium ratio of seawater on carbonate biomineralization throughout the Phanerozoic**

This research showed that oscillations in the Mg/Ca ratio of seawater have determined whether organisms producing aragonite or calcite have been major reef-builders or carbonate sediment producers during the Phanerozoic. It connected plate tectonics to seawater chemistry, biomineralization, paleontology, and mineralogy.

Stanley, S. M. and Hardie, L. A. 1998, Secular oscillations in biological calcification driven by tectonically forced shifts in seawater chemistry. *Palaeogeography, Palaeoclimatology, Palaeoecology* 144: 3-19.

Stanley, S. M. and Hardie, L. A. 1999, Hypercalcification: Paleontology links plate tectonics and geochemistry to sedimentology. *GSA Today* 9: 1-7.

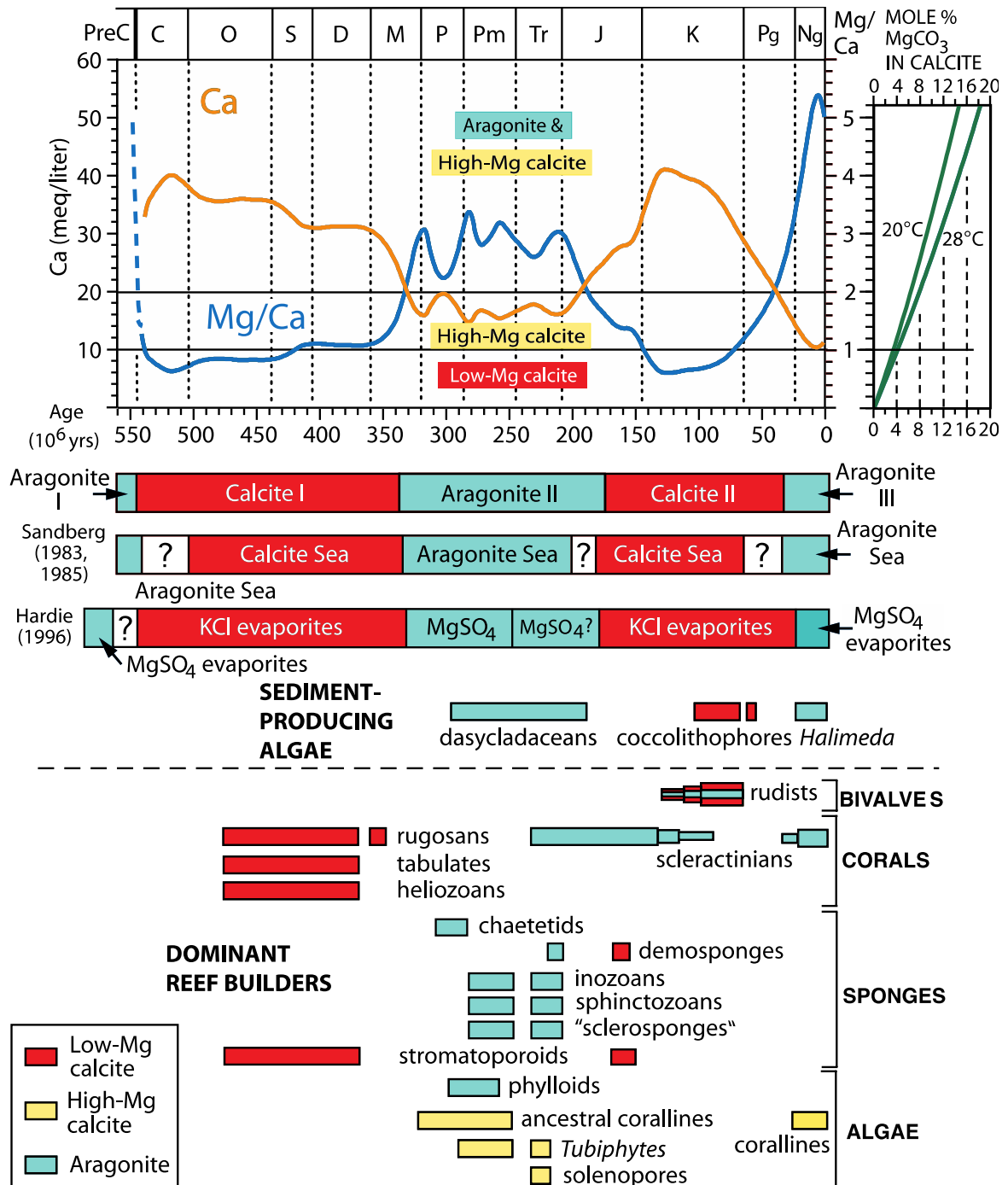
This research was stimulated by the brilliant work of my former colleague Lawrie Hardie, who showed that the ambient Mg/Ca ratio of seawater has governed the mineralogy of inorganic precipitation of calcium carbonate over the course of geologic time. Furthermore, he showed that the dominant control of this ratio is the rate of formation of oceanic crust via seafloor spreading and formation of basaltic plateaus. This global rate influences the rate of consumption of Mg from seawater in metamorphic reactions and the release of Ca into it by magma. My contribution has been to show that changes in the Mg/Ca ratio also influence biomineralizing organisms, which produce most of the lime sediment in the ocean. Relatively sophisticated taxa, such as mollusks and brachiopods, have been able to flourish in both "calcite seas" and "aragonite seas," but biologically simple organisms, such as algae, sponges, corals, and bryozoans have been able to flourish as major sediment producers and reef builders only when the Mg/Ca ratio of seawater has favored their particular mineralogy. The second of these papers was an invited contribution, designed to make the ideas of the first paper available to a broader audience. (Figure on the following page.)

### **Experiments demonstrating the relationship between the ambient Mg/Ca ratio and biomineralization**

I designed this research program to undertake experiments to further test the results obtained by the analysis of fossil data. The hypotheses to be tested were that reductions in the Mg/Ca molar ratio in artificial seawaters from its present level of 5.2 would result in enhanced growth rates for calcitic taxa and reduced growth rates for aragonitic taxa, and also that these alterations of seawater chemistry would result in progressive increases in Mg within calcitic skeletons and also increased production of calcite by taxa that produce today produce skeletons of almost pure aragonite. All of the experiments bore out these predictions. Some of the experimental results have been published by my former student and post-doc, Justin Ries.

Stanley, S. M., Ries, J. B., and Hardie, L. A. 2002, Low-magnesium calcite produced by coralline algae in seawater of Late Cretaceous composition. *Proceedings of the National Academy of Sciences* 99: 15323-15326.

This study established the basic protocol for which all of the other experimental work in my laboratory on the effects of seawater chemistry was patterned. In this first study, it turned out that the Mg content of the skeletal mineralogy of coralline red algae decreased with the Mg/Ca ratio of seawater, and the fractionation pattern resembled that for nonskeletal precipitation. These algae produced low-Mg calcite in "calcite" seawater, and the experiments in my lab on a wide variety of other taxa showed that they all did the same thing, though with unique fractionation patterns. The implication is that no marine calcifiers could have produced high-Mg calcite in the "calcite seas" of the Cretaceous or middle Paleozoic.

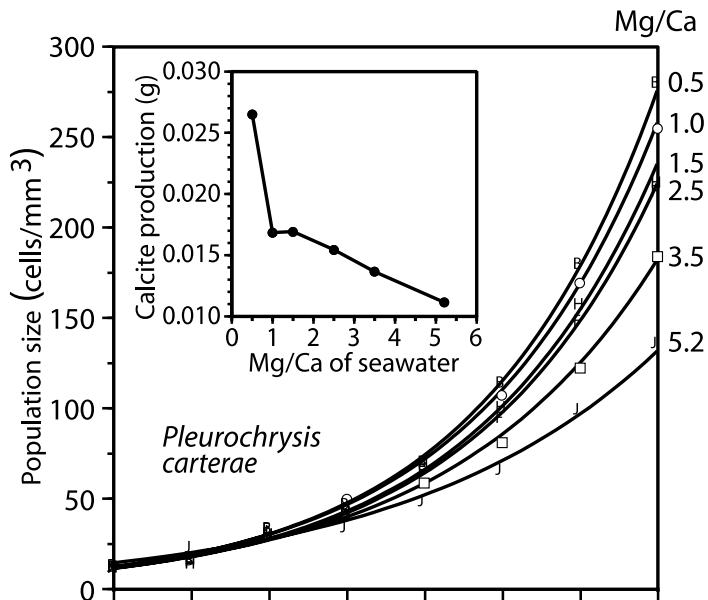


Comparison of the temporal distribution of mineralogies for nonskeletal marine carbonates and evaporites with those of biologically simple carbonate-producing taxa that have functioned as important reef builders and producers of marine carbonate sediment. The large upper diagram shows nonskeletal precipitation of carbonate minerals as a function of the Mg/Cs molar ratio of seawater. The graph at the upper right shows Mg in nonskeletal calcite as a function of the Mg/Ca at two temperatures. The broad horizontal bars show (1) intervals of calcite and aragonite seas, as indicated by ancient ooids and early marine cement and (2) intervals characterized by KCl and MgSO<sub>4</sub> marine evaporates. Below are the ranges of biologically simple calcifying taxa.

Stanley, S. M., Ries, J. B., and Hardie, L. A., 2005, Seawater chemistry, coccolithophore population growth, and the origin of Cretaceous chalk. *Geology* 33: 593-596.

This study explains the extensive deposition of chalk in Late Cretaceous time that gave the Cretaceous Period its name. It was based on the suggestion of biologists that precipitation of calcium carbonate by algae may "fertilize" photosynthesis by releasing carbon dioxide. (The equation for the precipitation of calcium carbonate can be written as:  $\text{Ca}^{2+} + 2\text{HCO}_3^- \rightleftharpoons \text{CaCO}_3 + \text{H}_2\text{O} + \text{CO}_2$ .) Thus, I predicted that coccolithophores would not only calcify at a higher rate but would also experience a higher rate of cell multiplication as the Mg/Ca ratio of artificial seawater was reduced from its very high modern level of 5.2, which favors precipitation of aragonite, to levels of 1 and 1.5, which favor calcite, the mineral that coccolithophores produce. It turned out that the multiplication rate of coccolithophores increased dramatically as the ambient Mg/Ca ratio was lowered; for two of the three species we studied, this exponential rate itself increased exponentially! We further employed experiments in which either the Mg/Ca ratio or the absolute concentration of Ca of seawater was varied while the other was held constant. The results showed that both factors produced increases in the growth rates in "Cretaceous" seawater. In addition, whereas the conventional view is that coccolithophores all produce low-Mg calcite, we found that two of the three species we studied produced high-Mg calcite in modern seawater, although like all other taxa we studied, they produced low-Mg calcite in "Cretaceous" seawater.

In addition to showing how growth rates explained the coccolithophores' production of massive chalk deposits in the "calcite seas" of the Cretaceous, this research implied that population growth rates of typical coccolithophore species in modern seawater are limited by the low concentration of Ca and high Mg/Ca ratio; this explains why they fail to respond to attempts to fertilize them with nitrates, phosphates, or iron and why they tend to be confined to the central regions of oceans, where nutrients are scarce. (The famous, highly productive *Emiliania huxleyi* is an exception; it appeared only about 270,000 years ago and is an aberrant supercalcifier.)



Increase in growth rates of the coccolithophore species *Pleurochrysis carterae* in laboratory experiments in which the magnesium/calcium ratio was lowered progressively from that for the modern ocean (5.2) to Cretaceous levels (0.5-1.0).

Stanley, S. M., Ries J. B., and Hardie, L. A. (2011) Scleractinorals produce calcite, and grow more slowly, in artificial Cretaceous seawater. *Geology* 34: 525-528.

This paper showed that scleractinian corals, which secrete skeletons consisting of almost pure aragonite today, produce calcite as an increased percentage of their skeletal mineralogy as the ambient Mg/Ca ratio is

reduced in laboratory experiments. Three species produced skeletons containing more than 30% calcite in when grown in seawater with  $Mg/Ca = 1$  ("Cretaceous" seawater). Furthermore, all species grew progressively more slowly as the ambient  $Mg/Ca$  ratio was lowered.

Stanley, S. M., Ries, J. B., and Hardie, L. A., 2010, Increased production of calcite and slower growth for the major sediment-producing alga *Halimeda* as the  $Mg/Ca$  ratio of seawater is lowered to a "calcite sea" level. *Journal of Sedimentary Research* 80: 6-16.

The subject of this research was a calcareous green alga that is a highly prolific producer of carbonate sediment on shallow tropical seafloors. One aspect of this research had a premise similar to one in the coccolithophore project, because it had been suggested that *Halimeda*, in effect, fertilizes its photosynthesis by calcifying. Indeed, we found that *Halimeda* calcified and also grew progressively more slowly as the ambient  $Mg/Ca$  ratio was lowered. It produced only a small percentage of calcite in modern seawater, but increasing percentages as the ambient  $Mg/Ca$  ratio was lowered, with an average of 46% in "early Eocene" seawater ( $Mg/Ca = 1.5$ ); as for other taxa, the  $Mg$  content of calcite decreased as the ambient  $Mg/Ca$  ratio was lowered. Calcium is a poison for many plants and algae, but by holding the  $Mg/Ca$  ratio of ambient seawater constant and varying the concentration of  $Ca$ , we found that calcification and growth rates increased with increases in ambient  $Ca$ , although the effect of  $Ca$  was weaker than that of the  $Mg/Ca$  ratio.

Stanley, S. M. 2006, Influence of seawater chemistry on biomineralization throughout Phanerozoic time: paleontological and experimental evidence. *Palaeogeography, Palaeoclimatology, Palaeoecology* 232: 214-236.

Stanley, S. M. 2008, Effects of global seawater chemistry on biomineralization: past, present, and Future. *Chemical Reviews* 108: 4483-4498.

These are both invited review papers, which introduced a few new ideas and generalizations -- for example that the great increase in primary production by *Halimeda* during the past 30 m.y. must reflect the pronounced increase in the molar  $Mg/Ca$  ratio of seawater rather than an increase in atmospheric  $PCO_2$  because the latter underwent little change. Also, contrary to the previous views of many biologists who have studied biomineralization, my research program has shown that many organisms exert only partial control over the mineralogy of their skeletons. In particular, the skeletal mineralogy of biologically unsophisticated organisms tends to be strongly influenced by the  $Mg/Ca$  ratio of seawater.

### **Reef ecology and diagenesis**

This paper summarized my undergraduate thesis work, which I undertook independently (my advisor was on sabbatical).

Stanley, S. M. 1966, Paleogeology and diagenesis of Key Largo limestone, Florida: *Bulletin of the American Association of Petroleum Geology* 50:1927-1947.

Here the case was made that the coral reef that formed the upper Florida Keys, which lived about 125,000 years ago during the last glacial maximum, was not a group of patch reefs, as others had suggested, but a bank reef that grew below wave base. It is much too continuous to be a group of patch reefs, and there was no barrier reef offshore to produce a lagoon in which patch reefs could form. I also showed how the interstitial sediment was being lithified by freshwater solution of aragonite and reprecipitation of the calcium in calcite cement.

### **Mass extinctions**

I have published a paper that introduces new methods for calculating the magnitudes of mass extinctions. It corrects previous calculations in several ways, but most fundamentally in subtracting out background extinction to assess the actual number of extinctions that can be attributed to a mass extinction. I have concluded that the frequently cited estimate that 90-95% of species died out at the end of the Permian (i.e. that life nearly died out in the terminal Permian crisis) is a great exaggeration: slightly more than 80% of

species died out. Previously I uncovered four global mass extinctions not previously recognized (three mass extinctions during the Early Triassic and, with a former student, the Guadalupian event of the Permian). With coauthors, I have also uncovered regional mass extinctions that occurred in the Atlantic Ocean early in the recent Northern Hemisphere ice age. I have also provided what I think is convincing evidence from published oxygen isotope ratios that all major global mass extinctions have been associated with global climate change. However, I have also shown why, at times of sea level lowering, faunas of marginal epicontinental seas have suffered heavy losses because of being disgorged into waters that were thermally inhospitable. With former student Matthew Powell, I have shown that the late Paleozoic ice age caused the disappearance of narrowly adapted tropical species and produced a new state of the marine ecosystem by leaving alive taxa with broad ecological niches that experienced remarkably low rates of origination and extinction.

Stanley, S.M. 2016. New estimates of the magnitudes of major marine mass extinctions in earth history. *Proceedings of the National Academy of Sciences*  
[www.pnas.org/cgi/doi/10.1073/pnas.1613094113](http://www.pnas.org/cgi/doi/10.1073/pnas.1613094113).

By way of new mathematical methods, this paper that (1) showed, for the first time, that background extinction is a reality -- and that it definitely preceded mass extinctions; (2) introduced a new mathematical method for estimating the amount of this background extinction and, by subtracting it from total extinction, correcting estimates of losses in mass extinctions; (3) presented a new method for estimating the size of the Signor-Lipps Effect, which results from the imperfection of the geologic record; and (4) introduced a new method for correcting the rarefaction approach for calculating species losses in a mass extinction by taking into account clustering of extinctions. The contribution concluded that the great terminal Permian crisis eliminated only about 81% of marine species, not the frequently quoted 90-96%. **Life did not almost disappear at the end of the Permian, as has often been asserted.**

Stanley, S. M. and Yang, X., 1994. A double mass extinction at the end of the Paleozoic Era. *Science* 266: 1340-1344.

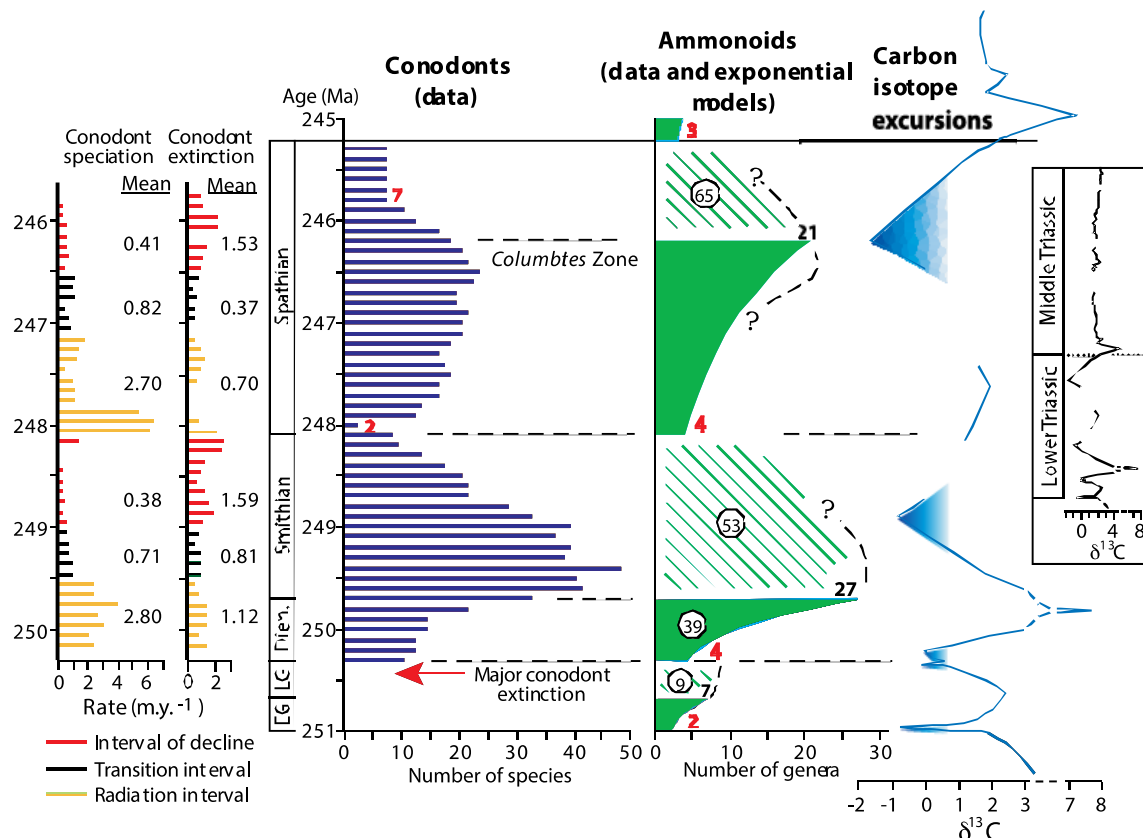
At the time this work was begun, it was widely debated whether a separate Permian mass extinction had preceded the great terminal Permian crisis or instead the incompleteness of the fossil record made it falsely appear that many victims of this event died out earlier (the Signor-Lipps effect). We showed how patterns of extinction for particular taxa indicate that there was indeed an earlier (Guadalupian) mass extinction : one of the largest of the Phanerozoic. Here we estimated that the terminal Permian mass extinction eliminated only about 80% of marine species, not the 90 or 95% quoted by earlier workers. This estimate was confirmed by my estimate of 81% based on better methodologies in my 2116 *PNAS* paper.

Stanley, S. M. 1990, Delayed recovery and the spacing of major extinctions. *Paleobiology* 16:401-414. This paper showed that the imputed periodicity for mass extinctions can be explained by the fact that a mass extinction can seldom closely follow another for taxa with relatively low rates of evolutionary turnover because time is required for recovery from the earlier crisis. A histogram of intervals between randomly spaced mass extinctions will be strongly right-skewed, and truncation of the left side of the distribution by imposition of a recovery time will produce a strongly peaked quasi-periodic distribution.

Stanley, S. M. 1979, *Macroevolution: Pattern and Process*: San Francisco, W.H. Freeman & Co., 332 pp. Among its contributions, this work showed that taxa characterized by high rates of background extinction have also experienced unusually heavy losses in mass extinctions. This relationship results from the fact that background rates of extinction are intensified in a mass extinction (they are multiplied by a large factor). In other words, diversities of taxa with high background rates of extinction are volatile. More aspects of this book are described below under the **Macroevolution** heading.

Stanley, S. M., 2009, Evidence from ammonoids and conodonts for multiple early Triassic mass extinctions. *Proceedings of the National Academy of Sciences* 106: 15264-15267.

This research showed that both the ammonoids and conodonts experienced three mass extinctions in rapid succession during the Early Triassic, each coinciding with a negative carbon isotope excursion, which probably reflected global warming (see 2010 entry below). These two taxa experienced extremely rapid evolutionary turnover under normal circumstances, and thus were prone to heavy losses in mass extinctions (see previous entry). Other marine taxa with lower background extinction rates probably also experienced losses, but ones that were too small to have been detected as of yet.



Three Early Triassic mass extinctions for conodonts and ammonoids that coincided with positive carbon isotope excursions, which presumably reflected global warming.

Stanley, S. M. 1984, Temperature and biotic crises in the marine realm. *Geology* 12:205-208.

This paper made the argument that global climate change has been the most important agent of mass extinction throughout the Phanerozoic. Part of the evidence was that many mass extinctions have struck tropical taxa preferentially; furthermore, some of these occurred at times of recognized global cooling.

Stanley, S. M., 2010, Relation of Phanerozoic stable isotope excursions to climate, bacterial metabolism, and mass extinctions. *Proceedings of the National Academy of Sciences* 107:19158-19189.

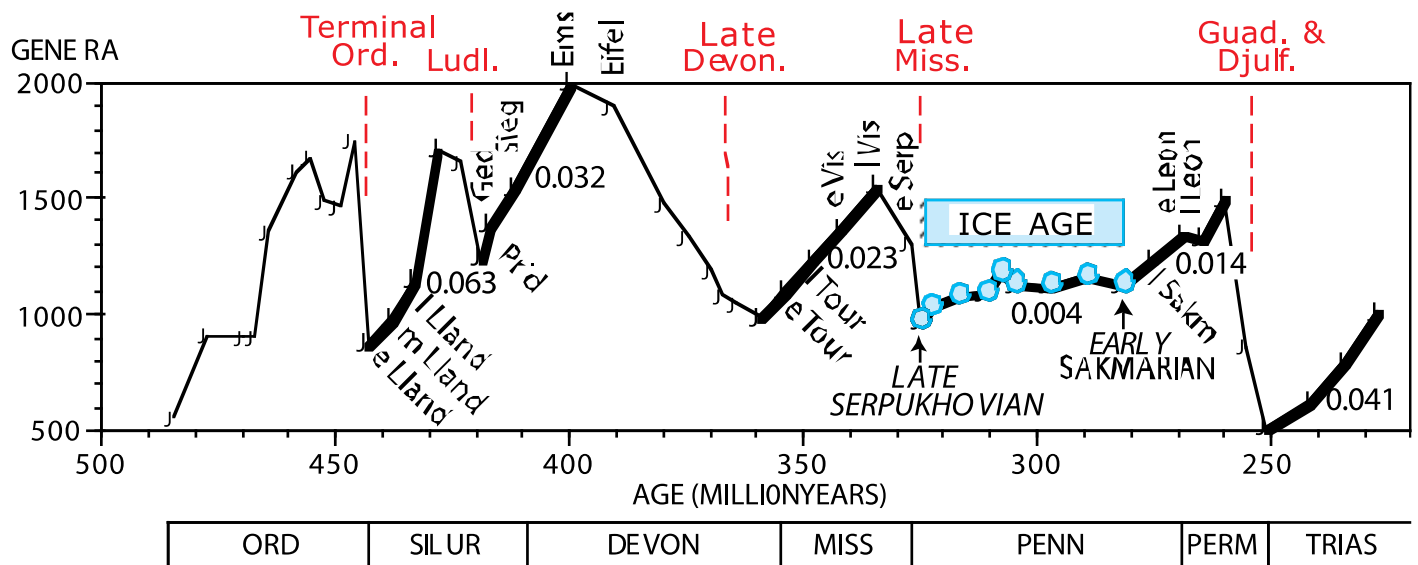
This paper confirmed the central point of the previous entry. It showed, via published oxygen isotope ratios that virtually all major extinctions have been associated with global cooling and all of the rest, with global warming. Thus, it made a strong case that climate change has played a dominant role in global mass extinctions. (See figure on page 2.)

Stanley, S. M. and Powell, M. G. 2003, Depressed rates of origination and extinction during the late Paleozoic ice age: A new state for the global marine ecosystem. *Geology* 31: 877-880.

Here it was shown that a major global extinction during the onset of the late Paleozoic ice age left a residual marine fauna in which all major taxa experienced reduced rates of turnover (evolution and extinction); this constituted a new state of the marine ecosystem. The proposition that tropical faunas suffered severe losses



and that the surviving fauna consisted of eurytopic taxa with broad geographic distributions was confirmed by my student Matthew Powell's dissertation work on brachiopods (*Geology* 33:381-381 (2005).



Low global diversity of marine genera during the late Paleozoic ice age following a mass extinction at the start of this event. Numbers below the curve are net rates of increase (fractional change per million years). The low rate for the ice age is the result of very low rates of origination and extinction.

Stanley, S. M. and Campbell, L. D. 1981, Neogene mass extinction of Western Atlantic molluscs. *Nature* 293:457-459.

This study employed Lyellian percentages (percentages of survival for species in fossil faunas) to show that Western Atlantic Mollusca experienced at least two pulses of extinction in late Pliocene and early Pleistocene time. It also provided evidence that these events resulted from climatic cooling.

Stanley, S. M. 1986, Anatomy of a regional mass extinction: Plio-Pleistocene decimation of the Western Atlantic bivalve fauna. *Palaos*. 1:17-36.

Here the case for climatic cooling as a cause of the Plio-Pleistocene mass extinction of Western Atlantic mollusks was solidified by the observation that all of the mid-Pliocene bivalve species of the tropical Pinecrest fauna of southern Florida that survived to the present (~30% of the original number) range around the Gulf Coast to Texas or up the Atlantic coast to Cape Hatteras -- they have broad thermal tolerances. All of the purely tropical forms died out. The global reduction of the areas of shallow sea floors during glacial expansions had little effect, because faunas of the Eastern Pacific, where continental shelves were reduced to a very small total area, did not experience heavy extinction.

Raffi, S., Stanley, S. M., and R. Marasti, 1985, Biogeographic patterns and Plio-Pleistocene extinction of Bivalvia in the Mediterranean and southern North Sea. *Paleobiology* 11:368-389.

Here it was shown that, with the onset of the Northern Hemisphere ice age and again about 2.5-2.4 million years ago, the Bivalvia of the Mediterranean and southern North Sea experienced patterns of extinction similar to those for Western Atlantic bivalves, although survivorship was higher. Climates became more seasonal, with colder winters. As a result, stenothermal tropical species disappeared preferentially. Only about 54% of early Pliocene species survived to the present, and they are largely eurythermal forms.

Stanley, S. M. 2010, Thermal barriers and the fate of perched faunas. *Geology* 38: 31-34.

The conclusions of this paper were based largely on two factors: (1) the differing heat capacities of land and water, which cause epeiric seas to experience greater climatic seasonality than neighboring seas of open continental shelves, and (2) latitudinal ranges of shallow marine species are determined by thermal tolerance for survival or by temperatures that are critical for triggering reproduction.

As a result, when an epeiric sea is drained, its occupants usually face thermal marine conditions that prevent either survival or reproduction. This paper shows that the fates of taxa in the Jurassic Sundance Sea illustrate this phenomenon.

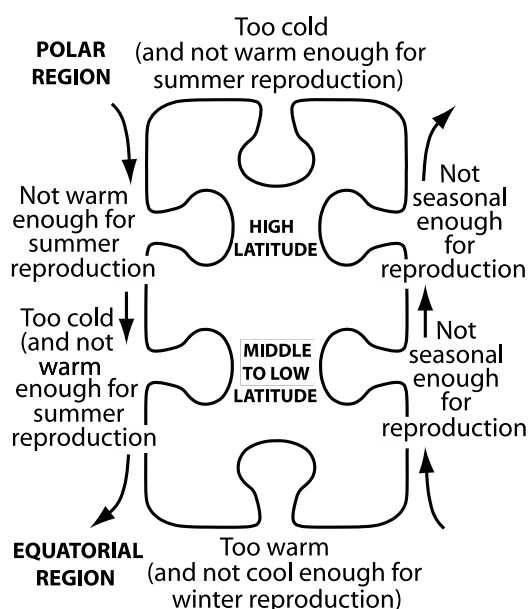
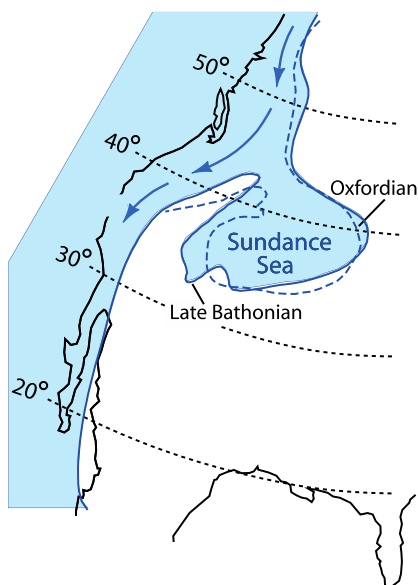


Diagram showing why climates of seas of open continental shelves are lethal to faunas dumped into them from epicontinental shelves by sea level lowering.



Map showing how the warm-adapted Jurassic Sundance Sea fauna could not have survived when the Sundance Sea was drained, and its fauna was dumped into the open ocean. The

Pacific Ocean's cold waters here flowed from the north as part of the Coriolis circulation. (The extent of the Sundance Sea is shown for two intervals.)

### Macroevolution

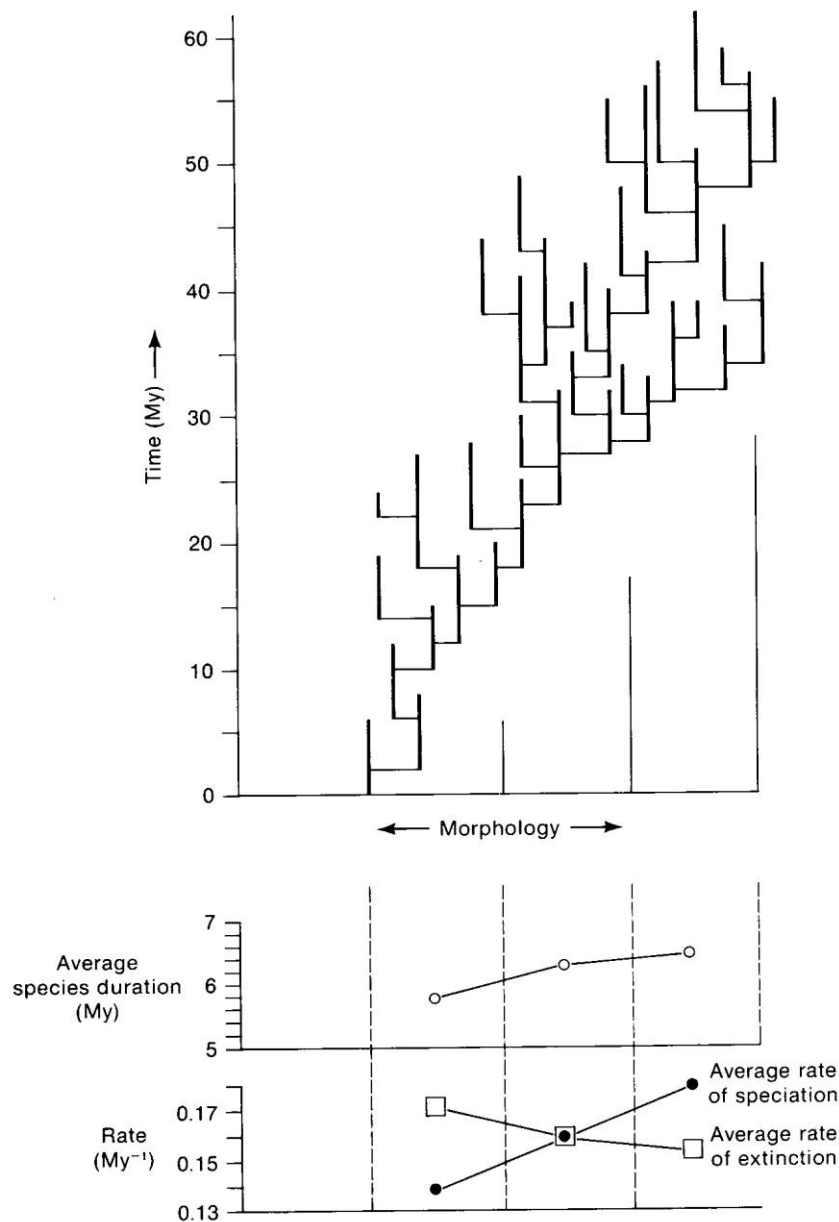
Stanley, S. M. 1973, An explanation for Cope's Rule: *Evolution*, 27:1-26.

Cope's Rule is the generalization that evolutionary increase in body size has been very common among animal taxa. At the time when this paper was written, the prevailing view was that this pattern existed because there were inherent advantages of becoming larger. But a fundamental point of this paper is that size increase is only advantageous if the founding members of a group are smaller than the optimum body size for animals of their basic type. Therefore, Cope's Rule reflects the origination of taxa at small body size relative to the size distribution that develops through subsequent diversification. In other words, the rule should be viewed as describing evolution from small size, not evolution toward large size. A second point is that adaptive innovations (origins of new animal taxa) tend to occur at small body size because scaling problems dictate morphological specializations at large body size that inhibit evolutionary innovation. This paper has had a large impact (more than 600 literature citations).

Stanley, S. M. 1975, A theory of evolution above the species level: *Proceedings of the National Academy of Sciences*. 72:646-650.

This paper provided the first tests of the punctuational model of evolution, and the model passed the tests. The paper generated more than 1,400 reprint requests. It began by providing rigorous definitions: the gradualistic model asserts that most evolutionary change is phyletic (= anagenetic, meaning that it entails the transformation of existing species). The punctuational model, in contrast, asserts that most evolutionary change occurs during speciation (branching) events. One test conducted here was "the test of adaptive radiation," which shows that species longevities in the dramatic early Cenozoic radiation of mammals were very long compared to the intervals during which higher taxa originated; gradual transformation of one species into another would have been much too slow to account for the origin of the distinctive new higher taxa. Instead, rapid, strongly divergent speciation events were required. A second test was "the test of living fossils." it was based on the observation that if the punctuational model is valid, one kind of segment of the tree of life should display little evolutionary change: one in which, over a long interval of time, there were very few branching events (where, according to the punctuational model, most of the action is). In fact, all such examples of narrow phylogenies that extend to the present, the one or very few extant species are regarded as "living fossils," being remarkably similar to their ancient ancestors.

This paper also developed the concept of species selection: selection in which species rather than individuals are the basic units, and differential rates of speciation and extinction account for directional change, rather than differential rates of reproduction and mortality. Although modern scientists have overlooked it, this idea traces back to Darwin, who shifted back and forth between individuals and taxa in discussing his selection process. **It is important to recognize that the concept of species selection is compatible with a situation in which all evolutionary change in speciation events results from natural selection at the level of the individual.**

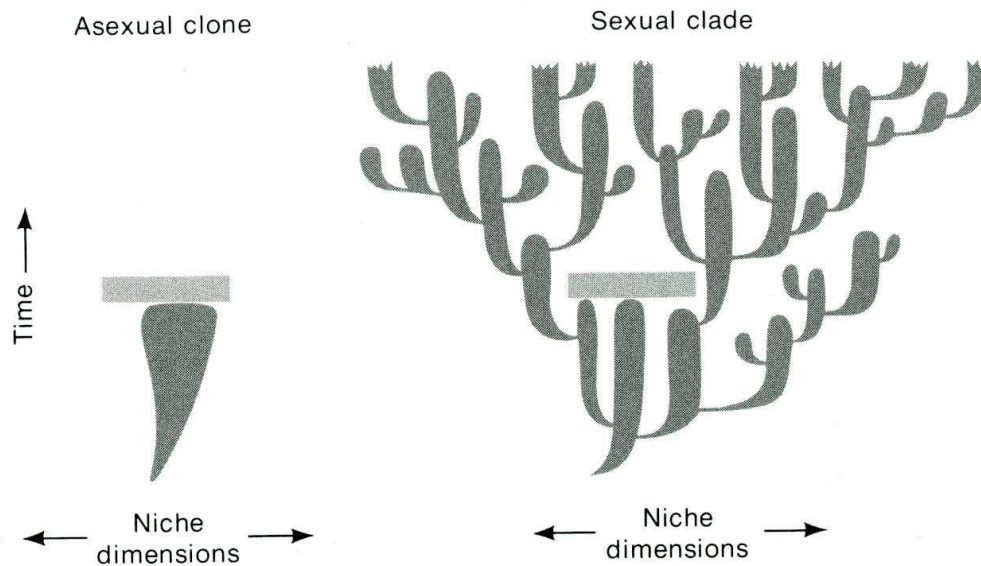


A diagram and plots illustrating species selection. This process is analogous to natural selection at the individual level, with speciation taking the place of birth and extinction taking the place of death. With regard to variation in some morphologic feature (horizontal axis here), rate of speciation increases toward the right while rate of extinction decreases. The result is that morphology of the clade shifts to the right. Either rate of speciation or rate of speciation operating alone can drive this kind of shift. Species selection is compatible with a condition in which all of the evolution in speciation is a result of natural selection at the level of the individual.

Stanley, S. M. 1975, Clades versus clones in evolution: Why we have sex: *Science* 190:382-383.

The basic idea for this paper began with a puzzle as to why sexual reproduction prevails among eukaryotic organisms: sex had been viewed as speeding up evolution, but if phyletic evolution is so slow, sex must have some other value. However, if rapid evolution occurs during speciation events, then that is where sex should play its important role. Here, my basic idea was that sexual reproduction is important primarily in accelerating evolution in small populations that are emerging as new species. Thus, through sexual reproduction a higher taxon could diversify rapidly and, via the persistence of some species, survive major

environmental changes. Comparable environmental changes would wipe out a slowly diversifying, narrowly adapted asexual clone. Thus, sexual clades are widespread, but asexual clones are rare. I also devoted an entire chapter of my *Macroevolution* book to these ideas. I presented them in more refined form at a meeting of the Evolution Society in 1990. John Maynard Smith, arguably the most prominent population biologist in the world, spoke after I did and opened his talk with this statement: “I have no problem with what Steve Stanley says, but I don’t think he has the *whole* story.” This never appeared in print, and biologists have almost entirely ignored my contribution, although it was originally published conspicuously in *Science*.



Diagrams illustrating a role for sexual reproduction. Evolutionary diversification occurs for a clone (left) and a clade (right). The two patterns begin from identical species, except that one is asexual and the other is sexual. The asexual diversification is slow, but the sexual diversification is rapid, producing a large clade because of the role of sexual reproduction in producing rapidly divergent speciation events. At some point, an environmental change causes extinction of a similar set of organisms in the clone and the clade. The result is disappearance of the clone and survival of the broad clade. This fate of this hypothetical clone, resembles the fates (early extinction) of actual clones that appear now and again in nature but quickly disappear.

Stanley, S. M., Addicott W.O., and Chinzei, K. 1980, Lyellian curves in paleontology: possibilities and limitations. *Geology* 8:422-426.

Here Lyellian curves (plots of the percentages of species of faunas of various ages that survive to the present) were used to show that rates of extinction have varied from place to place and taxon to taxon.

Stanley, S. M. 1979, *Macroevolution: Pattern and Process*: San Francisco, W.H. Freeman & Co., 332 pp. This book expanded on the concepts of the three previous entries. Its most general contribution was to introduce methodologies by which species, not simply genera and families, can be used in paleontology to study macroevolution. By analysis of Lyellian percentages and other approaches, it provided evidence that evolutionary stasis for species has pervaded the history of life. On the other side of the punctuational coin, this book reviewed many examples of rapid speciation events that have produced extant species. Also included were a further explication of the concept of species selection and an introduction of the two other concepts: phylogenetic drift, which can produce significant evolutionary trends within small segments of phylogeny, just as genetic drift can produce significant trends within small populations, and directed

speciation, in which a tendency for speciation to move in a particular adaptive direction can produce an evolutionary trend.

Two of the most important contributions of this book relate to rates of speciation and extinction: (1) It was shown that higher taxa have characteristic rates of speciation and extinction, and that these rates are correlated (for example, are both relatively high or relatively low for a taxon). It was further shown that species selection should tend to separate the rates for a taxon (elevate speciation rate and depress extinction rate), but that these rates do not easily diverge because they are fortuitously linked by common biological traits that tend to shift them in the same direction: both rates are correlated with both behavioral complexity and dispersal ability. Only a few “supertaxa” have relatively high rates of speciation and low rates of extinction. (2) As noted above, it was also shown that rates of extinction for higher taxa in biotic crises have been correlated with characteristic rates of background extinction and that this pattern reflects the fact that mass extinctions intensify background rates (multiply them by some general factor).

Stanley, S. M. 1986, Population size, extinction, and speciation: the fission effect in Neogene Bivalvia. *Paleobiology* 12:89-110.

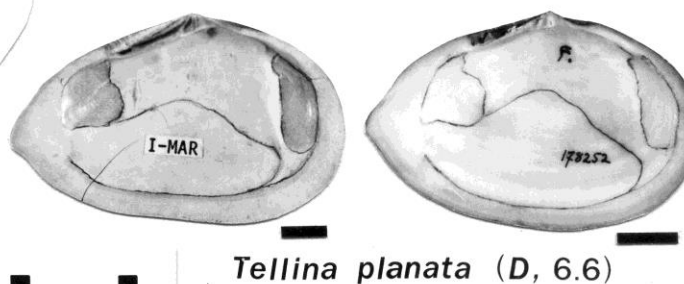
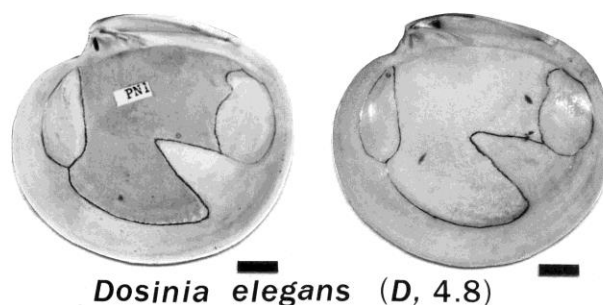
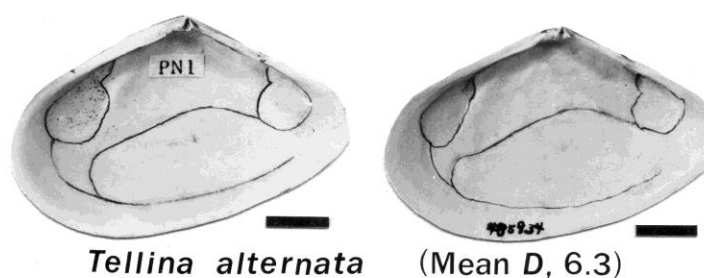
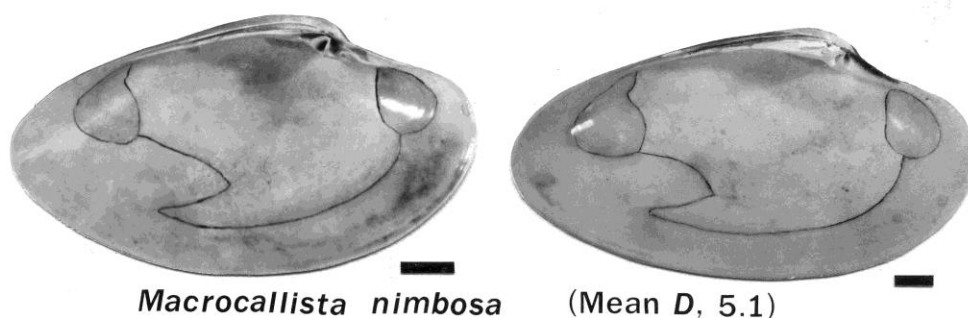
Stanley, S. M. 1990, The general correlation between rate of speciation and rate of extinction: fortuitous causal linkages. pp. 103-172, in R.M. Ross and W.D. Allmon, eds., *Causes of Evolution* (University of Chicago Press).

These contributions showed that the correlation among taxa between rates of speciation and rates of extinction results not only from the influence of behavioral complexity and dispersal ability but also varies with population size and stability: taxa with small, unstable populations, tend to experience relatively high rates of both extinction and speciation. Therefore, taxa such as the Pectinidae (scallops) that suffer from a decline in the size of their populations over evolutionary time (in the case of the scallops because of increased intensity of predation) not only experience higher rates of extinction but also, because of fragmentation of populations, higher rates of speciation. Also, geographic range results in differences in extinction rates only when differences in geographic range are quite large.

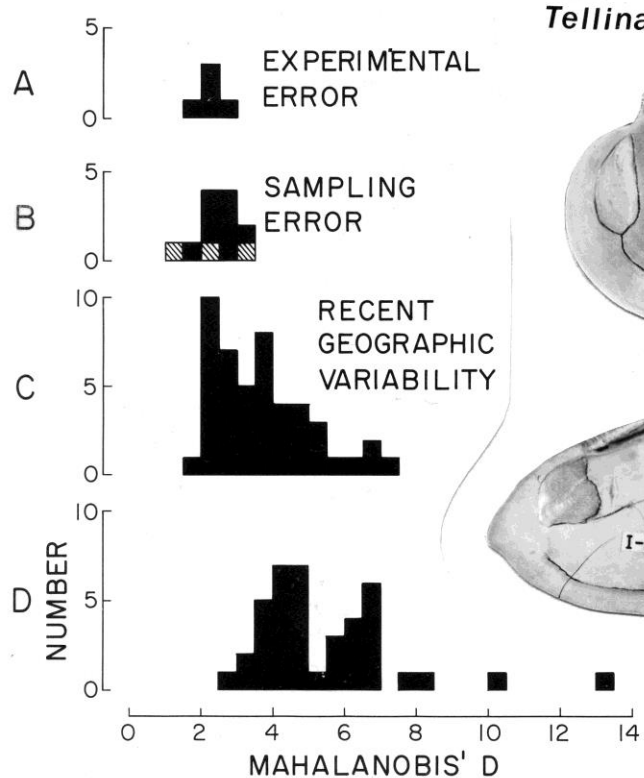
Stanley, S. M. 1982, Species selection involving alternative character states: An approach to macroevolutionary analysis. *Third North American Paleontological Convention Proceedings* 2:505-510. Here it was shown that the heavy ice-age extinction of bivalves in the Western Atlantic differed from background rates of extinction with respect to relative intensities for particular life-habit groups.

Stanley, S. M. and Yang, X. 1987, Approximate evolutionary stasis for bivalve morphology over millions of years: A multivariate, multilineage study. *Paleobiology* 13:113-139.

My original contributions supporting the punctuational model relied heavily on evidence that species identified in the fossil record survived for millions of years, and thus experienced approximate evolutionary stasis. Critics (notably John Maynard Smith, arguably the most prominent population geneticist in the world) dismissed these identifications, stating that species are in the eye of the beholder. I responded that if two populations of a lineage are separated by millions of years and are placed in the same species by a taxonomic expert, then they must record very little evolutionary change over millions of years whether or not they are actually given the same species name. It seemed, however, that a more rigorous analysis was required, and my study with my graduate student Xiangning Yang was designed to provide it. This study ignored species names and employed multivariate statistics to impartially assess the degree of similarity between Pliocene bivalve populations of 19 species 3-4 m.y. old and populations of the living species that were most similar to the fossil species, regardless of whether the fossil and living populations had been assigned to the same species. The Pliocene species were selected arbitrarily: they were all species of 4 superfamilies for which adequate samples could be obtained. It turned out that fossil and living populations were nearly as similar to each other as populations within the living species were to each other. Thus approximate evolutionary stasis has been the rule for these taxa.



Species of bivalve mollusks that experienced almost no morphologic change in the course of 3 or 4 million years. Various populations of the living forms (right) are nearly as similar to each other as they are to the fossil forms (left).



Stanley, S. M., Signor, P.W., Lidgard, S., and Karr, K.F. 1981, Natural clades differ from "random" clades: simulations and analyses. *Paleobiology* 7:115-127.

This paper refuted the conclusion of several papers that, by way of computer simulations, purported to show that major fluctuations in the diversities of species-rich higher taxa might have resulted from random walk under conditions in which probabilities of origination and extinction were equal. We showed that this conclusion is invalid because of scaling problems: the numbers of entities within the taxa in the original simulations were much smaller than the numbers of species within these taxa in the real world. When realistic numbers are employed, such simulations result in very little change of diversity.

## Evolutionary Radiations

Stanley, S. M. 1973, An ecological theory for the sudden origin of multicellular life in the Late Precambrian: *Proc. Nat. Acad. Sci.* 70:1486-1489.

Stanley, S. M. 1976, Fossil data and the Precambrian-Cambrian evolutionary transition: *Amer. Jour. Sci.*, v. 276, p. 56-76. Reply to K.M. Towe: *Ibid* 266:1180-1181.

Stanley, S. M. 1976, Ideas on the timing of metazoan diversification: *Paleobiology* 2:209-219. The central conceptual point of these papers was that before the advent of effective predation on phytoplankton, the population sizes of marine phytoplankton species would have been established by nutrient availability, so that competition among species would have been much more intense than in the modern ocean. Thus, the phytoplankton ecosystem would have been saturated with species: there was little room for the origin of new species, and evolution would have been stifled. This conclusion is supported by the observation that, before the appearance of animals, a typical species of acritarchs survived for about a billion years.

Stanley, S. M. 1968, Post-Paleozoic adaptive radiation of infaunal bivalve molluscs – a consequence of mantle fusion and siphon formation: *Journal of Paleontology* 42:214-229.

This contribution, submitted when I was a graduate student, showed that fusion of the bivalve mantle, which underlies and secretes the shell, triggered the enormous post-Paleozoic evolutionary radiation of infaunal bivalves. First, mantle fusion creates siphons, which permit animals to burrow more deeply than nonsiphonate forms. Second, mantle fusion makes the burrowing mechanism more efficient by sealing the mantle cavity so that, when adduction of the valves applies pressure to the water in the mantle cavity, blood is squeezed more effectively into the foot, which then anchors the animal for the rocking motion of burrowing. Nonsiphonate burrowing bivalves are shallow burrowers, and they are nearly all slow burrowers (the trioniids are exceptions because of their highly muscular foot). Nonsiphonate burrowing bivalves have undergone little net diversification since the Paleozoic.

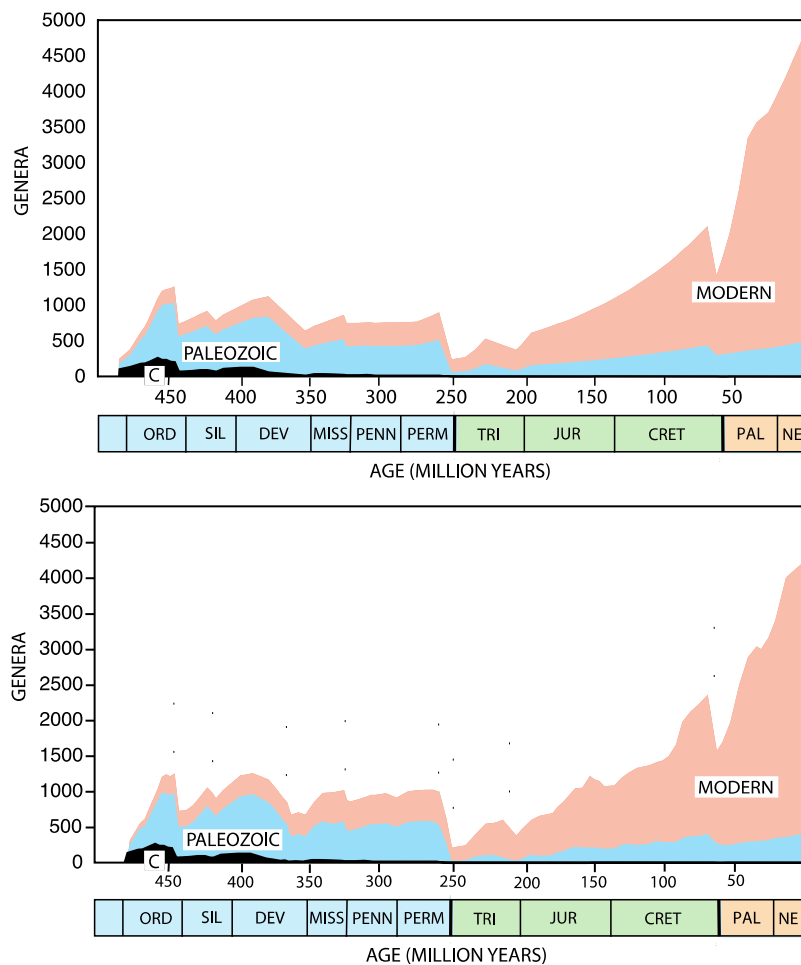
Stanley, S. M. 1974, What has happened to the articulate brachiopods? *Geological Society of America Abstracts with Programs* 6:966-967.

In this contribution, I advanced the notion that Geerat Vermeij later labeled “the Mesozoic marine revolution.” This is the notion that the initial evolutionary radiations of three groups of advanced marine predators caused the decline of taxa that were relatively defenseless against them. The new predators were teleost fishes, which were more mobile and had more sophisticated feeding apparatuses than their predecessors; crabs, which had powerful claws, and predatory snails, many of which were able to attack victims by boring into shells. Here I focused on the decline of the articulate brachiopods.

Stanley, S.M. 2007, An Analysis of the History of Marine Animal Diversity. *Paleobiology* 33(4 Supplement), Memoir 4. 55pp.

Here it was shown that individual higher taxa of marine animals generally increase in diversity exponentially on a global scale unless this increase is interrupted by a mass extinction. Total global marine animal diversity has also increased exponentially except when interrupted by mass extinctions. Empirically based simulations confirm this pattern and show that the logistic model, which was based on the idea that rates of diversification are suppressed by crowding, fails to replicate the empirical pattern when empirically based rates of origination and extinction are employed. It was also shown, for many more taxa than in my *Macroevolution* book, (1) that individual taxa have characteristic rates of origination and background extinction, (2) that these rates are correlated with each other, and (3) that in any mass extinction these rates are multiplied, so that taxa characterized by high background rates experience extremely heavy losses. In other words, taxa characterized by high rates of origination and background extinction are volatile, diversifying rapidly but also suffering heavy losses in mass extinctions





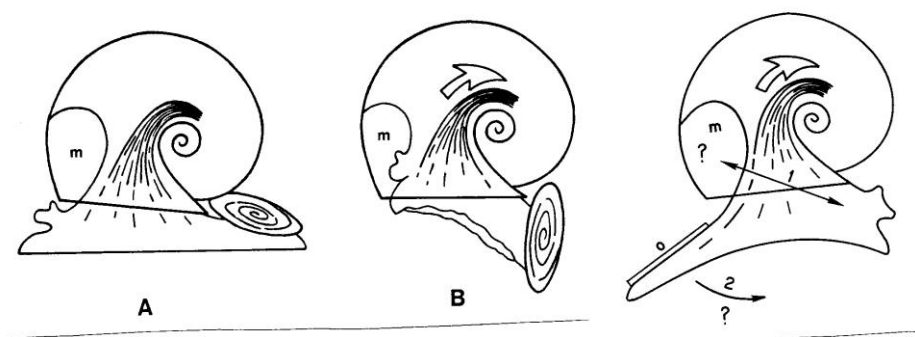
Simulation employing standardized empirical rates of diversification and magnitudes of mass extinction for marine genera (top). This closely resembles the empirical plot of Phanerozoic marine animal diversity (bottom). This comparison demonstrates that marine animal diversification has been simply been a matter of exponential increase punctuated by mass extinctions. Crowding has not stifled diversification.

Stanley, S. M. 1977, Trends, rates, and patterns of evolution in the Bivalvia. pp. 209-250 in A. Hallam, ed. in *Patterns of Evolution* (Elsevier, Amsterdam).

This was a general review of bivalve evolution, but in it I further developed the idea that the evolutionary radiations of teleost fishes, crabs, and predatory snails caused the Mesozoic decline of taxa that were particularly vulnerable to their attacks. Among their victims, I concluded, were not only articulate brachiopods but also endobyssate bivalves and crinoids. Geerat Vermeij cited this book chapter in his 1977 paper but failed to indicate that it had contained the event that he labeled “the Mesozoic marine revolution” -- an event for which he has been widely given credit for recognizing but which he actually learned about from me.

Stanley, S. M. 1982, Gastropod torsion: predation and the opercular imperative. *Neues Jahrbuch für Geologie und Paläontologie* 95:95-107.

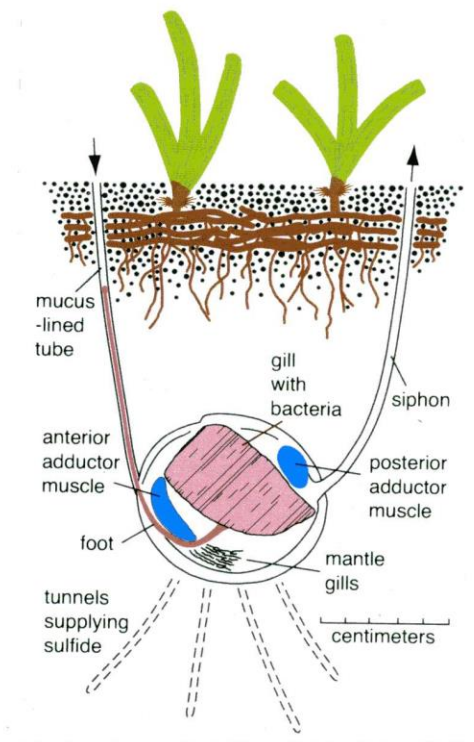
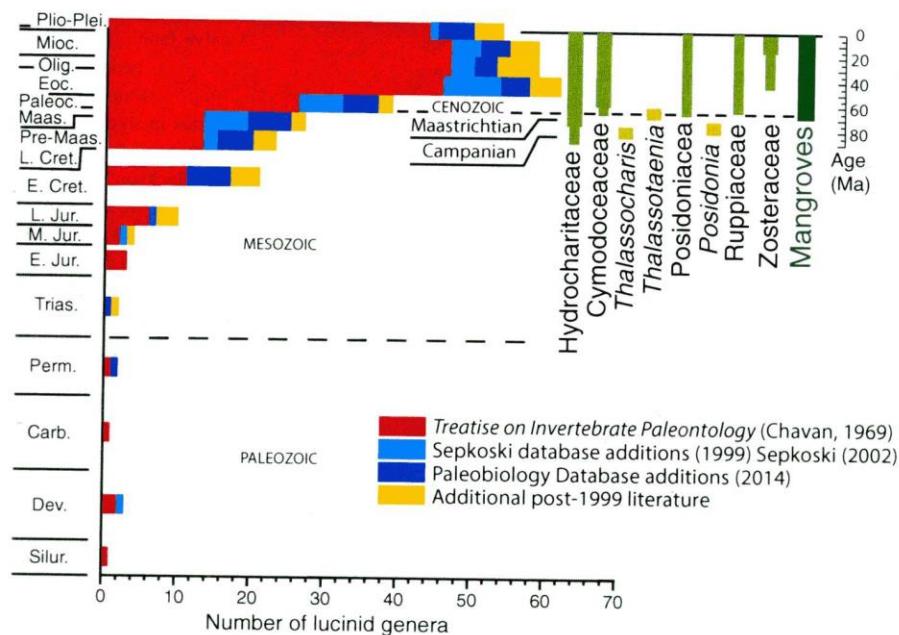
Gastropods (snails) are an extremely diverse group today. The fundamental trait that defines them is torsion. This has nothing to do with the coiling of the shell of many snail species. Torsion results from an event early in life history when the alimentary tract is twisted into a “U,” so that the anus is positioned more-or-less above the head. Many biologists have suggested that this seemingly strange evolutionary event may be the product of a single mutation. When I considered the value of torsion, several ostensible advantages for it had been suggested, but none seemed to me to make sense. I recognized that a key result of torsion is that, when the snail pulls into its shell, it goes in head-first. For the monoplacophoran ancestors of snails, the head went in last, and they declined rapidly in diversity after the Early Cambrian, probably because new predators could attack them even after they pulled into their shells. Snails quickly evolved an operculum: a pluglike structure on their posterior that allowed them to shut themselves in their shells with what amounts to a closed door. Modern snails that lack an operculum are limpets, which in effect use the substratum as an operculum, and naked snails that are poisonous. I believe that I have explained the function of the feature that not only defines the gastropods but also explains their great success, but this contribution has been largely ignored (even though this interpretation of torsion is included in my *Macroevolution* book).



The value of torsion in orienting a gastropod so that its head goes in first so that it can protect itself with an operculum (A and B). The head of an untorted monoplacophoran had to go in last, and the body could not have folded to protect the animal (right)

Stanley, S.M., 2014, Evolutionary radiation of shallow-water Lucinidae (Bivalvia with endosymbionts) as a result of the Late Cretaceous rise of seagrasses and mangroves. *Geology* 42:803-806.

This study explained the very unusual evolutionary history of the Lucinidae. This family arose in the Silurian and remained at very low diversity until very late in the Cretaceous, when it suddenly underwent a remarkable radiation. I connected this expansion to the origin of mangroves and especially seagrasses. The highest diversity of modern lucinids is in meadows of seagrass meadows, and many species occupy mangrove habitats. These flowering plants create environments in which anoxic sediment beneath them is rich in sulfides occupied by sulfide-oxidizing bacteria, and lucinids harvest these organisms and grow them in their gills, digesting them for nutrition.



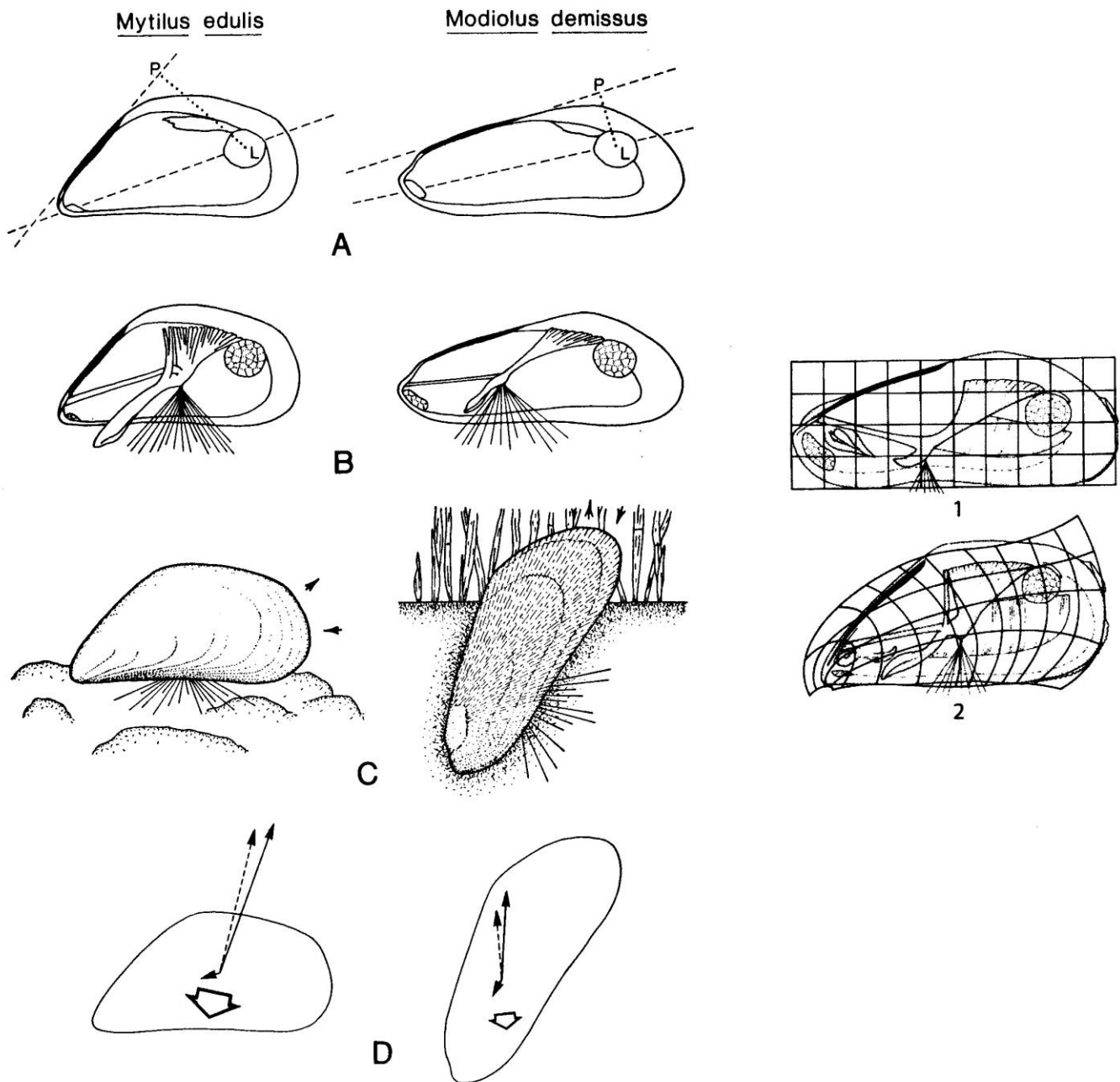
Lucinid bivalves, which today in shallow water live predominantly at the anoxic/oxic boundary beneath mangroves and, especially, seagrass, were present in very low diversity until the very late Cretaceous, when these groups of plants arose, providing these animals' favored habitat. This was clearly no accident.

### Evolutionary ecology (Adaptive breakthroughs were often involved here as well.)

These are various contributions that have related patterns of evolution and extinction for major taxa to ecological changes involving them and often also associated taxa.

Stanley, S. M. 1972, Functional morphology and evolution of byssally attached bivalve mollusks: *Journal of Paleontology* 46:165-212.

Focusing on bivalves attached by byssal threads, this study complemented the 1968 paper on the evolutionary consequences of mantle fusion for free-living burrowers. All burrowing bivalves above the level of the Protobranchia employ a byssus to attach to sedimentary particles during their postlarval stage, when they are vulnerable to disruption by waves and currents. C. M. Yonge therefore logically concluded that byssal attachment became established in adults of bivalve taxa by neoteny, the evolutionary process in which a juvenile feature is retained to later stages of ontogeny. My analysis showed that neoteny in fact led to adult byssal attachment independently in a number of bivalve groups. In each case, the first byssate forms were infaunal (endobyssate), but from them epifaunal (epibyssate) forms evolved. In other words, the byssus allowed bivalves to emerge from the sediment and attach firmly to the substratum without support from surrounding sediment. It happens that in some epifaunal bivalves, juveniles retain endobyssate shapes, and this has made it possible for evolution to produce reversions from epibyssate to endobyssate modes of life. In general, however, the percentage of endobyssate taxa has declined since the Ordovician, presumably because of their vulnerability to predators.



Functional morphology of two byssally attached mytilid bivalve mollusks, the epifaunal form, *Mytilus*, and the semi-infaunal form, *Geukensia*, representing an earlier stage of evolution, has musculature that pulls it downward into marsh peat. The anterior of *Mytilus* is reduced and the posterior hypertrophied, so that strong musculature anchors it firmly to the substratum. Deformation coordinates on the left show how the shape of *Mytilus* came about.

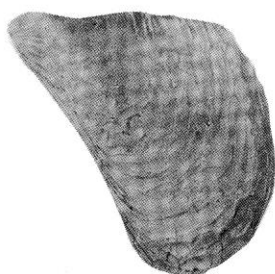
M.  
(Orthomyalina)  
subquadrata



M. glossoidea



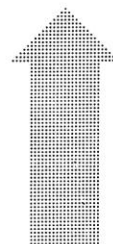
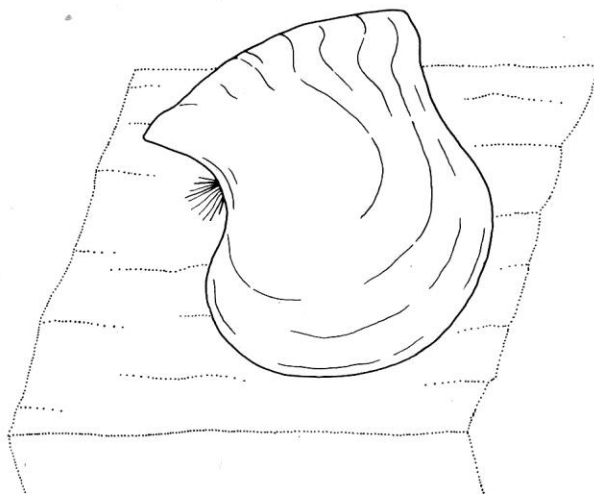
M.  
wyomingensis



M. lepta



M. copha

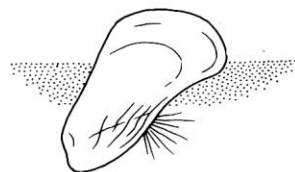


Loss of anterior lobe

Increase in size

Trend from prosocline to acline

Trend from subequivalve to markedly inequivalve



The late Paleozoic myalinid bivalves display a general evolutionary transition that, by analogy with mytilids and other living bivalves, can be shown to have involved a transition from semi- infaunal byssate species to epifaunal byssate species. Note the similarity of *M. copha* (bottom photo) to *Geukensia* (top figure).

Stanley, S. M. and Newmn, W. A. 1980, Competitive exclusion in evolutionary time: the case of the acorn

barnacles. *Paleobiology* 6:173-183.

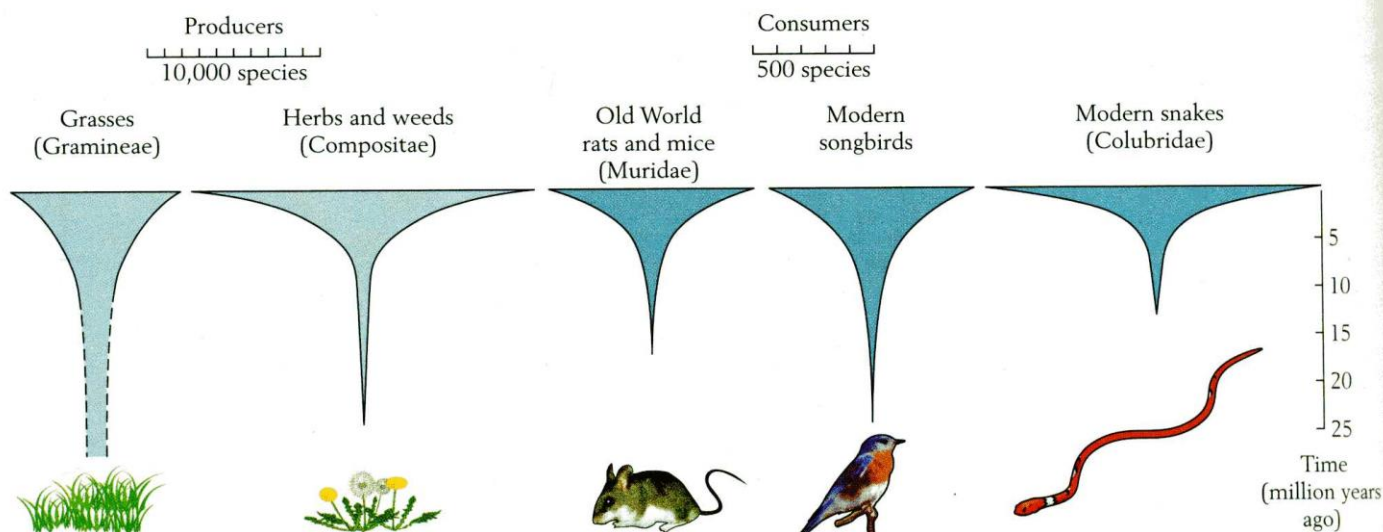
There is overwhelming evidence that for most marine taxa, competition for food or living space does not play a dominant role because predation and physical disturbance limit population sizes for most species. There is one clear exception, however, which entails barnacles, and it is the result of the very weak role that predation plays in the upper intertidal zone. Today the barnacle genus *Chthamalus* is restricted to the uppermost intertidal zone, where balanoid barnacles are physiologically incapable of living. Below this level, balanoids physically eliminate *Chthamalus*. Because of their porous wall structure, balanoids grow more rapidly and attach more firmly than *Chthamalus*. As a result, they tend to overgrow and dislodge *Chthamalus*. Balanoids arose about 50 million years ago, and have been undergoing an enormous adaptive radiation, which has produced about 273 living species. Chthamaloids originated earlier, at least 70 million years ago, but today include only about 53 species, some 40 of which are restricted to a high intertidal refuge. We concluded that balanoids suppressed chthamaloids and drove them largely into this refuge.

Stanley, S. M. Wetmore, K., and Kennett, J. P. 1988, Macroevolutionary differences between the two major clades of Neogene planktonic Foraminifera. *Paleobiology* 14:235-249.

Here we contrasted the globorotaliids and globigerinids. The former exhibit higher mean rates of speciation and extinction than the latter. We attributed this to the relative instability and small size of globorotaliid populations: globorotaliids lack the symbiotic algae harbored by globigerinids and live in relatively deep water, flourishing only under conditions of upwelling.

Stanley, S. M. 1990, Adaptive radiation and macroevolution. *Systematics Association Special Volume* 42:1-16.

The important new concept here was that the global spread of grasslands and contraction of forests caused by Neogene climatic cooling and drying led to the dramatic evolutionary radiation of weeds (the Compositae), rats, Old World mice, snakes, and songbirds. In other words, adaptive radiation was passes up through the food web on a global scale. I termed the results “cascading radiations.



Cascading radiations propagating upward through the food web of open terrestrial environments from the Miocene to the present.

Stanley, S.M., 2014, Evolutionary radiation of shallow-water Lucinidae (Bivalvia with endosymbionts) as a result of the Late Cretaceous rise of seagrasses and mangroves. *Geology* 42:803-806.

This contribution shows that the appearance of mangroves, and especially of seagrasses, late in the Cretaceous triggered a great adaptive radiation of the bivalve family Lucinidae after this group had existed at very low diversity for about 340 million years. By far the highest diversity of shallow-water lucinids today is in sediments cloaked by these angiosperms, which provide anoxic conditions that support the endosymbiotic bacteria consumed by the lucinids. (See illustration on page 19.)

Stanley, S. M. Evolutionary Ecology of the Bivalvia in *Treatise on Invertebrate Paleontology*. Part N. Volume 1, Bivalvia (revised, electronic version), Ch.19. 48pp.

This is a summary of my work on this subject, along with a smaller amount of work by others. As a return to my roots, its writing was very gratifying.

### Human evolution

**(This contribution could also be included within the categories “Evolutionary ecology” and “Adaptive breakthroughs”)**

This research showed that *Australopithecus* and its descendent, early *Homo*, represented entirely different organisms, both anatomically and ecologically. It attributed the evolution of the modern human genus, *Homo*, to climatic changes early in the modern ice age of the Northern Hemisphere that drove our ancestors from their partly arboreal mode of life to an entirely terrestrial mode of life.

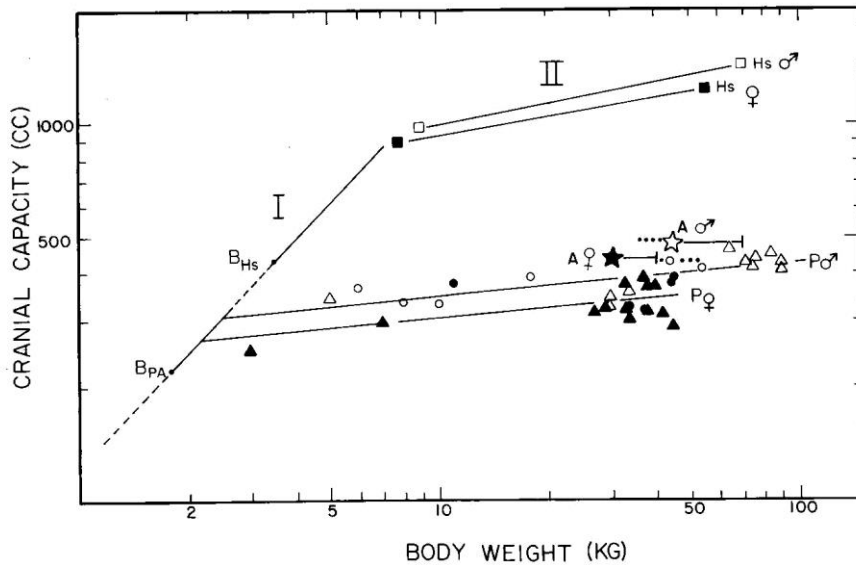
Stanley, S. M. 1992, An ecological theory for the origin of *Homo*. *Paleobiology* 18:237-257.

Stanley, S. M. 1996, *Children of the Ice Age: How a Global Catastrophe Allowed Humans to Evolve*. New York, Harmony Press, 278 pp. (Paperback ed. W. H. Freeman, New York, 1998).

It had become clear by the time that these publications were produced that *Australopithecus* retained numerous adaptations for climbing trees. I argued that it had to put these adaptations to use to obtain food and escape from predators (*Australopithecus* was an extremely slow runner and lacked sophisticated anatomical or manufactured weapons). A key point of this research was the fact that the evolution of the large brain of *Homo* produced helpless infants by depressing the overall rate of fetal and infant development. Our australopithecine ancestors, however, had mature neonates that clung to their mothers when they climbed. A population of *Australopithecus* had to abandon tree-climbing habits before it could evolve into *Homo* because the immature neonates of *Homo* could not have clung to climbing mothers and mothers could not have climbed while carrying a helpless infant. The drying of climates in Africa about 2.5 million years ago, when the Northern Hemisphere ice age got fully underway, caused woodland habitats to contract. The result was the extinction of *Australopithecus*, but one population, living a life fully on the ground, survived to evolve into *Homo* (probably an unlikely event!).

In this research I was able to show that *Australopithecus* was not characterized by delayed development (its infants were as mature as those of modern apes), whereas early *Homo* had delayed development and helpless infants. Values for a few parameters provided the evidence. Pelvic size indicates the size of a neonate, and higher primates at birth have brains that constitute 10 percent of total body weight, so it was possible to estimate both body and brain weight for neonates of *Australopithecus* and early *Homo* from the dimensions of fossil pelvises. We also have estimates for adult brain and body weights of adults of these taxa. Like modern humans, early *Homo* had to have retained its high fetal rate of brain growth for a time after birth in order to attain its large adult brain size. This means that early *Homo* had helpless infants that could not have clung to climbing mothers. *Australopithecus* did not; the trajectories of its brain and body growth were only slightly different from those of a chimpanzee or orangutan, so its infants were mature enough to cling to their climbing mothers.





*Homo  
rudolphensis*



*Australopithecus  
africanus*

Patterns of brain growth for apes, *Australopithecus*, and hominids. The steep curve

depicts the rate *in utero*, where for all higher primates brain weight is maintained at ~10% of body weight. At birth, for apes and *Australopithecus* the rate of brain growth declines sharply. The lower of the lower of the two low-angle curves is for chimps and oranges; the upper one is for *Australopithecus*, indicating that, like apes, this creature had relatively mature neonates that could have clung to climbing mothers. The upper low-angle curves represent male and females of *Homo sapiens*, for which the high neonatal rate of brain growth is maintained for about a year after birth, which produces a very big brain but also helpless infants. Early members of Homo, such as *H. rudolphensis*, had a growth pattern like *H. sapiens* and thus also had helpless infants.

### Bivalve functional morphology

This is the largest body of work that any researcher has produced on the functional skeletal morphology of any class of animals. I have interpreted the function of over 50 features of bivalve shells. Here are three of the relevant publications, the most important by far is GSA Memoir 125, which is my unaltered dissertation.

Stanley, S. M. 1969, Bivalve mollusk burrowing aided by discordant shell ornamentation: *Science* 166:634-635.

This paper showed how asymmetric ridges, with steep dorsal slopes and gentle ventral slopes, aid some bivalves in burrowing by alternately sliding and gripping as the shell rocks back and forth. The focus was on a tellinid species with parallel ridges at an angle to the shell margin and a lucinid species with parallel chevron-shaped ridges.

Stanley, S. M. 1970, Relation of shell form to life habits in the Bivalvia (Mollusca): *Geological Society of America Memoir* 125, 296 p.

This was the publication of my unmodified dissertation. It was based on study of 95 species representing 29 bivalve families. The goal was to make it possible to relate modes of life to environments in paleoecological studies and to interpret the adaptive significance of evolutionary trends. Bivalve life habits had previously been poorly understood and were studied extensively in the field and the laboratory. Many taxa turned out to live in ways that had never been reported in the literature. Burrowers were imaged by x-



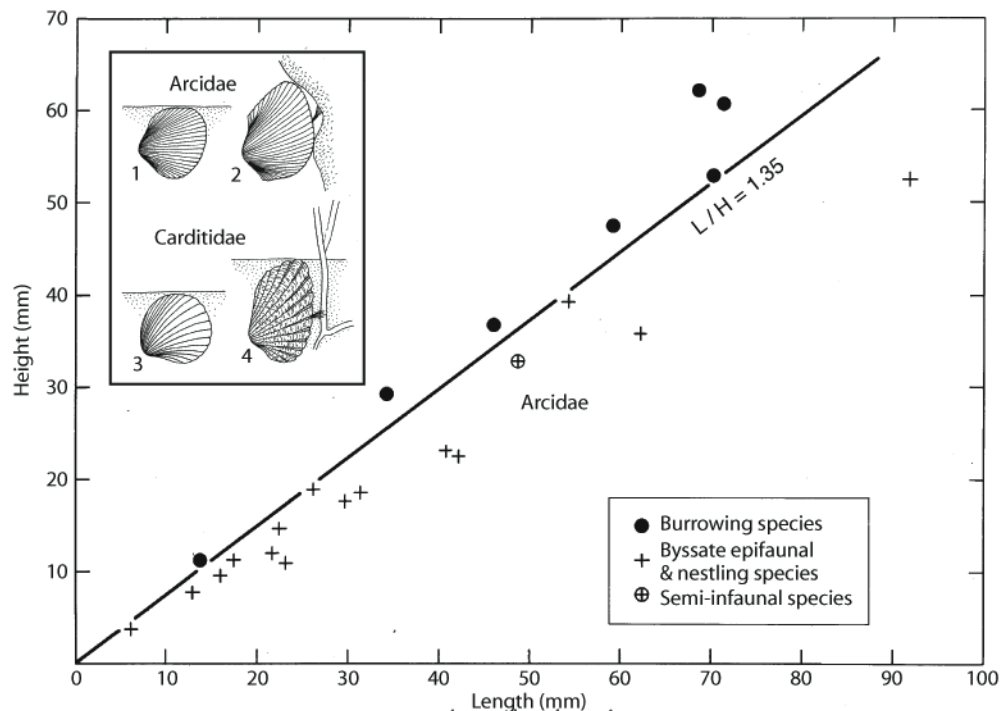
raying them in life position within narrow aquaria. Rates of burrowing were also measured using a new metric that standardized for body size.

Stanley, S. M. 1977, Coadaptation in the Trigoniidae, a remarkable family of burrowing bivalves: *Palaeontology* 20:869-899.

This paper showed how the bizarre shapes of the bivalve family Trigoniidae actually represented a coadapted complex of features. The large, muscular foot required a wide gape, so huge hinge teeth with secondary dentition evolved to maintain shell alignment. These crowded the umbonal region, so the family was forced to evolve orthoclinous and opisthogyrous shapes. Having lost the advantage that a prosogyrous shape provides for burrowing, the family evolved a variety of shell ornamentations that aided in burrowing. The cardiids solved the problem of having a large, muscular foot a different, much less complex way. They simply evolved large lateral teeth for shell alignment.

### Here are all of my functional morphologic interpretations for bivalves:

- (1) Epifaunal members of the Mytilidae have a triangular outline in lateral view, with a hypertrophied posterior dorsal region associated with large byssal retractor muscles that provide firm attachment. (See figure on page 20.)
- (2) Endobyssate (infaunal or semi-infaunal) members of the Mytilidae, are oblong in lateral view, retaining an anterior lobe, which has been lost in epifaunal lineages. Some have a byssal sinus. I later extended this analysis to Paleozoic taxa, such as the ambonichiids and myalinids. (Stanley, S. M. 1972, Functional morphology and evolution of byssally attached bivalve mollusks: *Journal of Paleontology* 46:165-212.) (See figure on page 20.)
- (3) Tridacnids, have a greatly reduced anterior region and greatly hypertrophied posterior region. This morphology results in an inflation of mantle tissue and exposure of numerous symbiotic algae to sunlight. The tridacnids' coarsely corrugated shell provides scalloped shell margins that increase mantle exposure because the marginal projections are narrow; they do not fill the embayments opposite them when the valves are adducted. I showed that simple zigzag margins would not change the area of gape for a given angle of gape.
- (4) The lower valve of byssally attached epifaunal species that live with the sagittal plane at a low angle is normally less convex than the upper valve, conforming to the substratum.
- (5) Byssally attached pteriids that live with the sagittal plane at a low angle have an adjacent byssal sinus that provides for firm attachment. This provides for firm attachment by positioning two points of contact with the substratum distal to the site of byssal attachment, so that the shell cannot be flipped over.
- (6) The genus *Pteria* habitually attaches to alcyonarians in an upside-down position, with its elongate posterior dorsal wing angled upward. The animal's exhalent current flows parallel to the wing, which, by way of experiments, I concluded must function to deflect any water currents that would otherwise sweep the exhalent water back to the animal's inhalant region. Experiments described in my 1972 paper on the evolution of byssal attachment confirmed this inference.
- (7) For firm attachment, byssally attached members of the Arcidae and Carditidae are more elongate than free-burrowing members of these families and thus lack convex ventral margins.



Graph showing the elongate shapes of byssally attached arcids and carditids.

(8) In the modern ocean only limids that nestle within cavities employ loose byssal attachment. Limids living in this way have a byssal gape bordered on each valve by a smooth lip that permits shell movement without detachment.

(9) Members of the Pinnidae are endobysate forms with an elongate shell whose pointed anterior permits the animal, as it grows, to pull itself downward occasionally by tugging against the byssus.

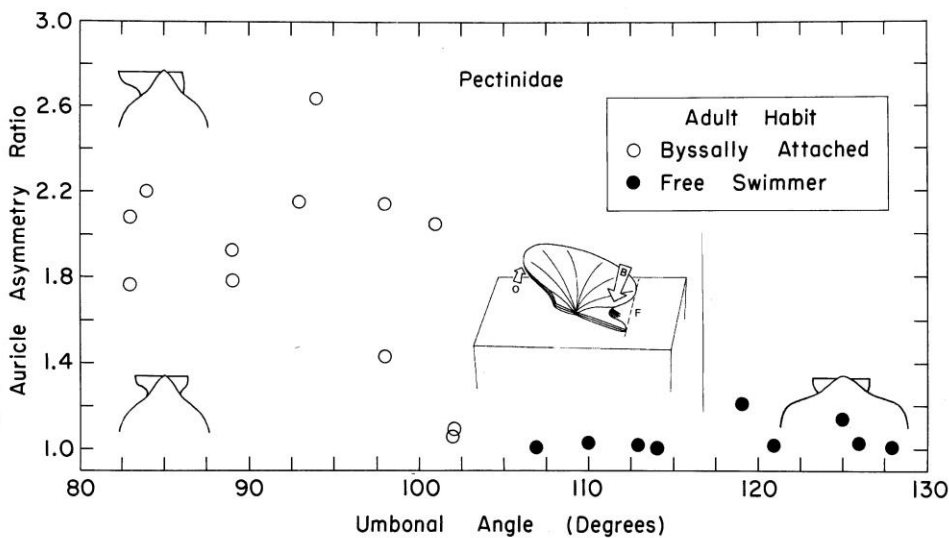
(10) Epifaunal species that attach by cementation generally have thick shells, and many have spines. Both of these features thwart predators.

(11) Many free-living recliners that are immobile have relatively large, broad shells, often with a flattened upper valve that offers little resistance to water currents.

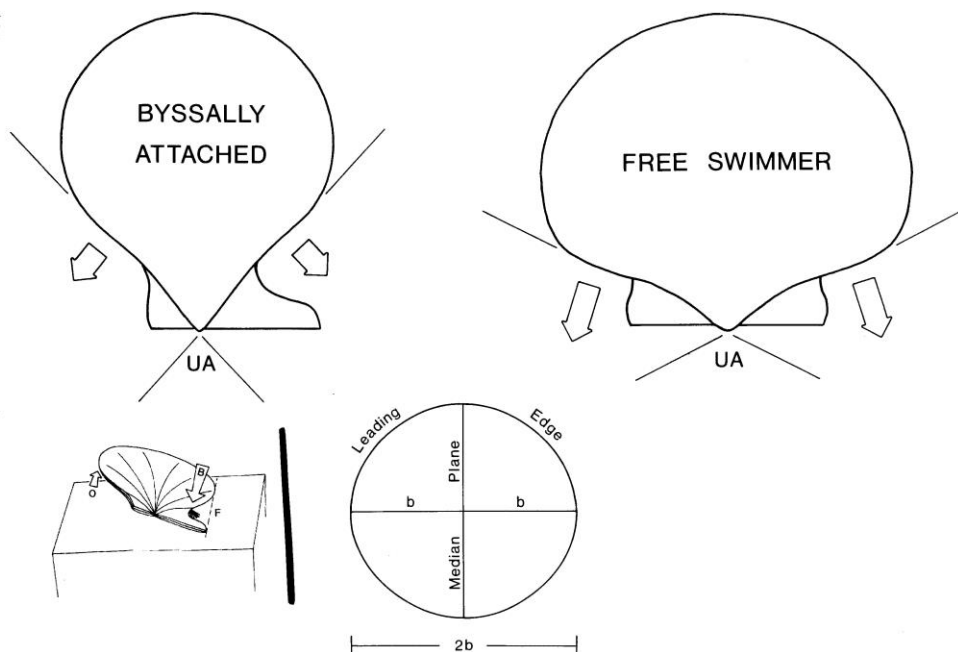
(12) Scallops (Pectinidea) that are free-living as adults and occasionally swim by jet propulsion have relatively thin shells, which endow them with a relatively low overall density.

(13) Most free-living scallops have permanent narrow gapes between their valves for water expulsion.

- (14) As one would expect, free-living scallops have an axis of almost perfect symmetry about an axis parallel to the direction in which they swim. Scallops that are attached as adults lack this symmetry.
- (15) Free-living scallops have shells with larger width-to-height ratios than scallops that are byssally attached. The large aspect ratio of the shell increases lift during swimming.
- (16) The wide umbonal angle of swimming scallops also expands the shell margins where water is expelled and results in expulsion of water directly backward.
- (17) A relatively narrow umbonal angle of byssally attached scallops provides for strong attachment.
- (18) Byssally attached scallops also have an elongate anterior auricle, which functions, along with the anterior shell margin, to provide two points of attachment distal to the site at which the byssus attaches. This configuration provides for firm attachment. In the absence of the elongate auricle, the animal could flip back and forth without firm attachment.



Free-living scallops, which are relatively good swimmers, and byssally attached scallops have different adaptive shapes. Byssally attached species have narrow umbonal angles and a wide auricle adjacent to their byssus. This configuration gives them two points of shell contact with the substratum beyond the attachment of the byssus, so they are stabilized (can't flip over). The wide umbonal angle of free-living species sends the currents they use for jet propulsion more directly backward and also increases lift by providing a large aspect ratio for their overall shape.



- (19) Some scallops that are rapid swimmers have an

upper valve that is more convex than the lower valve. Like the cross-section of an airplane wing, this morphology provides lift via the Bernoulli Effect

(20) Some free-living scallop species have a slightly concave upper valve. These forms clap their valves to excavate a pit into which they slide, ending up with the lower valve buried. Sand that settles on the concave upper valve then hides the animal. Only the commissure margin is visible.

(21) My research confirmed the generally understood notion that the size of a burrowing bivalve's pallial sinus correlates with the length of the animal's siphons and, hence, with its burrowing depth. On the other hand, because the diameter of siphons varies greatly among species, one cannot calculate a precise burrowing depth from the area of the pallial sinus, into which the siphons contract when retracted. Nonetheless, the area of the pallial sinus is better correlated with siphon length than is the length of the pallial sinus.

(22) A posterior gape, which is most often present in elongate bivalves, correlates with long siphons and deep burrowing. In some species with large gapes the siphons are not even totally retractable.

(23) For most infaunal bivalves, the orientation of a species as it burrows can be reconstructed from the fact that, in the absence of a gape, the site along the margin of the shell that opens widest is at the greatest distance from the hinge axis. This is normally the position of the center of the extended foot. Thus, the sediment surface is tangential to the shell at this point on the shell margin when the animal begins to penetrate the sediment. The hinge axis of the animal is therefore approximately horizontal when the animal is in its burrowing position.

(24) Shallow-burrowing bivalves whose shell margins are flattened in the posterior region where the inhalant and exhalant currents are located live with this flattened region oriented parallel to the surface of the sediment.

(25) A shallowly burrowing bivalve such as *Anomalocardia* that has an elongate posterior and short siphons lives with its long axis vertical. In effect, the elongate posterior takes the place of longer siphons, so that the animal's viscera are deeper in the sediment than they would otherwise be positioned.

(26) When a gape is present at the opposite end of an elongate bivalve shell from the end where the siphons emerge, the animal burrows in a direction parallel to the long axis of the shell. The foot is cylindrical.

(27) Interdigitation of ribs or denticulation along the inner shell margin of some bivalves serves to align the valves upon closing if they have become slightly misaligned by shearing pressure while gaping.

(28) Rapidly burrowing bivalves fall within two life habit groups: some occupy shifting sand and are required to reburrow frequently, and others are deposit feeders that must migrate frequently to obtain new food resources (nuculids, as slow burrowers, are exceptional deposit feeders, but they live in organic-rich fine-grained sediment and migrate slowly).

(29) Most rapidly burrowing bivalves have shapes that are blade-like, discoid, or cylindrical in general form, so that they encounter less physical resistance during sediment penetration than is encountered by more spheroidal species. Exceptions are the cockles (cardiids), which, though somewhat spheroidal, are unusual in having a highly muscular foot.

(30) Bivalves with elongate or pointed anterior-ventral regions tend to be rapid burrowers. Donacids and mesodesmatids, which occupy the swash zones along sandy beaches and have to reburrow frequently, have such shapes. The truncated posterior of these groups reorients the hinge axis, which locates the axis of the

extruding foot at the narrow anterior-ventral region of the shell. This allows them to wedge into the sediment very rapidly with a few downward movements and no shell rotation.

(31) Thick-shelled burrowing bivalve are generally slow burrowers. Their thick shells, however, provide stability against strong water movements.

(32) Burrowing species with pronounced ornamentation on their shells are also generally slow burrowers.

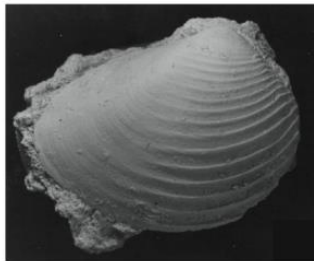
(33) Pronounced ornamentation on the shells of burrowers serves to stabilize them in the sediment.

(34) Asymmetric ridges, with steep dorsal slopes and gentle ventral slopes, aid bivalves in burrowing by alternately sliding and gripping as the shell rocks back and forth. In some species these are parallel ridges at an angle to the shell margin and in others they are parallel chevron-shaped ridges. Knobs on extinct trigoniids also aided burrowing by gripping the sediment during the backward rotation of burrowing

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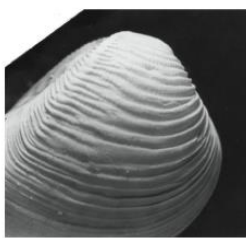
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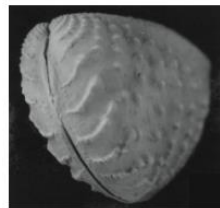
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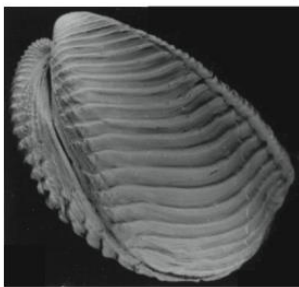
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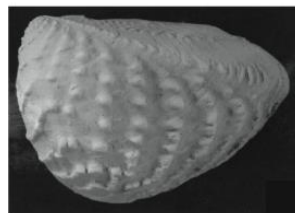
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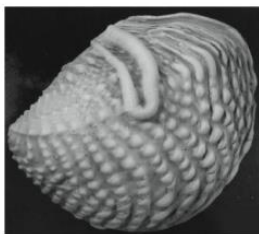
3a



4



3b



5



6

My experiments have shown that asymmetrical ridges on burrowing bivalve shells aid burrowing by alternatively gripping and sliding through the sediment. Similar experiments have also shown that knobs on shells of extinct trigoniids (Figs. 3b and 5) gripped the sediment during the backward rotations of burrowing. Fig. 2 is also a trigoniid.

(35) Cockles that possess ribs use them to saw into the sediment when they burrow, employing multiple, quick rocking movements after each time they anchor their foot.

(36) Many deposit-feeding tellinids have life positions in which the sagittal plane is horizontal. This orientation serves to keep them at a particular depth as they migrate laterally to obtain new food supplies. These forms are asymmetrical, with the siphonal region of the shell twisted upward in the animals' life position. This twist prevents crimping of the siphons where they bend sharply upward at the shell margin. Early tellinids lacked this asymmetry; living with the sagittal plane vertical, they probably had not yet become deposit feeders.

(37) Most bivalves that live in sediment with a mud fraction exceeding 25% are small (have a large surface-area-to-weight ratio) or are thin shelled. Both of these traits help these animals float in soupy sediment.

(38) Most bivalves that are very deep burrowers, being less susceptible to predation than shallow burrowers, are thin-shelled.

(39) Species that nestle in irregular cavities tend to be xenomorphic (have irregular shapes).

(40) Species that bore into hard substrata tend to be elongate. Some of these have cup-shaped projections on the surface of their shell that pick up bits of rock that serve as excavation tools.

Stanley, S. M. 1975, Why clams have the shape they have: An experimental analysis of burrowing: *Paleobiology* 1:48-58.

(41) Here I showed that the blunt anterior of a typical burrowing bivalve (one having the shape of most venerids) aids the animal in burrowing by means of its rocking motion.

The animal takes a step downward because the axis of backward rotation is located to the anterior of the axis of forward rotation. For this study, axes of rotation were determined from films of burrowing animals. Projections of still shots at the start and end of a rotation allowed the axis of rotation to be determined as the point on a grid applied to the shell images that remained unmoved. After being lowered by forward rotation of the shell, the blunt, prosogyrous anterior jams against the sediment during backward rotation, allowing the animal to slice downward. This was demonstrated by the use of robots. A robot with a discoid anterior required more rocking movements for burial than a robot of normal shape, and the axes of rotation of the altered form were closer together, showing why downward steps were smaller.

Stanley, S. M. 1977, Coadaptation in the Trigoniidae, a remarkable family of burrowing bivalves: *Palaeontology* 20:869-899.

This family, which was very diverse in the Mesozoic, posed a challenge for functional morphological analysis because of its curious features. By studying the burrowing of *Neotrigonia*, the only living genus of the family, observing the sedimentary environments of fossil forms, and making use of robots of fossil taxa, I found that the unusual morphological features of the family constituted a coadapted complex. The trigoniids' muscular foot has enabled them to be unusually rapid burrowers as nonsiphonate forms, and some also had ornamentation that aided them in burrowing. Many trigoniids have occupied shifting sands.

(42) To maintain valve alignment at the wide angle of gape required for extrusion of their muscular foot, trigoniids evolved large hinge teeth with secondary dentition.

(43) The large teeth occupied so much space in the mantle cavity that the trigoniids were forced to evolve orthogyrous or opisthogyrous shapes in place of the ancestral prosogyrous shape.

(44) To compensate for losing the benefit that a prosogyrous shape provides for burrowing, trigoniids evolved a variety of knobs and ridges that my experiments with robots showed to accelerate their burrowing by gripping the sediment during backward rotation.

(45) The Cardiidae (cockles), which also possess a muscular foot, evolved elongate lateral teeth, far from the beak, to maintain valve alignment at wide angles of gape; this was a much simpler solution to the problem than the trigoniids' evolution of their unusual coadapted complex of morphologic features.

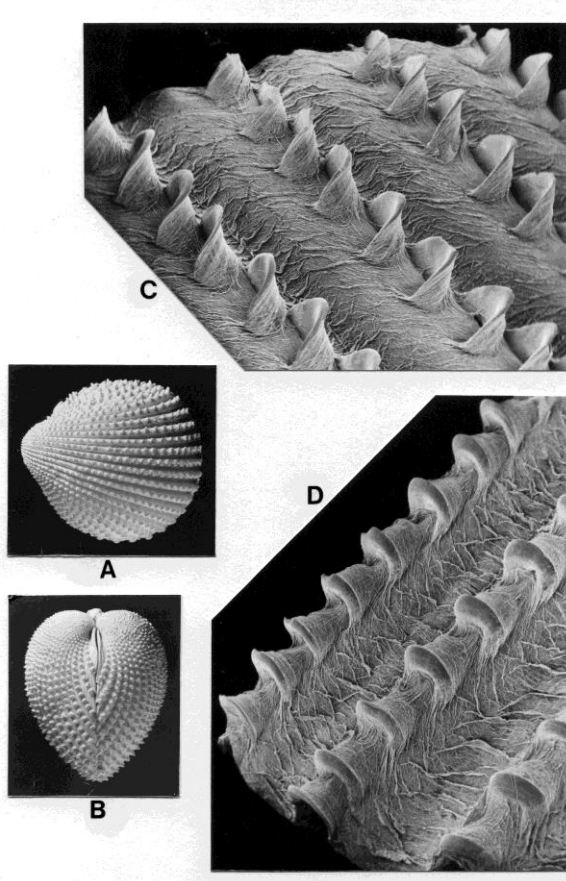
Stanley, S. M. 1981, Infaunal survival: alternative functions of shell ornamentation in the Bivalvia (Mollusca). *Paleobiology* 7:384-393.

This paper reported on a series of experiments, some of them employing models in a wave tank, to examine adaptations of bivalves for maintaining infaunal life positions. Bivalves can maintain infaunal life positions in two ways. They can reburrow if exhumed by a water current, or they can avoid being dislodged in the first place. Some of the models in the wave tank experiments had normal ornamentation, and others lacked ornamentation.

(46) Sharp costae on the venerid *Chione cancellata* reduced scour of sediment adjacent to partly exposed shells by breaking up bottom currents (creating turbulence, which amounts to random motion).

(47) Spines shaped like a cat's ear on the posterior of the cardiid *Trachicardium* reduced scour in the same way.

(48) Experiments with live animals showed that recurved spines on the anterior of *Trachicardium* accelerate burrowing by gripping the sediment during the backward rotation phase of the rocking movement



The two types of spines of *Trachicardium* have different shapes and different functions. The upper photo shows the spines resembling cats' ears, which my wave-tank experiments showed to reduce scour when the posterior of the shell is exposed. The lower photo shows the recurved spines on the anterior, which my experiments with live animals showed to grip an slide as the animal rocks back-and-forth to burrow.

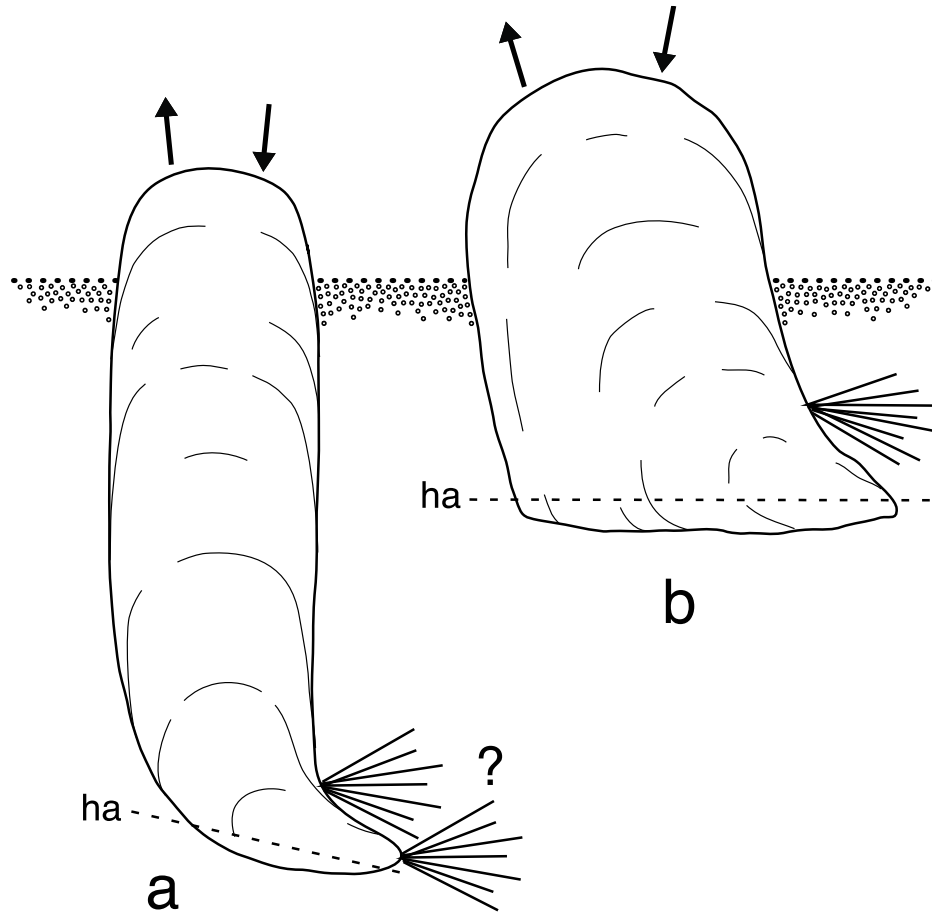
(49) Similar experiments showed that asymmetric ridges on the anterior of *Anomalocardia* accelerate burrowing in the same way (see page 17, Figs. 1a, 1b, and 1c).

Stanley, S. M. Functional morphology of non-cementing Bivalvia. in *Treatise on Invertebrate Paleontology*. Part N. Volume 1, Bivalvia (revised, electronic version), Ch.5. 46pp.

This is a summary of the work described in the previous five entries, along with a smaller amount of research by others.

(50) A zigzag commissure functions to increase the total rate of flow of water into the mantle cavity for a given width of valve gape by increasing the length of the gape for a given angle of gape.

(51) An elongate endobyssate species benefits from having an L-shaped shell because of the location of its inhalant and exhalent currents.



Elongate semi-infaunal myalinids, the Triassic *Novaculoperna* (a) and the Jurassic *Mytiloperna* (b), whose L-shaped shells benefited them by orienting the hinge axis (ha) nearly horizontally so that the maximum gape would be at the posterior end of the shell, where the inhalant and exhalent currents were located. (The workers who initially described *Novaculoperna* reconstructed its byssus as emerging from the beak, but I favor the more orthodox view that it emerged to the posterior of this position.)



Supporting my interpretations of the functions of burrowing shapes is the remarkable similarity of shapes of the members of the Veneracea and Mactracea that have similar modes of life:

Deep burrowing in firm, stable substrata

Elongate and tubular:

to minimize siphon length

Siphonal and pedal gapes:

for extrusion of siphons and foot with little danger from predators

Valves thin:

metabolically economical and permitted by a deep life position

Loss of hinge teeth:

for rocking of shell about a dorsoventral axis for extension and contraction of siphons and foot

Shallow burrowing in stable substrata

Posterior elongate:

to minimize siphon length

Center of gravity near anterior:

for stability

Valves thick:

for stability

Rapid burrowing in shifting sand

Anterior triangular:

for easy penetration

Exterior smooth:

to reduce friction during burrowing in the absence of ornamentation that facilitates burrowing

Rapid burrowing in swash zone of sandy beaches

Anterior elongate:

to accommodate large foot

Posterior truncate:

to provide maximum gape at tip of shell for pedal extrusion

Shell compressed, with maximum width near posterior:

to reduce resistance to burrowing

Valves thick (*Spisula*):

for stability

Shallow burrowing in soft, muddy substrata

Small:

to reduce surface/weight ratio for flotation

Valves thin (*Mulinia*):

for flotation

