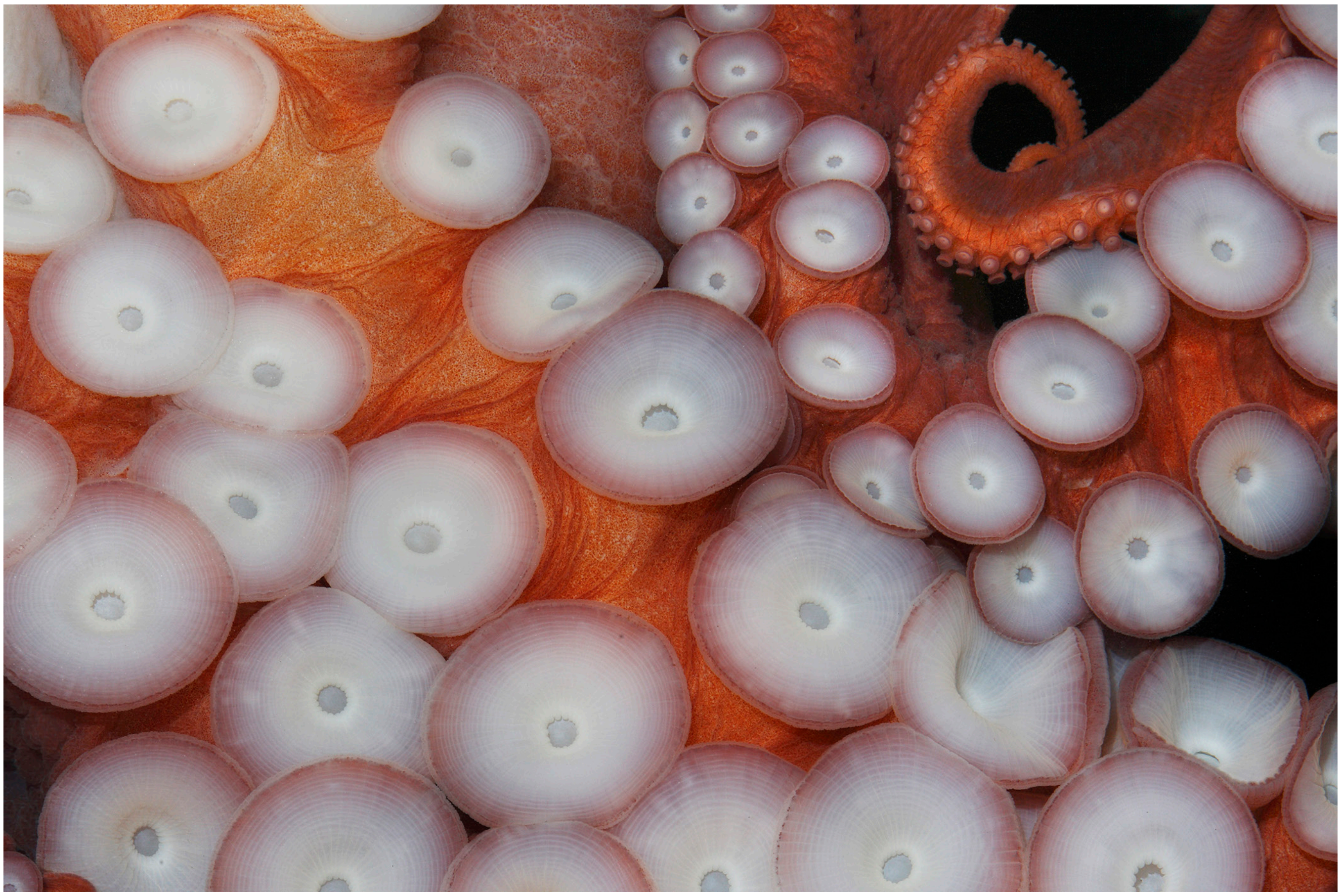
Shape of Life

Armor and Speed
The Survival Game



As the tide rises, the closed mollusc

Opens a fraction to the ocean's food,

Bathed in its riches. Do not ask

What force would do, or if force could.

A knife is of no use against a fortress.

MAY SARTON, POET

Oysters. Photo by NNSS

Most of us encounter molluscs for the first time on our forks. With the exception of the occasional chocolate-covered grasshopper, a worm or two on a dare, and the always delicious lobsters and crabs, molluscs are at the top of the invertebrate menu for humans. We eat tons of oysters, clams and mussels live, barbecued, and broiled with cheese and spinach. We devour queen conchs in chowder, scallops en brochette, escargot drenched in garlic butter, octopus on our sushi platters, abalone steaks, and deep-fried calamari to soak up the beer in sports bars. We hunt them, farm them and, for centuries, have treasured their delicate flavors. Special runners and pack trains were dispatched over the Alps from the Mediterranean to bring oysters to Roman legions in their inland garrisons of conquered Europe.

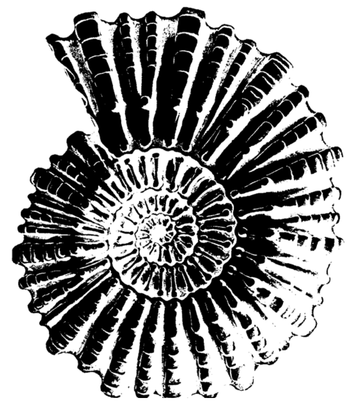
Our particularly intimate relationship with molluscs is due largely to their tasty, fleshy bodies, which have been an easy meal for millions of other animals in the food web since they first emerged during the Cambrian explosion. With that kind of vulnerability, and because they couldn't outrun predators, early molluscs came up with armor to survive. Their shells make them easy to handle in a New England shore dinner, but they gave molluscs an enormous advantage in playing the survival game over the millennia. Of the million or so named species of animals alive on earth today, molluscs account for about 70,000. That's more than the 60,000 species in our tribe, the chordates, but far behind the 1.2 million species of arthropods. (The number of existing mollusc species is subject to rancorous debate, but ranges from 50,000 to 110,000, depending on whom you talk to.) The adaptations that enabled molluscs to cope with day-to-day danger, and threats of mass extinction, were made possible by the most versatile body plan in the animal kingdom.

Molluscs and Mass Extinctions

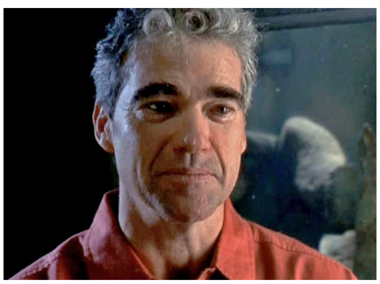
Earth has always been a dangerous place for animals. The climate swings between ice ages and searing heat, bringing cyclones, floods, and droughts. The oceans rise and fall, volcanoes and earthquakes fracture the land and sea floor, and even the continents themselves change shape and move around on the surface of the globe. Day by day, animals contend with the constant pressures of finding food and safe places to bear young. They must always be on guard against each other because most animals are both a meal and a hunter in the indifferent drama of prey and predator. These conditions drive the biological engine of evolution and force the adaptations upon which the survival of life depends.

> *Death is the mother of beauty; hence from her, alone, shall come fulfillment to our dreams*
>
> Wallace Stevens
> "Sunday Morning"

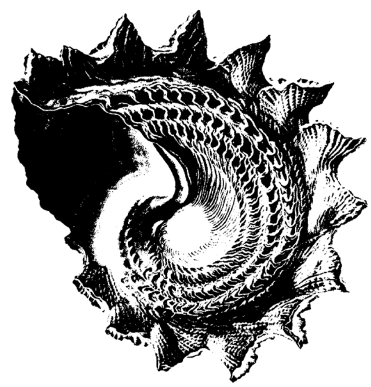
And every so often, like loaded dice in a rigged craps game, destructive events of such enormous magnitude occur that all life is threatened. Over the six-hundred-million-year history of complex multi-cellular animal life on earth, these mass extinctions have been a steady pulse in the heartbeat of the planet, and like the deadly outcomes of predator and prey, they are paradoxically essential to the existence of life. These sudden episodes of great mortal consequence come in varying shades of destruction about every twenty million years or so, ranging from relatively minor die-offs that wipe out a few hundred species to the five major events that have threatened the very existence of life on earth. The extinction at the end of the Cretaceous period claimed 65 percent of all life, including the dinosaurs and the lesser-known but equally dominant creatures called ammonites, the ancient molluscan relatives of clams, oysters, snails, mussels, squid, and octopus.



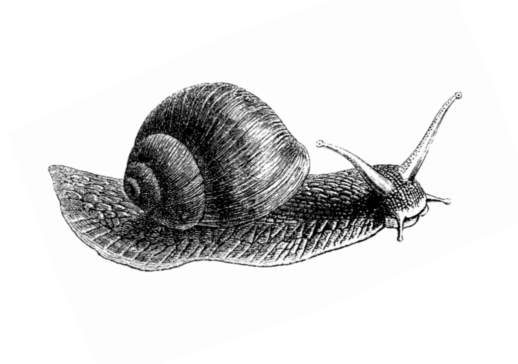
The evidence of one of these stupendous catastrophes is indisputable. At many sites around the earth, there is a clear demarcation in the rocks below which lay the fossils of dinosaurs, ammonites and many of the other extinct species, and above which there are absolutely none. Zero. Those rocks can be precisely dated by measuring the amount of certain atoms that decay at a predictable rate, so we know the exact time of their formation. There is no doubt that extinctions of massive proportions have occurred.



Paleontologist Peter Ward



Peter Douglas Ward is a paleontologist known for his work on molluscs and, more recently, breakthroughs in our understanding of mass extinctions, the conditions that precede them, and the effects on the survivors. Ward and others cite a number of possible causes of these great die-offs including: a dramatic shift in climate; a sudden change in the composition of the atmosphere; volcanic global winter; changes in the fauna and flora that were deadly to dinosaurs, ammonites and the other species that died; a shift in the earth's magnetic poles that left portions of the globe exposed to solar wind and radiation from space; the explosion of a supernova near the sun; and the most likely, the impact of an asteroid or comet that plunged the earth into a period of fire, then darkness.



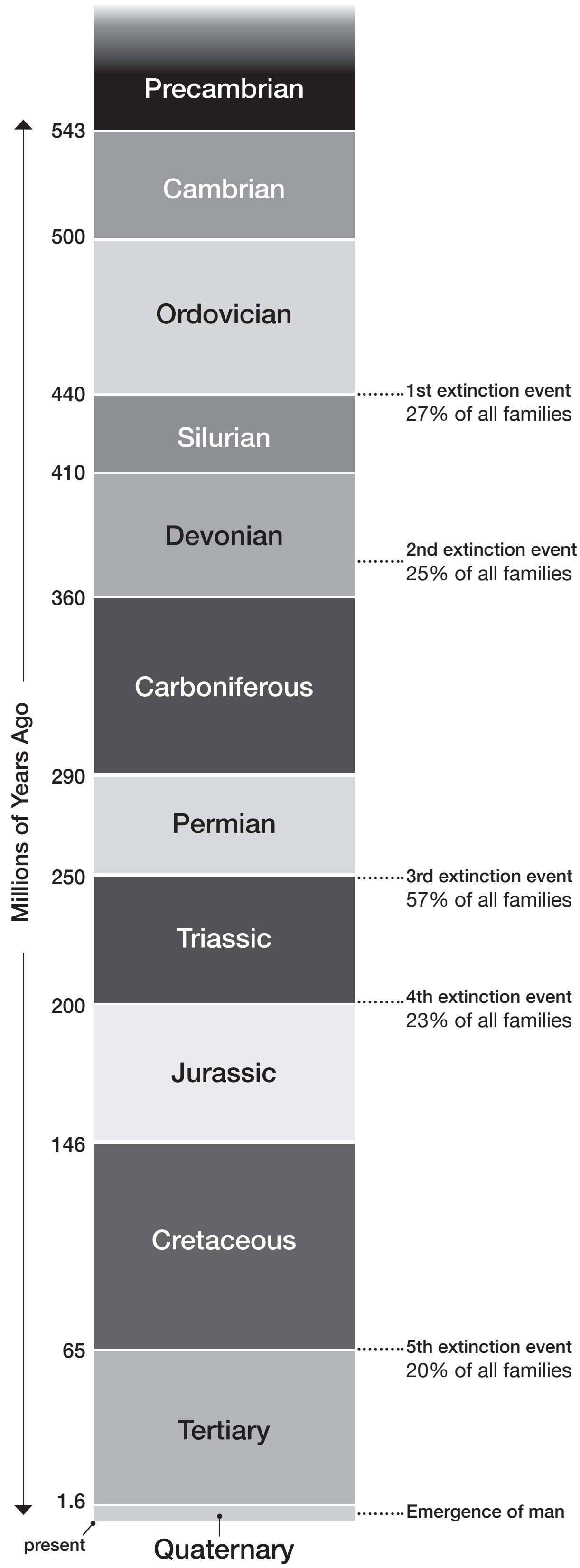
"Some theories have been fanciful, such as world-covering floods; others have been religious, citing God's will," Ward says of the explanations for extinction events. "Many of these have been crackpot ideas, while others emerge from great good humor. A tabloid headline blaming 'Big Game Hunters from Outer Space' and Gary Larson's view that cigarette smoking did in the dinosaurs are my two favorites." Very likely, Ward and other scientists believe, the catastrophic events that mark the greatest of mass extinctions were both extra-terrestrial and terrestrial.

Because the number of species is currently in precipitous decline, Peter Ward and a growing number of paleontologists, biologists, and others tracing the course of life on earth are becoming increasingly convinced that the planet is in the middle of the sixth great extinction event. The other five mass extinction events are indicated on the timeline on this page.

It is difficult for us, as creatures capable of viewing life as precious, to look beyond the ultimate horrors of such declines in animal life and the violence of a culminating asteroid strike or other final catastrophic event that marks a mass extinction on the geologic calendar. The truth is, though, that such terrible times result in periods of equally sudden bursts of creativity among the survivors. "Little evolution is likely to occur unless extinction has greatly shaken up -- and diminished the numbers of -- species already in existence," writes paleontologist Niles Eldridge. "Extinction is absolutely vital to the evolutionary process. When vast areas open, evolution is rampant. And it is then that the large-scale transformations take place." When the dinosaurs were extinguished, for example, mammals found the way cleared for them to evolve into larger species to occupy that niche in the land ecosystems and, eventually, lead to us.

The most remarkable part of the extinction story, though, is that of all the major body plans of animals that emerged during the Cambrian explosion half-a-billion years ago, at least one representative of each has lived through all of the great and small mass extinctions. This stunning fact means that the genes that govern the creation of a particular body plan have also survived the long and dangerous trip into the present. When the last of the ammonites died with the dinosaurs, after a run of three hundred million years in the sea, for instance, enough other molluscs survived to continue that basic line of animal life, which began when that kind of animal diverged from its more primitive ancestors to begin its voyage through time.

GEOLOGIC TIME LINE



The Innovators

In so dangerous a place as earth, however, the molluscs have always been good candidates for survival because they quickly diversify when the opportunity presents itself. The arms race of predator against prey has pushed the molluscs to grand new innovations, and extinctions have provided opportunities for rapid evolution within the group resulting in an incredible range of variation on that single body plan.

The molluscs most familiar to us are the bivalves—the clams, oysters and mussels that show up so often on our plates. Each features a pair of hinged shells and a single, muscular foot with which it moves and burrows. Cephalopods (one of the great names in the animal kingdom, meaning 'foot-on-head') are the Ferraris of molluscs—the squids, octopus, and cuttlefish. The hauntingly beautiful chambered nautilus is a cephalopod, too, the closest living relative of the once powerful ammonites. To those of us who prowl in tide pools, the members of the chiton branch of the family are also familiar as sluggish little creatures we call sea cradles scraping algae from the bottom and capable of clamping onto rocks like super-magnets. Chitons have remained essentially

Molluscan diversity: (from top left clockwise) kellet's whelk; octopus; mussels; thorny oyster; chitons; and giant clam (clam photo by Elias Levy) unchanged for 500 million years and were most likely one of the earliest molluscs to emerge during the Cambrian, sporting their armor in a simple arrangement of eight plates laid in an arch over their backs. About 650 species of chitons still exist. And then there are the snails, known as gastropods ('foot-on-stomach,' of course) those slow-moving creatures of fables that have managed to colonize both land and sea, produce beautiful shells and torment gardeners who slaughter them by the zillions. Some gastropods, like slugs, have no shells and use stealth and camouflage to survive even gardeners. Shell-less slugs in the ocean are flamboyantly colored to advertise the fact that they taste bad to most other animals.

It takes quite a feat of the imagination to see how this diverse tribe sports the same body plan. How can a clam, a snail, a slug, an octopus, and an extinct ammonite all be part of the same race? It's very easy to see if you know what to look for, because each has taken the same complement of body parts and crafted them for radically different tasks. The basic architecture of all the molluscs that drives their adaptability is a fleshy soft body. They get their name from a Latin word, mollis, which means 'soft'. Most molluscs have hard shells but some have shed them in favor of speed. They retain only vestiges of that external armor.

All molluscs have a fold of tissue that covers the body, called a mantle, which is a spectacular piece of biological equipment that builds and shapes the incredible diversity of shells. Among those bottom-dwelling species, the soft molluscan body has evolved a versatile foot, supported by internal fluids, against which powerful muscles can work. In the abalone the foot is a broad, flat platform capable of clinging tenaciously to rocks, and in clams it becomes a tool for digging deep within the mud. Also unique to molluscs is a special kind of tongue called a radula, which would be the envy of any woodworker or machinist. This raspy strap is backed by strong muscles and is coated with tooth-like serrations used for scraping up food, lacerating flesh, or even for boring holes in other hard-shelled animals. Modern molluscs range in size from microscopic critters no bigger than a grain of sand to five-foot-wide clams to the biggest invertebrate of all, the giant squid, which reaches lengths of seventy feet.

Scanning electron microscopic view of radula with rows of sharp teeth (top). Underside of an abalone showing the radula in its circular mouth (bottom).

The Evolutionary Arms Race

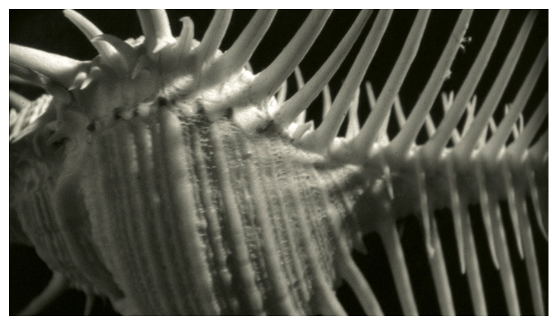
Pushed by constant threats from predators, the molluscan body plan showed its versatility early on in its history. The first molluscs in the early Cambrian were ground-bound like all the other animals on the sea floor, with shells to protect them against the dominant trilobites and other predators. The ability to manufacture that hard, versatile shell has been the key to the success of the molluscs, and they have become known as aesthetic masters to us because of the magnificent shapes and colors that turn beaches and knick-knack shells into art galleries.

Of course, molluscs do not create those beautiful shells for our adoring human eyes, but as part of their strategy for survival. Gary Vermeij, who probably knows more about molluscs and their shells than anyone alive, has been blind since he was a child has never seen one with his eyes.. "I was first shown some shells from Florida by my fourth grade teacher. I was prepared to like what I saw. Back in the Netherlands, I had already grown fond of shells. A successful day at the beach meant a good haul of cockles, wedge shells, and razor clams. I was overwhelmed with their beauty," Vermeij remembers of those Florida shells. "You know, they had such smooth interiors and such rather nicely sculptured and shaped exteriors. The contrasts were beautiful, the ribbing was even and the whole thing just struck me as a real work of art. And I never turned back. That was for me the beginning of a career, really. My teacher had not only given my hands an unforgettable aesthetic treat, but she aroused in me a lasting curiosity about things unknown."

> *All animals endure an arms race, all organisms endure an arms race. We have bacteria and antibiotics, that's kind of an arms race. We have shells and shell-breaking predators, that's a classic arms race. Everything in biology really is an arms race.*
>
> Gray Vermeij, Biologist

Geerat Vermeij as a child

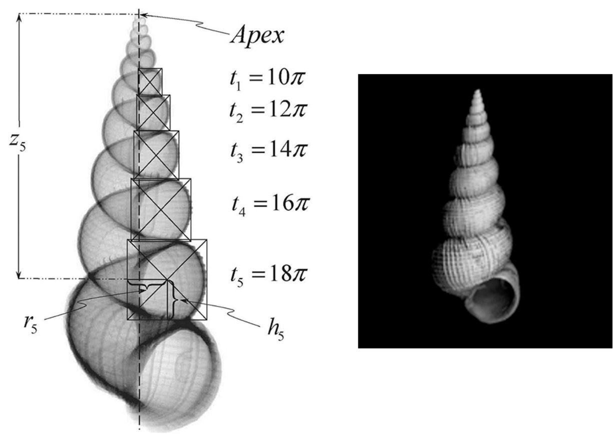
Now, in his lab at the University of California at Davis and at field sites all over the world, Gary Vermeij sees molluscs very clearly, interpreting the ancient history of these remarkable survivors and their elegant armor with his fingers and the power of his imagination. He marvels at molluscs and their ability to survive in nature's arms race. "I think that a body plan can be pushed incredibly far," Vermeij says, turning one of his spectacular whorled shells in his hands. "When you think about molluscs, they're everything from slow, tank-like snails, to very, very fast squid, which have large brains and very, very good eyes. There is virtually nothing that you can't do with a molluscan body plan. It may take evolutionary time to get there, but you can get there. And, well, for me, the most amazing things about molluscs is their sheer beauty. The diversity on a simple theme of spiral growth, how much you can do with a simple theme like spiral growth. They show all these wonderful variations, it's kind of like listening to Bach all your life."



Venus comb shell

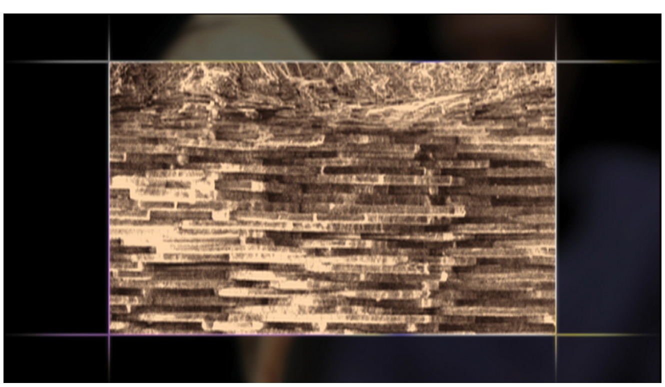
Geerat Vermeij at work

More than a hundred years ago, another mollusc interpreter named Canon Moseley gave a mathematical account of the spiral forms of snail shells in one of the classics of natural history. To a mathematician, the shape of a shell can be read in Moseley's series of numbers and symbols, but in words . . .the surface of any shell, whether shaped like a disc or a turban, revolves around the fixed axis of a closed curve, which continually increases in dimensions. (The shells of bivalves – clams, oysters, mussels, and scallops to name a few – are not spirals but grow outward in the same direction.) Since the scale of a whorled shell increases in geometrical progression while the angle of rotation increases arithmetically, and the center remains fixed, the curve traced in space is a spiral with equal angles. In molluscs shaped like disks, such as the chambered nautilus, the shell grows in a plane perpendicular to the axis. In turban-shaped shells, such as those of garden snails, conchs, or so many of the other collectable beach treasures, it grows in a spiral along the axis of the shell in the shape of a helix.



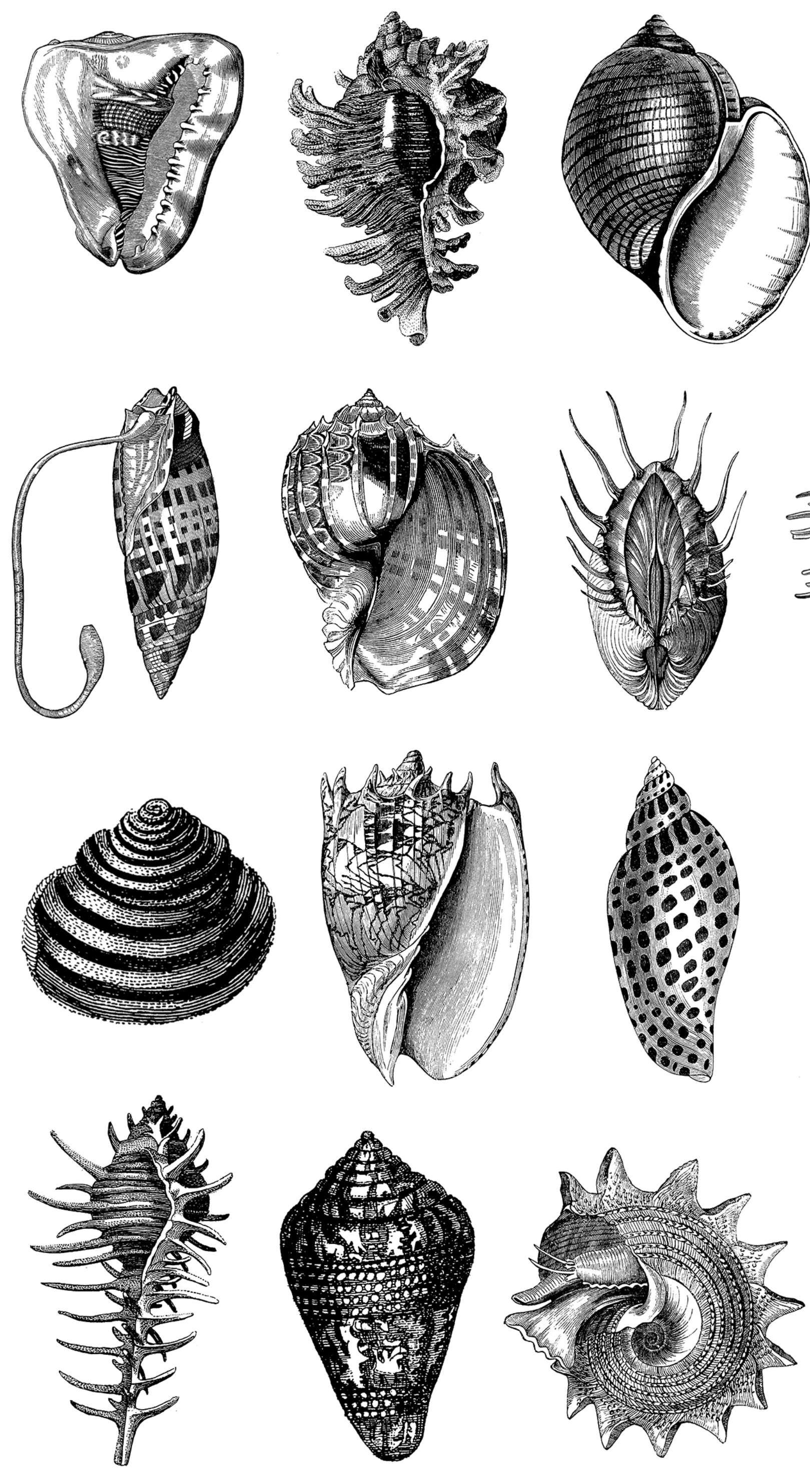
Modeling Shell Morphology, George L. Ashline, et. al. 200o9, COMAP, Inc. | UMAP/ILAP Modules 2009

Molluscs can't do math, or express themselves in complex relational terms, so how do they make shells? Their secret lies in that unique mollusc body part called the mantle, which is a filmy sheath surrounding its soft inner flesh like a cape. The mantle secretes the layers of shell from its outside edge, building with ingredients it takes into its body as it feeds and breathes. The mantle lays down a matrix of protein that determines the shape of the shell as it grows, and also extracts calcium carbonate from the seawater to harden it. The spectacular colors that are unique to each species of mollusc, have evolved over time as a result of the combination of each particular animal's diet, habitat, and internal chemistry. Shells grow in stages from the leading edge outward, and each spurt of construction is usually marked by a clear line in the finished shell, giving them their distinctive and graceful patterns. Many mollusc shells sport spikes and protrusions, which have evolved to make them more difficult to break or eat. Most mollusc shells continue to grow until they reach maturity, which may take several years, and then stop. An immature mollusc shell usually looks like a smaller version of the adult.



The internal structure of a shell overlaps to prevent breakage.

Most molluscs are either male or female, shedding their sperm and eggs into the sea. Some, including land snails, nudibranchs and some clams, are hermaphroditic, although they usually need another mollusc to get the job done, and self-fertilization is rare. The fertilized eggs of marine molluscs hatch to become drifting larvae, called veligers, except for those of squid, octopus and the other cephalopods which, like the eggs of terrestrial molluscs, develop directly into juveniles without passing through a larval phase.



Molluscan shell diversity

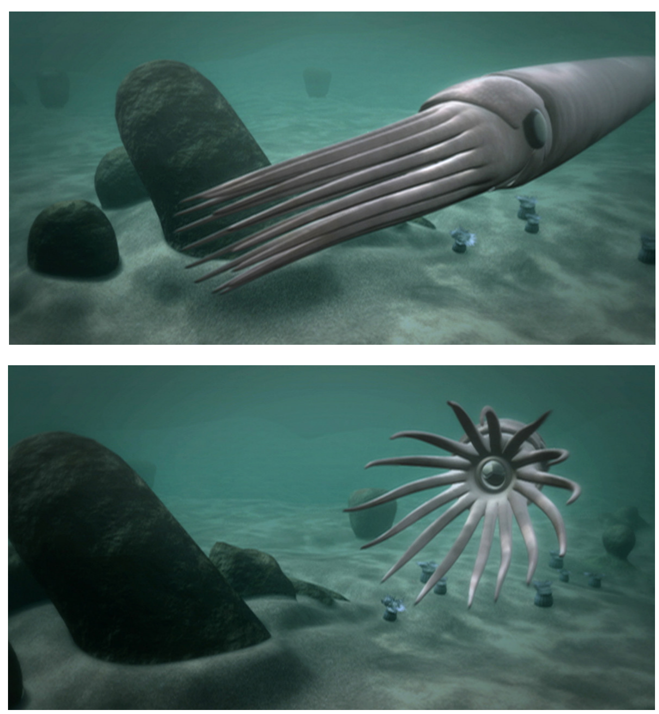
Gastropods – the marine snails that make all those beautiful shells – perform a unique bit of molluscan gymnastics while they are developing from larvae to adults. Nobody is quite sure why this peculiar process evolved, but in an architectural modification called torsion, a snail flips its innards 180 degrees, turning the mantle, and shell upside down in relation to their head and foot. Molluscs, and all animals except sponges and cnidarians, form two openings as they grow from fertilized egg into either larvae or adults, one opening becoming the mouth, the other

Gastropods snails. Drawings by Ann Caudle.

the anus. As they grow, these two openings usually remain as widely separated as possible on the adult body. With torsion, however, a mollusc throws a figure-eight twist into this arrangement after which both the mouth and anus are pretty much situated at its head. This doesn't sound like much of a good deal, unless you happen to live in a shell for defense, and it only has a single opening, and your elastic body plan can do just about anything to survive, including defecating on your own head. Despite such a compromise, torsion gives snails more room in their shells to which they can withdraw and avoid being eaten. They have also devised ways of creating currents within their shells that sweep their waste away from their heads.

Life in a hard shell has enormous advantages if you are soft and slow. To us, the variations of molluscan armor have become objets d'art, but in the vicious reality of the Cambrian ocean where its inventors were scrambling to stay alive, it was pure animal genius. The creation of shells was a matter of following the essential law of natural selection, which allowed those members of a particular mollusc generation whose mantles secreted thicker coverings to survive and reproduce. Those that were eaten because they were the softest among them did not pass on the grow-a-thicker-shell trait to their offspring. Molluscs, and most of the survivors that emerged in the early going of animal life on earth, were quick studies. Given millions and millions of years they refined their original ability to produce shells because they were driven to do so by the pressures of snapping claws and trilobite jaws.

In nature, though, every dog has its day, as we say, and eventually molluscs had diversified so widely and refined their adaptive powers so well that they found a way to grow jaws of their own, start moving around in the water, and become fierce predators. It was yet another demonstration of the grand versatility of their body plan. They evolved a way to seal off their shells and control buoyancy, and a new branch of their race – the cephalopods — rose off the bottom. This was an enormous step forward in the arms race for survival, and very bad news for trilobites and the other animals that could only get off the bottom in brief spurts, but



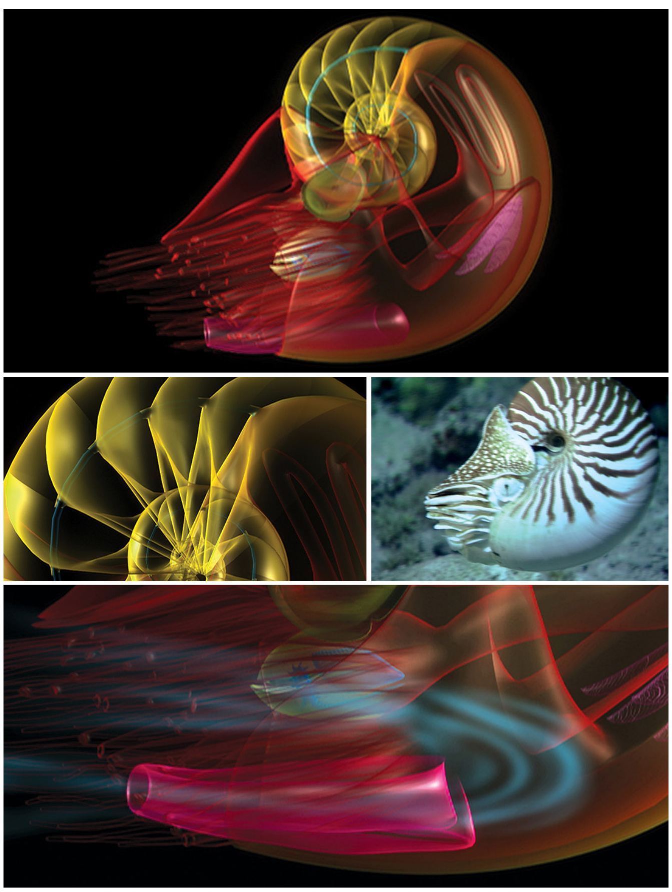
Orthocerus *was an early chambered-shelled cephalopod* were not truly mobile in the water column. Those first swimming molluscs were the ancestors of the modern nautiloids, squid, cuttlefish and octopus, and they revolutionized the uneasy relationships between the hunter and the hunted. The swimming molluscs quickly dominated the marine food web and their descendants have spread to every ocean on the globe terrifying lesser creatures, including us.

Living Fossils

The history of life can be great theater. . . The development of the gas and liquid filled chamber in the shell liberated the nautiloids from the sea bottom and set in motion an evolutionary history that is still unfolding today..

Peter Ward, Paleontologist
On Methuselah's Trail: Living Fossils and the Great Extinctions

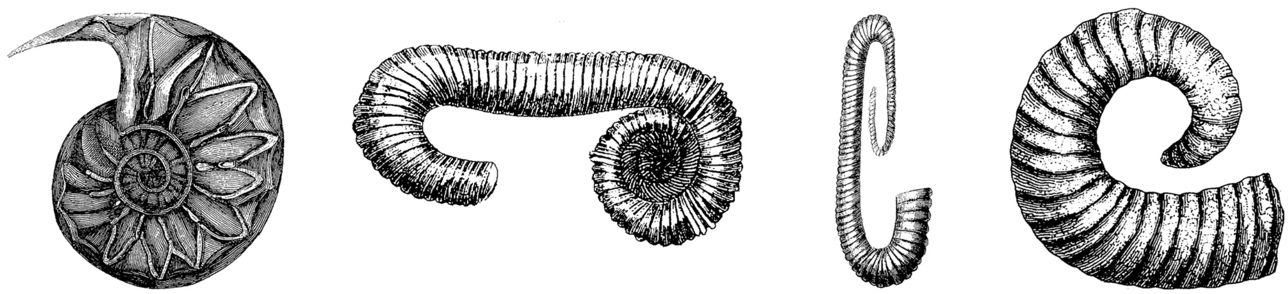
Getting off the bottom of the ocean while wearing a hard shell was no simple piece of biological business. Nature selected this path to survival and dominance, of course again demonstrating the ability of a single major body plan, in this case the molluscan, to evolve a variety of solutions to a problem. As it happened about 400 million years ago, the shells of the earliest swimming molluscs were elongated cones. As the animal grew, it sealed earlier shell growth into chambers with tubes connecting each compartment from the front, which housed the animal's body, to the rear. This connecting tube, called a siphuncle (from the word siphon), allowed the animal to empty the water from its chambers, leaving a gas-filled shell that was light in the water and could even counter the added weight of a growing animal.



An animated still of a nautilus showing its internal structure (top). The siphuncle runs through all the chambers (middle left). A living nautilus (middle right). Water is pumped for jet propulsion (bottom).

You can see the blueprint for molluscan buoyancy the next time you are in a trinket shop at the beach where the split shell of that living fossil, the chambered nautilus, is always a star attraction. This stupendous development meant that the animal had the architecture for controlling its buoyancy, and the rest of its anatomy evolved with wonderful possibilities. By modifying their mantles into a kind of pump that can eject water at velocities great enough to push them through the water, the swimming molluscs became masters of jet propulsion. Add to that the evolution of big, complex eyes, a hard beak capable of crushing just about anything else that crawls or swims, and a forest of suckered tentacles on its head, and you have one of the most powerful killing machines of the ancient ocean.

Even when fish and giant reptiles showed up in the sea, nautiloids and their cousins the ammonites, held their own. They even survived the greatest extinction event of all time at the end of the Permian, 235 million years ago. From their beginnings as cone-shaped monsters that could be six feet long, the nautiloids morphed into hundreds of species, most of which curled their shells into discs. These relatives, the ammonites, grew to gigantic size. The largest ever found measured over nine feet in diameter, and by the end of their run as a branch of the cephalopod class of molluscs, ammonites had bent their shells into every imaginable shape, including very weird saxophone-like creatures that lived while the last of the dinosaurs were running things on land. When the asteroid ended the Cretaceous 65 million years ago, the ammonites went with them, so nobody has ever seen one alive. One ancient, patient nautiloid lives on, though, as an example of durability and wonder contained in a single animal body plan.



Various fossil ammonites

Squid and Kin

And the story of the wildly adaptable molluscan body just gets better. After the cephalopods lifted themselves and their shells off the bottom of the oceans, speed became a key to survival for some of them and so nature selected for that trait when the fast-swimming fishes arrived on the scene as predators. Like modern airplanes, power systems improved, bodies grew more streamlined, and in some species, the increased speed meant a heavy defensive shell became less and less important. Eventually, the exterior shell all but vanished, leaving only a vestigial strip of flexible tissue running lengthways in their otherwise soft bodies. This feather-shaped remnant of a hard exterior shell, called a pen, has a plastic-like texture and lies beneath the mantle, enveloping the squid itself, now morphed into a thick, tubular muscle.

Starbuck still gazing at the agitated waters where it had sunk, with a wild voice exclaimed – 'Almost rather I had seen Moby Dick and fought him, than to have see thee, though white ghost!'

'What was it, Sir?' said Flask.

'The great live squid, which, they say, few whale ships ever beheld and returned to their ports to tell of it.'

Herman Melville
Moby Dick

Enter the squids, torpedo-shaped, jet propelled predators that range in size from a few inches to sixty-foot giants that can move at speeds up to twenty miles per hour and fear no creature on the planet. Squid, and their cousins the octopus, are the most highly organized invertebrates that ever lived.

School of squid

A squid has three hearts to process oxygenated blood through a complex closed capillary system not unlike our own. Their nervous system is centralized and also highly complex, with part of it fused into a brain center between its eyes, which are very large in proportion to the rest of its body. These are real eyes, too, capable of forming images and remarkably like our own, built on the same principal as a camera which consists of a dark chamber into which light is admitted only through a lens. (The eyes of humans and squid are examples of convergent evolution, evidence that the same anatomical structures have evolved more than once in different animals.) Some squid add the ability to produce disorienting clouds of ink, toxins, and bioluminescence to their defensive and offensive arsenals, and all have hard beaks capable of doing immense damage to anything else that swims. Their tentacles and arms are adorned with powerful suckers that have appeared in the nightmares of many a blue-water sailor. And as if mobile armor and speed are not enough of a triumph of adaptation, molluscs also came up with intelligence. Octopuses and cuttlefish think, learn and react to their environments in ways surpassed only by vertebrates like us. But they are still molluscs, using the same body plan as clams, snails, limpets, and the rest of their relatives running the evolutionary race against destruction and transforming themselves to survive in a very dangerous place.

Red octopus drawing by Ann Caudel

Cuttlefish

Think about all that the next time you sit down to a plate of linguini con calamari.

One wonders why some animals last and others go extinct. In a humble clam, a beautifully evolved squid, or a nautilus, we can tell that certainly they all evolved from a single, common ancestor. A mollusc.

Peter Ward, Paleontologist