Whatever criteria for success one cares to adopt, the animals with legs keep coming out at the top of the list. Whether one rates success in terms of numbers, number of species, range of habitats exploited or simply as total mass of animal tissue, the limbed creatures clearly have the advantage.

MARTIN WELLS, LOWER ANIMALS
A New Kind of Animal

The history of the animals whose descendants would be the first to breathe air and live on land begins over half-a-billion years ago, when the earliest members of a group called arthropods branched off from their ancestral roots – primitive, bilateral animals. These creatures quickly became powerful hunters and scavengers, and established patterns of adaptability and dominance that continue into the present. One group, the trilobites, were the top predators in the sea for more than 325 million years, beginning in the Cambrian when their primitive legs, complex armored bodies, and the first true eyes in the animal kingdom gave them immense power over less-endowed prey. Trilobites look a bit like modern pill bugs common in gardens, but they are only distantly related. Still, just about everybody knows what a real trilobite looks like because there were simply so many of them and because their hard shells endured through time as perfectly preserved fossils. Trilobites have been mined from quarries by the millions to be sold as paperweights, pocket rocks, tie tacks, cuff links, necklaces, and bracelets in just about every rock shop in the world. These rulers of the sea achieved immense diversity, branching into thousands of species over time. They and their other arthropod cousins began the noble lineages that would lead to the crustaceans, which include crabs, lobsters, shrimp and barnacles; the arachnids, which include spiders, scorpions and mites, and the largest group of all, the insects and their close cousins the millipedes and centipedes. But the trilobites were all marine creatures capable of living only in the sea.

Various arthropod groups: (clockwise, starting from top left) insect, centipede, spider, shrimp, crab and scorpion.
During the two-hundred-and-fifty-million years or so after arthropods first appeared in the ocean, their basic body plan adapted to an enormous variety of niches in which they were able to live, creating new species and groups of species. The first members of their group had inherited their biological architecture from more primitive bilateral ancestors. The coded instructions for bilateral architecture carried in every cell were controlled by those mighty Hox genes that choreograph the building of a bilateral segmented body. The earliest arthropods took the basic ingredients of a segmented body – appendages, tissues, organs, nervous system and brain – and diverged to become an entirely new kind of animal.

The arthropod body plan has adjusted itself many times since it first appeared, adapting to the pressures of changing environments and the dance of predators and prey, but then, as now, it is defined by a segmented body, jointed legs, and a hard external skeleton. The name, *Arthropod*, means ‘jointed leg.’ From its Greek root we also get the modern word art, which in its conception was defined as a *joint* between reality and abstraction.
The segmented body is a powerful arthropod evolutionary tool that is common elsewhere in the animal kingdom. People are segmented, too, though not as obviously as earthworms or lobsters, and you have to know how to look at our spine and muscles to see the segmentation. This kind of construction allows a body to build itself in identical segmented units that become specialized for particular functions. Many of the tasks of arthropod living, like eating or sensing the world in the water or on land, are handled by appendages attached to each segment of the body or the head of an arthropod. These appendages, in turn, are segmented, which makes them both flexible and easily altered to become antennae, claws, jaws and other mouth parts, and especially legs—legs for walking, legs for clamping, legs for holding onto egg sacs, legs for swimming, legs for digging. Sections of the legs even evolved into gills for obtaining oxygen from the surrounding seawater. These corresponding appendages are said to be serially homologous, that is, similar in position on a particular segment but not necessarily similar in function.

**Skeletons on the Outside**

Arthropods were the first bilateral animals with exoskeletons, in their case hard shells made of a nitrogen-rich sugar called chitin. In the simplest of terms, this suit of armor keeps the inside in and the outside out, and it also anchors the muscles of claws, legs and antennae against which those muscles can work. Inside, an arthropod has all the organs of a complex higher animal, but its blood just sloshes through loose channels surrounding these organs, unlike our refined circulatory system that distributes blood throughout our bodies under pressure. Outside of an arthropod is, well, the rest of the world, so the hard shell offers protection from predators and environmental conditions that might harm the animal. An arthropod controls the intake of water just like we do, and, while it is moist on the inside, the sea does not flow through it freely. Crustaceans like crabs and lobsters go a step further in reinforcing their armor with calcium to make it extra hard.

One of the enormous drawbacks to life with a hard shell is that once it forms and hardens it doesn’t grow, unlike our own internal bones, which are surrounded by flesh and organs but grow as our bodies grow. It’s impossible, therefore, for the animal to grow for very long without just filling up the shell. Arthropods deal with this apparent design flaw by shedding their exoskeletons when their insides grow too big for their outsides in a process.
called molting. It's one of the most fascinating tricks in the animal kingdom. When a crab, for instance, is plumped up against its shell to the point of bursting, it forms a new exoskeleton beneath the old one and separates the new from the old by pumping in water. What happens next is some complicated chemistry, controlled by special molting glands and hormones. The crab basically loosens itself and its still-soft new exoskeleton from every part of its old hard body, legs, and claws, and slips out of its old shell in about thirty minutes. Some take more or less time to do the job, but before the new exoskeleton hardens, they quickly expand their body to make sure the new hardened skeleton has extra room for growth. While molting is underway, arthropods are extremely vulnerable and very likely to become a meal, as anyone who loves soft-shell blue crabs can tell you.

Even though arthropods have solved the problem of growing from juvenile to adult by periodically molting, their hard, heavy shells are one of the reasons Hollywood nightmare visions of giant insects terrorizing the world could never be real. Among the smallest of arthropods is a mite that lives on your eyelashes, and the largest is a crab with a twelve-foot leg span. All the bigger arthropods still live in the ocean, where the buoyancy of water reduces the force of gravity and the effort needed to pack around a heavy shell, allowing them to convert into growth the energy they would otherwise be using for hauling themselves around. In the ocean, too, gravity does not deform the new shell of a molting arthropod before it can harden into the right shape.

Another reason an arthropod could never be the size of a *Tyrannosaurus rex* is that its legs are much too fragile to bear a lot of weight. Jointed appendages are perfect for facile movement and speed, up to a point; but balancing a lot of pressure on them is impossible. An apt comparison is the ability of the broad flat surfaces of hiking boots to carry more weight than a pair of high-heeled tango pumps.
Marine arthropods: (left-top to bottom) Coral crab, slipper lobster, hermit crab and spider crab and (right) kelp crab.
Breathing Underwater

Arthropods, like all animals, must find ways to extract oxygen from either water or air and distribute it to all parts of their bodies. In water, which contains forty times less oxygen than an equal volume of air, the standard tools are gills. These vary from very small waving tentacles in small marine animals to the much larger, more extravagant arrays of feathery structures in larger creatures such as lobsters and crabs (and, of course, fish). A simple oxygen concentration gradient between the interior of a respiratory system and the open water allows gills to draw in oxygen molecules from the water through a thin membrane. The oxygen dissolves in the blood’s fluids and is then whisked away to all parts of the body.

Some marine arthropods, including the scorpion and spider ancestral lines, breathed with a system called book gills. These are much less complicated than gills, really just a row of flaps, which are kept in constant motion so an ample supply of dissolved oxygen can enter the respiratory system. During their time as exclusively marine animals, along with all the rest of life on the planet, the arthropods evolved several breathing strategies that helped pave the way for the invasion of land.