

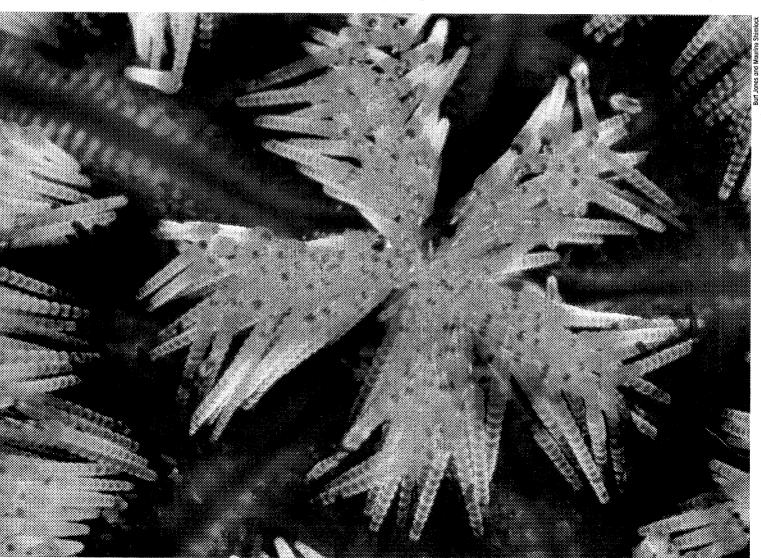
By Gregory A. Wray and Rudolf A. Raff

Previous page: A detail from the underside of a sea star from Sulawesi reveals the animal's five-sided, radially symmetrical body plan. Even the toxic spines, below, of an Indonesian sea urchin are clearly five-sided.

Il the world's animals—from earthworms burrowing in the soil and eagles soaring overhead to giant clams and diaphanous jellyfish in the sea-fall into thirty-five major groups, or phyla, each defined by a distinctive body plan. Species within a phylum often vary enormously, but they all share certain physical traits. Insects may have six legs and spiders may have eight, for example, but the legs of both are jointed—a characteristic of the arthropod body plan. Similarly, members of the phylum Chordata (which includes humans and all other vertebrates, along with tunicates and other less familiar organisms) have distinct zigzag blocks of muscles along the trunk and, at least in embryonic stages, a notochord. Each body plan repre-

sents a different anatomical and functional solution to the fundamental challenges of life, such as feeding, breathing, and reproducing. Evolutionary biologists have long wanted to know how different body plans arise and change over time. Recent research on the genes of a variety of animals is providing some answers and suggesting that some of these changes may not be so difficult to achieve after all.

Animals in the phylum Echinodermata, which includes the familiar sea stars (or starfish) and sea urchins, have a particularly unusual body plan: they have no head and are organized into a pentamerous, or five-"sided," radially symmetrical shape. Humans and other vertebrates are bilaterally symmetrical: our left side is a mirror image of the right. This symmetry, together with a forward-facing head at one end of the body and (often) means of locomotion toward the other, has an



Echinoderms began experimenting with body design a

enormous impact on how we function. It gives us, for example, a front and a back and thus a preferred direction of movement. In most echinoderms, the five sides radiate out from the mouth. For these animals, there is no such thing as forward or backward.

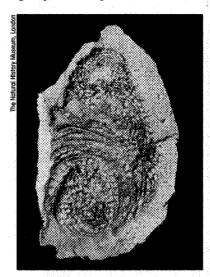
Early in their evolutionary history, which began more than a half billion years ago, echinoderms experimented with a variety of anatomical designs (see "Bygone Body Plans"), but as the rich fossil record reveals, most of the approximately twenty-five known groups of anatomically distinctive echinoderms perished before the age of dinosaurs; only five groups survived to the present. In terms of sheer numbers of species and geographical distribution, however, echinoderms are a modern evolutionary success story. Some 6,500 species of various shapes and sizes exist today, occupying nearly every seafloor habitat, from the Tropics to the Poles and from the edge of the sea to its deepest abyss.

Up to two feet across from tip to tip, sea stars pry open mussels and clams with their muscular "arms," although they are not above scavenging a meal as well. Brittle stars, their more slender cousins, capture live fish, squid, and crabs with highly mobile, graceful arms. Omnivorous sea urchins scrape the surface of kelps and algae-encrusted rocks with an elaborate jaw apparatus, named Aristotle's lantern for its first describer. Sand dollars, which are basically flattened sea urchins, burrow through sediment in search of microorganisms that dwell on sand grains. Other echinoderms filter small creatures from seawater: the swaying arms of sea feathers, deep-water sea lilies, and some brittle stars reach out to capture tiny plants and animals floating by. Many of the soft, sausage-shaped sea cucumbers use elaborately branching tentacles to shovel mud loaded with microorganisms into their mouths.

The ecological success of echinoderms is the heritage of their unique anatomy—not only radial symmetry and lack of a head but also a distinctive skeleton, composed of a meshwork of calcite that is both light and strong, and a unique assemblage of hydraulic organs. The most important function of this water vascular system is to power—with the help of muscles—hundreds of highly mobile, fleshy appendages known as tube feet. In most species, powerful suckers on the tips of the tube feet turn these little appendages, which can be rapidly extended and retracted, into the echinoderm's hands and feet. Tube feet also serve as the animal's gills—enabling it to take up oxygen from the seawater—and, since they are packed with sensory neurons, as its primary sense organs.

Bygone Body Plans

The earliest echinoderm fossils, which are about 535 million years old, have many of the features we associate with living representatives of the group, including a calcite skeleton and a water vascular system that pro-



A 525-million-year-old helicoplacoid

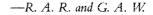
vided hydraulic power to the tube feet. However, these most primitive echinoderms lacked the trait we most associate with the group: five-sidedness.

One of these ancient echinoderms, a carpoid, had a front and a back end but lacked bilateral symmetry. A single arm carried its water vascular system and was presumably also used for feeding. Carpoids were probably not very active animals, but because their fossils invariably occur in rocks that formed from sand and mud, which are inherently unstable, we can assume they were not sessile either. Our best guess is

that carpoids moved about slowly on the seafloor, sweeping their arm back and forth to gather up food from the sediment.

The helicoplacoid, above, was a spindle-shaped animal covered by skeletal plates in a spiral arrangement. Its water vascular system had three branches wound around the body. The reason for this peculiar anatomy is unknown. Like carpoids, helicoplacoids lived on soft seafloors and gathered food with their tube feet. Since no living equivalent of either animal exists today, we know frustratingly little about their relationship to living forms.

The first echinoderms with fivefold symmetry appeared a few million years later. These animals had bodies raised above the seafloor on stalks and fed by filtering plankton from the water. During their Paleozoic heyday, eocrinoids, right, and many other groups of stalked echinoderms were often the most abundant animals on the seafloor. Most of these groups were extinct by 250 million years ago, however; the only living echinoderms with stalks are some crinoids (the sea lilies).



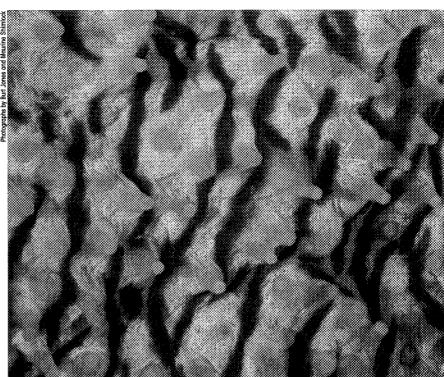


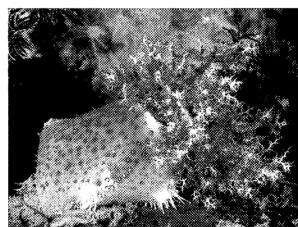
A 520-million-year-old eocrinoid

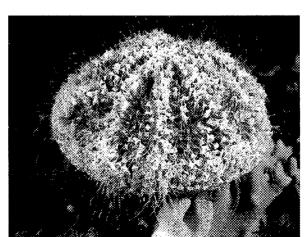
half billion years ago.

Some of the same genes regulate the development of









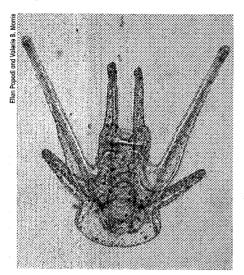
sea urchin from New Zealand, far left, protect the animal from predators. Tube feet, above, help echinoderms walk, feel, and even "breathe." As a softbodied sea cucumber searches for food with bushy tentacles, it feels its way on little yellow tube feet, left, middle. A sea urchin, left, bottom, extends its tube feet through openings in its hard skeleton.

The long spines of a

both mammal heads and echinoderm tube feet.

Evolving Larvae

Life cycles in which larvae and adults are dissimilar are quite common in the animal kingdom. Butterflies develop from caterpillars, frogs from tadpoles, and most animals in the sea start life as tiny larvae that look



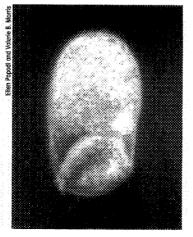
Two-week-old Heliocidaris tuberculata larva

very different from the adults they will become. The larval forms of many marine organisms have remained largely unchanged for hundreds of millions of years. Partly because of this, evolutionary biologists long thought that larval anatomy evolved very little, if at all. The apparent similarity of vertebrate embryos, whether fish, bird, or mammal, also contributed to the notion that most evolutionary changes involved adult anatomy (see "Beauty Beyond Belief,"

page 56). Research over the past few years, however, has shown that in fact larvae can evolve in radically dissimilar ways.

Two closely related Australian sea urchins provide a good example. The adults of these two species are anatomically similar, but the larvae are strikingly different. The relatively complex larva of Heliocidaris tuberculata, above, has rigid arms covered with tiny hairlike cilia that it uses to swim and to sweep single-celled algae into its mouth. After a few weeks of swimming near the water's surface, it metamorphoses into a little sea urchin. In contrast, the larva of H. erythrogramma, below, is anatomically simple, swims near the bottom, and does not feed; instead, it develops from a much larger egg with enough nutrients for the larva to metamorphose in just a few days. Some other

echinoderms also display dramatic larval differences. Some sea star genera include species that utilize a dizzying variety of developmental strategies, including feeding larvae and nonfeeding larvae that develop apart from their parents, as well as juveniles that are brooded in their mother's stomach, ovaries, or even on her back. Significantly, the gene sequences of some of these species are very similar, indicating that big changes in larval anatomy can evolve in as little as a half million years.-G. A. W. and R. A. R.



Two-day-old H. erythrogramma larva

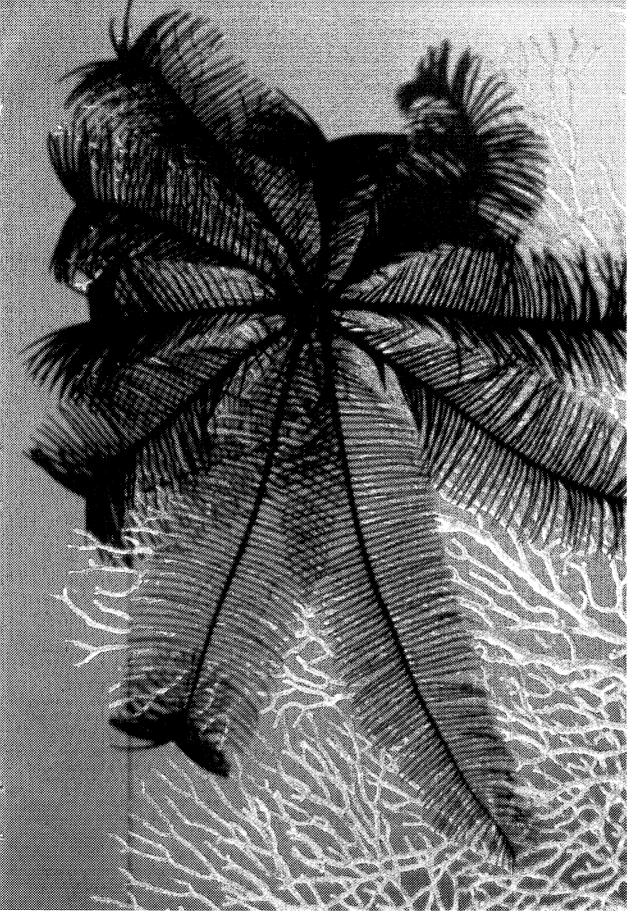
Early attempts at classifying these anatomically peculiar animals grouped echinoderms with branches of the animal kingdom quite distant from our own, often with jellyfish and corals. But echinoderms are actually quite closely related to the chordates. This surprising kinship was initially proposed early in this century, following the discovery that echinoderm and chordate embryos have similar patterns of cell division and cell movements, and it has since been confirmed through extensive comparisons of DNA sequences.

If echinoderms and chordates are so closely related, how did they evolve such distinct body plans? In the last fifteen years, researchers have discovered an extraordinary commonality in the genetics of embryonic development throughout the animal kingdom. It turns out that fruit flies and mice, the workhorses of the geneticist's laboratory, as well as organisms as diverse as worms, sea stars, snails, and humans, share many of the same key regulatory genes. But how, with so many of the same genes at work, does one embryo develop into a fruit fly and another into a mouse?

Part of the answer is that regulatory genes are general-purpose switches that can turn a variety of embryonic processes on and off. Just as you may flip a wall switch to turn on a lamp or a fan, depending on what its wires are connected to, so too can a regulatory gene cause a cell to divide or change shape depending on which developmental process it activates. (Although all the cells in an animal contain all its genes, a given gene will only be active at certain times and in certain cells.) Along with several other biologists, we began to suspect that modified interactions among regulatory genes, rather than the mere presence or absence of these genes, are responsible for many evolutionary changes in anatomy. Regulatory genes, for instance, might be active at different times or in different places within an embryo, depending on the species. Even more surprising, some of these genes might come to control entirely different processes. To test this idea, we joined forces with colleagues Chris Lowe and Ellen Popodi to raise thousands of echinoderm larvae of various species in the laboratory. We then examined embryos and larvae of different ages under the microscope, using highly specific chemical tags to label the proteins made from particular regulatory genes. The tagged proteins allowed us to trace when and where these genes are active during echinoderm development.

Echinoderm embryos develop into tiny, swimming larvae that bear no resemblance whatsoever to their parents; at this early stage of their life, they are bilater-

For headless, five-sided



Resting on a gorgonian coral, a sea feather waves its branched arms to capture tiny organisms floating by.

echinoderms, there is no forward or backward.

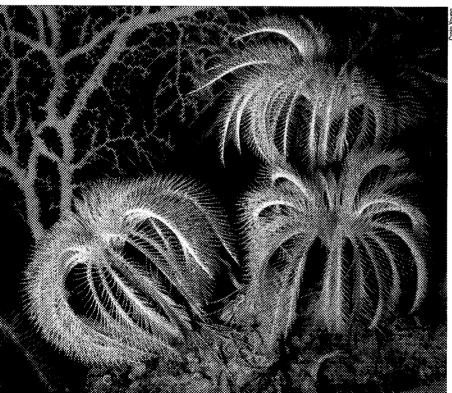
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All echinoderm larvae begin as bilateral organisms, with a left and a right side, right, but soon form a pentagonal disk, far right, that develops into a five-sided juvenile the size of a pinhead. Below: "Standing" on thin stalks, sea lilies live on the ocean floor in deep water. Most sea stars, opposite page, inhabit shallow water near the shore.

ally symmetrical (as were their ancestors), with a left and a right side, as well as distinct front and rear ends (see "Evolving Larvae," page 44). The transition from larva to adult is dramatic. Special groups of cells on the left side of the larva begin to grow into a pentagonal disk, all the while embedded in the larva. Then, during the most eventful half hour of an echinoderm's life. the disk turns inside out and produces a miniature radial body that engulfs the larval cells that formerly housed it. The resultant juvenile, which already looks a lot like its parents but is just about the size of a pinhead, immediately takes up life on the seafloor. A year







or so later, it will have grown large enough to reproduce and begin the next generation.

The very first embryos we examined revealed how profoundly different echinoderms really are from other animals. Some of the differences were not particularly surprising but gratifying to observe nonetheless. A gene called engrailed, for instance, regulates the development of several bilaterally situated structures in chordates. One of its roles is to help set up muscles on each side of the vertebrate head. In the geometrically more complicated echinoderm, engrailed is active in radially symmetrical patterns—for example, in each of the five major branches of the nervous system that run down the arms of sea stars. We have found similar spatial "rewiring" in numerous other genes.

A more surprising finding was that, in most cases, regulatory genes in echinoderms are not even active in the same regions of the body or in the same kinds of cells as they are in members of other, bilateral phyla; instead, they are involved in the development of structures unique to animals in this phylum. Two such genes are orthodenticle, which helps define the part of an insect or mammal embryo that will go on to become the head, and distal-less, which is active in limb formation. Echinoderms have neither heads nor limbs in the traditional sense (whether the legs of a vertebrate or the wings of an insect). This might seem to put these genes out of a job, but natural selection has put them to work in the development of tube feet. Thus, "old" genes can be used to regulate entirely new developmental processes that lead to the origin of new organs and, ultimately, radically different body architecture. Many changes of this kind undoubtedly occurred during the evolution and diversification of echinoderms, and we continue to find new examples. Orthodenticle, for example, also appears to be involved in the development of Aristotle's lantern in sea urchins.

The evolutionary history of animals is crammed with extraordinary anatomical transformations. Wings, eyes, and skeletons, each of which has evolved more than once, are just a few examples. We have only begun to view this rich panorama through the lens of the genes that helped shape some of these events. The first images, although somewhat blurry, are already changing the way we perceive the history of life. Evolving new anatomical features—or changing existing ones-probably doesn't require new genes. Natural selection works with the genetic tools at hand, forging new interactions among them that can resculpt an organism's anatomy and alter its destiny forever.

Echinoderms occupy nearly every seafloor habitat.

