TELL TALE SHELL-ING

UNCOILING A SNAIL'S LIFE

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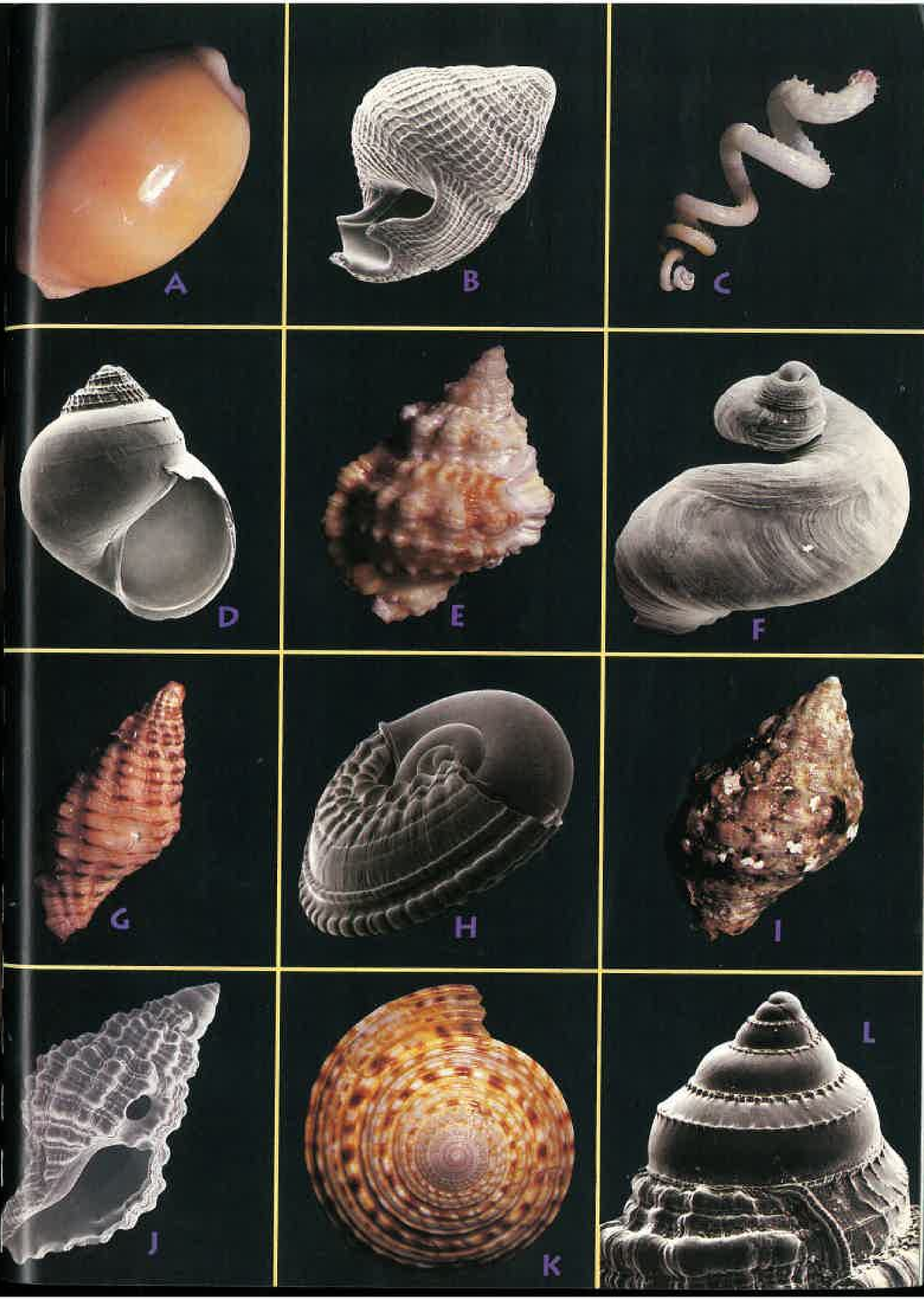
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ONLY a drifting speck in the water column, the tiny marine-snail larva inside its transparent shell survives weeks of exposure to potential predation by larger plankton and larval fishes. Larval growth demands lots of nutrients and energy, but meals are sparse, arriving unpredictably when the larva collides with patches of single-celled algae and other microorganisms. Once more the larva will rely on chance to overcome crucial obstacles as it transforms into an adult. Survival depends on whether or not the tiny snail falls on the right kind of bottom during the period of metamorphosis.

Most shelled, bottom-dwelling marine mollusks—clams, oysters, and snails—spend at least a small part of early life as plankton, free-living drifting organisms, settling on substrate as they become adults. Bottom organisms as diverse as benthic fishes, lobsters, barnacles, corals, marine worms, and sea urchins also evolve through ocean-drifting larval stages. In the open ocean, competition for food is not as fierce as in the almost always crowded bottom environment.

In order to grow and gain bulk, many marine invertebrates—such as crustaceans—successively shed their larval shells through molting. Corals begin life as soft-bodied larvae and transform to soft polyps with hard, calcified skeletons. In contrast to these animals, snails usually carry with themselves a record of earlier stages. Mollusk shells grow by accretion: The animal adds calcium carbonate crystals to the shell in small increments, usually without destruction or drastic modification of the parts already built. A snail's shell grows at its "mouth," or aperture, which increases in size around its axis. As a result, a fully grown shell includes not only the part built during adult life, but also the remains of the tiny shell formed by the animal during larval life. What remains of the larval shell is called protoconch.

Scientists can determine at any point in the adult life of a snail how the larval shell looked, if the shell isn't damaged or broken. They use a binocular microscope to appraise general details, but make micrographs with a scanning electron microscope (SEM) to study the fine structural details and sculpture of protoconchs.

Larval and adult snails grow under distinctive ecological conditions, and the shape and features of their shells reflect to some extent the differences. The delicate larval snails make shells that are thin and light, with the buoyancy necessary to a life adrift in midwater. They measure between 0.05 and 0.15 inch, are usually transparent, and often are externally sculptured with fine ribs or a reticulated pattern that reinforces the thin shell without much added weight. Adults make shells that are thicker and heavier, with much coarser sculptures that provide extra protection against predators. Researchers use these distinctions to learn about the reproduction and early life histories of different marine snails.

DURING plankton sampling at sea, marine biologists often collect larval creatures that can be identified only by rearing them in lab aquariums. Fortunately, biologists now know what many common crustaceans and echinoderms look like as larvae, but new puzzles arrive in most plankton tows. Matching a planktonic snail larva to its adult form, however, has become relatively easy for biologists who have learned to recognize a larval shell from its "record" in a well-preserved adult snail. For example, in the adult Caribbean coralsnail (*Coralliophila caribaea*), the peculiar shape and ribbed sculpture of the larval shell are easily identifiable in the preserved protoconch located in the apex of the grown shell.

In the early 1900s, zoologists hinted at the properties revealed by protoconchs and, in 1950, Danish marine biologist Gunnar Thorson made generalizations about protoconchs in his "shell apex theory." He found that a large number of protoconch turns, or whorls, and a small initial whorl such as occurs in the rock snail (*Stramonita haemastoma*) correlate to a long pelagic larval life: The rock snail may drift for more than three months before settling at the bottom. In the Caribbean coralsnail and twin drupe (*Trachypollia turricula*), the many whorled protoconchs also reveal long larval periods.

SOME snails deliver the young directly to the bottom. The shape of a protoconch also gives a clue to whether a species bypasses the planktonic, pelagic phase. Thorson realized that protoconchs with a single, large whorl, barely distinguishable from the adult shell, had no pelagic larval stage. As an egg-encased embryo, for example, the white hoofsnail (*Hipponix antiquatus*) feeds on a large yolk reserve, and its shell grows large to accommodate for the yolk before the larva crawls away from its egg capsule. In contrast, larval Caribbean coralsnails and twin drupes get tiny yolks or none, and so must feed quickly on plankton. A small initial whorl in the protoconch corresponds to a little parcel of yolk.

A yet-unnamed latirus shell collected from South Atlantic seamounts illustrates the predictive power of protoconch shape. This particular snail shows four protoconch whorls, suggesting that this animal has a long-lasting pelagic larval stage. Crescent-shaped ribs at the boundary between the protoconch and adult shell indicate the former position of one of the two velar lobes—prominent winglike expansions that help the larva get food particles from the water.

Protoconchs often look strikingly different from the fully grown shell. In the false cup-and-saucer (genus *Cheilea*), the protoconch is golden-yellow, finely reticulated, and coiled, with about three and a half whorls. The adult shell, which is white, lacks coiling and is only a broadly open, cup-shaped structure. Adult keyhole limpets in the genera *Fissurella* and *Diodora* also typically have uncoiled, flattened, or conical shells, hiding the fact that they built coiled shells during their brief larval life. The protoconch disappears in worn adult keyhole-limpet shells, but it can be seen near the orifice at the top of the shell in incompletely formed, young specimens.

The slit wormsnail (*Tenagodus squamatus*) provides another example. As a larva, its shell is regularly coiled, but after it settles on the sea bottom, the shell begins to uncoil. It becomes elongated and irregularly twisted, a shape that helps the slit wormsnail anchor itself to the sponge in which it lives as an adult.

DURING the 19th century, some zoologists misidentified larval shells because the differences between protoconch and adult shells were so grand. One of the most impressive changes from larval to adult shell occurs in shiny, colorful cowrie shells. Most cowries have long-lasting, pelagic larval stages, during which they build a thin, delicately reticulated protoconch. A pair of notches at the outer part of the aperture indicates the position of velar lobes. After metamorphosis, the sculpture pattern changes, and the cowrie shell starts to grow around itself, wrapping and hiding the older whorls. The fully grown snail has the egg-shaped, smooth, and brilliantly colored shell that sets cowries apart from other snails. The protoconch remains hidden midway along the core of the adult shell.

In the family of the sundials, or Architectonicidae, the direction of shell growth reverses 180 degrees during metamorphosis. The adult shell grows exactly in the opposite direction of the larval shell. As a result, sundials have upside-down protoconchs.

IN THE 1980s, marine biologists began to recognize that some species of marine snails could switch from producing pelagic to nonpelagic offspring, a phenomenon known as poecilogony. Evidence indicates that polychaete worms and nudibranchs with long-lasting planktonic larvae can produce offspring with shorter or no larval life when faced with adverse environmental conditions. A few marine-snail species that appear practically identical as adults show vastly different lengths of larval stages. The West Indian alvania (*Alvania auberiana*) and Faber's alvania (*Alvania faberi*) are good examples. The West Indian has a many-whorled protoconch, suggesting that the larva had a long planktonic life, but Faber's displays a little-whorled protoconch, indicating either a short planktonic stage or complete early development inside the egg capsule.

In a few snail species, the little embryos growing inside egg capsules do not depend on a yolk source to feed, but instead feed upon each other, a phenomenon called embryonic cannibalism. The cannibals' initial whorl is small, and their protoconchs end up with many whorls, resembling those of planktonic larvae. These species' protoconchs can confuse the researchers' attempts to predict their development.

SHELL collectors regard protoconchs as an extra bonus hidden in a beautiful shell. Like the fully grown adults, protoconchs can be contemplated solely for their delicate and sometimes intricate beauty. Coexistence of both the larval and adult shell in the same "package" occurs because of peculiar growth patterns of marine snails. Despite the bedazzling change at metamorphosis, these animals preserve their original shelter as remnants of more turbulent, bygone days.

The author made the black-and-white scanning electron micrographs at the Electron Microscope Laboratory at the University of Miami Rosenstiel School of Marine and Atmospheric Science.

Many shells change form dramatically as they grow from larval stage to adult stage. The Atlantic gray cowrie (A, preceding page) grows around its reticulated larval shell (B). When the adult slit wormsnail (C) settles at the bottom, normal coiling seen in the protoconch (F) stops. The protoconch of a frog shell (D) is first reticulated, then smooth; its grown shell is knobby (E). The adult twin drupe (G) develops from a distinctive protoconch, visible at the top of its juvenile shell (J). Sundials have smooth, upside-down protoconchs (H) that grow in an opposite direction to that of the adult shell (K). The rock snail (I) has a many-whorled protoconch (L) that reflects its long planktonic larval life.