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How Did Insect Metamorphosis Evolve?

The evolution of metamorphosis remains somewhat mysterious, but biologists have gathered enough evidence to plausibly explain its origins

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In the 1830s a German naturalist named Renous was arrested in San Fernando, Chile for heresy. His claim? He could turn caterpillars into butterflies. A few years later, Renous recounted his tale to Charles Darwin, who noted it in *The Voyage of the Beagle*.

Gregory Phillips via Wikimedia Commons

Imprisoning someone for asserting what today qualifies as common knowledge might seem extreme, but metamorphosis—the process through which some animals abruptly transform their bodies after birth—has long inspired misunderstanding and mysticism. People have known since at least the time of ancient Egypt that worms and grubs develop into adult insects, but the evolution of insect metamorphosis remains a genuine biological mystery even today. Some scientists have proposed outlandish origin tales, such as Donald Williamson's idea that butterfly metamorphosis resulted from an ancient and accidental mating between two different species—one that wriggled along ground and one that flitted through the air.

Metamorphosis is a truly bizarre process, but an explanation of its evolution does not require such unsubstantiated theories (for a critique of Williamson's hypothesis, see this study). By combining evidence from the fossil record with studies on insect anatomy and development, biologists have established a plausible narrative about the origin of insect metamorphosis, which they continue to revise as new information surfaces. The earliest insects in Earth's history did not metamorphose; they hatched from eggs, essentially as miniature adults. Between 280 million and 300 million years ago, however, some insects began to mature a little differently—they hatched in forms that neither looked nor behaved like their adult versions. This shift proved remarkably beneficial: young and old insects were no longer competing for the same resources. Metamorphosis was so successful that, today, as many as 65 percent of all animal species on the planet are metamorphosing insects.

The egg of an idea

In 1651 English physician William Harvey published a book in which he proposed that caterpillars and other insect larvas were free-living embryos that abandoned nutrient-poor "imperfect eggs" before they matured. Harvey further argued that the cocoon or chrysalis a caterpillar entered during its pupal stage was a second egg in which the prematurely hatched embryo was born again. He entertained the idea that a caterpillar was one creature and a butterfly was an entirely different beast.

Some of Harvey's ideas were prescient, but he mostly misinterpreted what he observed. In 1669 Dutch biologist Jan Swammerdam rejected Harvey's notion of the pupa as an egg and the butterfly as a different animal than the caterpillar. Swammerdam dissected all kinds of insects under a microscope, confirming that the larva, pupa and adult insect were phases in the development of a single individual, not distinct creatures. He showed that one could find immature moth and butterfly body parts inside a larva, even before it spun a cocoon or formed a chrysalis. In some demonstrations, for example, Swammerdam peeled the skin off silkworms—the larval stage of the domesticated silk moth (*Bombyx mori*)—to reveal the rudimentary wings within.

Today, biologists know that these adult structures arise from clusters of cells called imaginal discs, which first form when an insect embryo develops in its egg. In some species, imaginal discs remain largely dormant until the pupal stage, during which they rapidly proliferate and grow into adult legs, wings and eyes, using dissolved larval cells as fuel and building blocks. In other species, imaginal discs begin to take the shape of adult body parts before the insect pupates (See Sidebar: How Does a Caterpillar Turn Into a Butterfly?)

Swammerdam also recognized that not all insects metamorphose in the same way. He proposed four kinds of metamorphosis, which biologists later distilled into three categories. Wingless ametabolous insects, such as silverfish and bristletails, undergo little or no metamorphosis. When they hatch from eggs, they already look like adults, albeit tiny ones, and simply grow larger over time through a series of molts in which they shed their exoskeletons. Hemimetaboly, or incomplete metamorphosis, describes insects such as cockroaches, grasshoppers and dragonflies that hatch as nymphs—miniature versions of their adult forms that gradually develop wings and functional genitals as they molt and grow. Holometaboly, or complete metamorphosis, refers to insects such as beetles, flies, butterflies, moths and bees, which hatch as wormlike larvae that eventually enter a quiescent pupal stage before emerging as adults that look nothing like the larvae. Insects may account for between 80 and 90 percent of all animal species, which means 45 to 60 percent of all animal species on the planet are insects that undergo complete metamorphosis according to one estimate. Clearly, this lifestyle has its advantages.

A new generation

Complete metamorphosis likely evolved out of incomplete metamorphosis. The oldest fossilized insects developed much like modern ametabolous and hemimetabolous insects—their young looked like adults. Fossils dating to 280 million years ago, however, record the emergence of a different developmental process. Around this time, some insects began to hatch from their eggs not as minuscule adults, but as wormlike critters with plump bodies and many tiny legs. In Illinois, for example, paleontologists unearthed a young insect that looks like a cross between a caterpillar and a cricket, with long hairs coating its body. It lived in a tropical environment and likely rummaged through leaf litter for food.

Biologists have not definitively determined how or why some insects began to hatch in a larval form, but Lynn Riddiford and James Truman, formerly of the University of Washington in Seattle, have constructed one of the most comprehensive theories. They point out that insects that mature through incomplete metamorphosis pass through a brief stage of life before becoming nymphs—the pro-nymphal stage, in which insects look and behave differently from their true nymphal forms. Some insects transition from pro-nymphs
to n pro-nymphs for anywhere from mere minutes to a few days after hatching.

Per Truman suggest, evolved into the larval stage of complete metamorphosis. Perhaps
280 ion, some pro-nymphs failed to absorb all the yolk in their eggs, leaving a precious
resc le situation, some pro-nymphs gained a new talent: the ability to actively feed, to slurp
up t uch pro-nymphs emerged from their eggs before they reached the nymphal stage, they
wou selves in the outside world. Over the generations, these infant insects may have
rem r longer and longer periods of time, growing wormier all the while and specializing in
diet ves—consuming fruits and leaves, rather than nectar or other smaller insects.
Eve ame full-fledged larvae that resembled modern caterpillars. In this way, the larval
stag to the pro-nymphal stage of incomplete metamorphosis. The pupal stage arose later as
a kind of condensed nymphal phase that catapulted the wriggly larvae into their sexually active winged adult forms.

Some anatomical, hormonal and genetic evidence supports this evolutionary scenario. Anatomically, pro-nymphs have a fair amount in common with the larvas of insects that undergo complete metamorphosis: they both have soft bodies, lack scaly armor and possess immature nervous systems. A gene named *broad* is essential for the pupal stage of complete metamorphosis. If you knock out this gene, a caterpillar never forms a pupa and fails to become a butterfly. The same gene is important for molting during the nymphal stage of incomplete metamorphosis, corroborating the equivalence of nymph and pupa. Likewise, both pro-nymphs and larvae have high levels of juvenile hormone, which is known to suppress the development of adult features. In insects that undergo incomplete metamorphosis, levels of juvenile hormone dip before the pro-nymph molts into the nymph; in complete metamorphosis, however, juvenile hormone continues to flood the larva's body until just before it pupates. The evolution of incomplete metamorphosis into complete metamorphosis likely involved a genetic tweak that bathed the embryo in juvenile hormone sooner than usual and kept levels of the hormone high for an unusually long time.

However metamorphosis evolved, the enormous numbers of metamorphosing insects on the planet speak for its success as a reproductive strategy. The primary advantage of complete metamorphosis is eliminating competition between the young and old. Larval insects and adult insects occupy very different ecological niches. Whereas caterpillars are busy gorging themselves on leaves, completely disinterested in reproduction, butterflies are flitting from flower to flower in search of nectar and mates. Because larvas and adults do not compete with one another for space or resources, more of each can coexist relative to species in which the young and old live in the same places and eat the same things. Ultimately, the impetus for many of life's astounding transformations also explains insect metamorphosis: survival.

The Biology of the Translucent Jewel Caterpillar, the Nudibranch of the Forest