

THE
LIVES
OF

MOTHS

A NATURAL HISTORY OF OUR PLANET'S MOTH LIFE

Andrei Sourakov
& Rachel Warren Chadd



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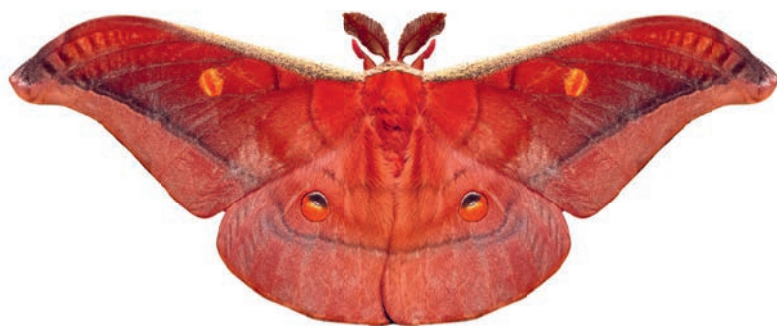
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INTRODUCTION

The world of moths

It's the 1970s, and I am walking from school past a high-rise apartment building. I suddenly stop in my tracks, while my heart begins to race. On the brick wall, I detect the unmistakable triangular shape of the Red Underwing moth. Slowly, not to startle it, I approach; even more slowly, I extend my hand and touch its hairy back. The moth flicks up its forewings, exposing a flash of red from hind wings normally hidden from view, in a desperate attempt to scare me off. When I touch it again, the moth zooms up and perches high above the ground, instantly becoming just another “scar” on the bark of the tall poplar.

The diet of their caterpillars sustains the intimate connection between moths and plants. Which plants occur where is determined by numerous factors, from geography and evolutionary history to soil composition and levels of sunlight and water. And while different continents may have different moth faunas, each moth community—whether in a rainforest or desert—bears a distinct imprint of its habitat. According to both habitat and geographic region, moths also interact with a host of other organisms—as large as grizzly bears and as tiny as viruses.

In the present volume, we first examine the moth's four stages of development, from egg to adult, and its biology and behavior in different environments, before venturing to explore examples of moths found in vast habitats of tropical forest, grasslands, deserts, and tundra. Certain moths have undergone interesting adaptations to occupy aquatic habitats, and it may come as a surprise to many that some species develop in water. There are also moths that live in sloths' fur, drink bird tears, or even, as caterpillars, predate on wasps or mollusks. The secret world of moths is truly remarkable!

Of course, moths are mobile creatures, and many of them move between habitats in search of nectar for themselves or plants to lay their eggs on. Some species even migrate seasonally and others are, like us, highly versatile, and have formed different races specifically adapted to the habitats of their geographic region. These, however, are exceptions rather than the rule, and I hope that showcasing moths as integral parts of their respective ecosystems will help in appreciating these species' roles in their environment. Today, when natural habitats are disappearing at an unprecedented rate, yielding to those created by humans, underscoring the connection between habitat type and the unique species that they harbor becomes vitally important. Only by conserving habitats can we preserve the precious species that inhabit them.

Andrei Sourakov



↑ → Two beautiful moths that the author first encountered as a child inside the city: the Red Underwing (*Catocala nupta*) that develops on poplar (top) and the Elephant Hawk Moth (*Deilephila elpenor*), whose caterpillars eat rosebay willowherb along rail tracks and in urban wasteland.



What is a moth?

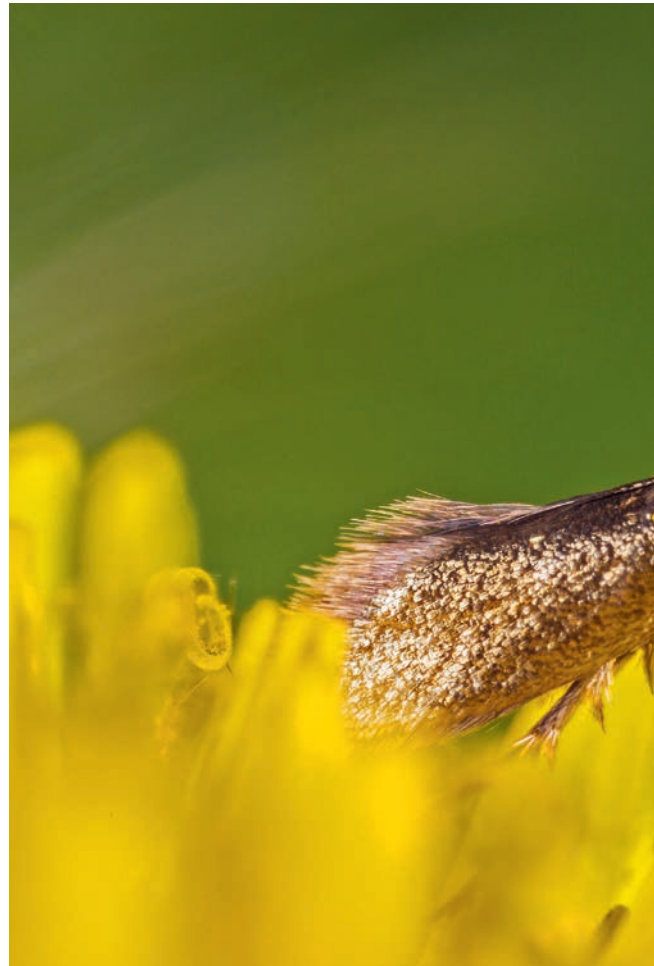
The evolution of moths—insects of ancient lineage in the order Lepidoptera—is intimately entwined with that of plants. While their diversification occurred during the rise of flowering plants from around 130 million years ago, gymnosperm plants 70 million years earlier appear to have played an important role in their origins and speciation.

THE ORIGINS

It was the recent discovery of a 200 million-year-old fossilized moth in Germany that pushed back the probable date of Lepidoptera origins and prompted the hypothesis that during the Jurassic period, before there were flowers, moths developed a sucking proboscis to sip droplets of moisture from the tips of immature seeds of plants related to today's conifers. The proboscis—part of the maxilla (mouthparts) called galeae, zipped together into a straw-like organ—continued to evolve and today distinguishes most (though not all) moths and butterflies from other insects, whose classification has traditionally been based on mouthparts. Some moths have retained their chewing mouthparts, but they are in a minority.

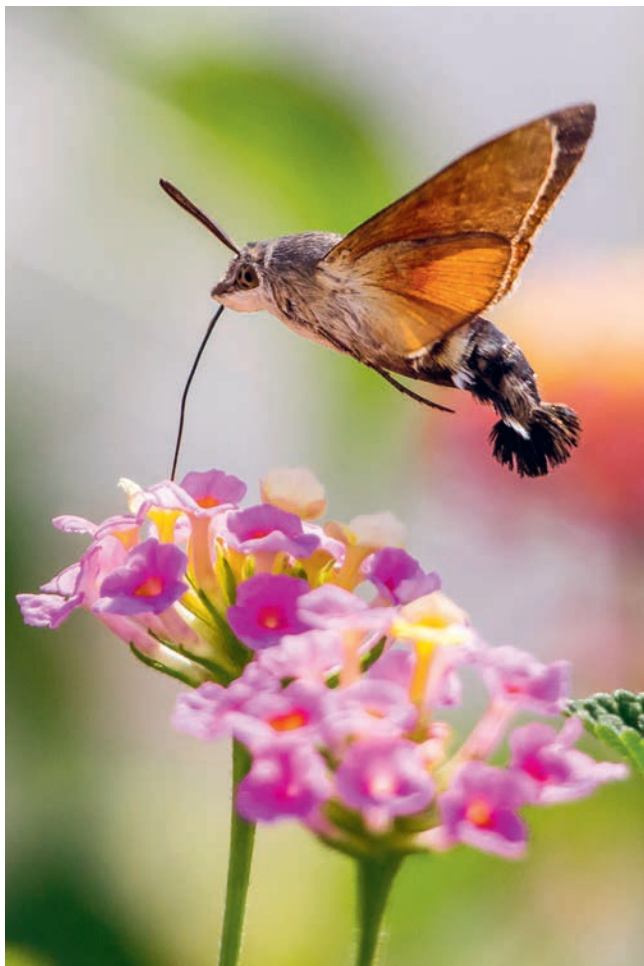
MOTH OR CADDISFLY?

Their closest relatives are Trichoptera (caddisflies), which also developed in the early Jurassic period, and together with Lepidoptera form a group called Amphiesmenoptera. While the two share some characteristics, such as larvae that can produce silk, there are major differences; the wings of moths, for instance, are covered in scales, while those of caddisflies are hairy.



MOTHS VERSUS BUTTERFLIES

People often wonder how butterflies relate to moths and may be surprised to know there are no major differences. Butterflies, which evolved from a common ancestor about 110 million years ago, form a group of just eight families within Lepidoptera, otherwise comprised of some 130 moth families, so are simply an offshoot of the moth evolutionary tree. Based on their genetic analysis, plume moths (Pterophoridae) are probably most closely related to butterflies. Like moths, certain butterflies, including many skippers and the American moth-butterflies (Hedylidae) fly at night, while numerous moths have independently evolved day-flying habits at least 30 times during their evolution.



ECOLOGICAL IMPORTANCE

Being more ancient, moths have experienced and adapted to a far greater range of conditions and environments than butterflies and thus are more diverse in their morphology and lifestyles. And while the caterpillars of a few moth species—those that eat crops—may have given moths a bad name, most species exist in balanced relationships with their ecosystems, playing crucial roles as pollinators and food for vertebrates. Many species have developed such intimate relationships with their hosts and the flowers they pollinate that neither can exist without the other. As this book reveals, across diverse ecosystems, moths play a crucial role.

↑ Among more advanced moths are the bombycoids, such as this Hummingbird Hawk Moth (*Macroglossum stellatarum*) with a fully developed proboscis that is used to sip nectar in flight.

↖ A member of the mandibulate archaic moth family Micropterigidae, this Marsh Marigold Moth (*Micropterix calthella*) as an adult feeds on pollen grains of various plants.

Moth classification

Of the millions of animal species on Earth, two-thirds are insects. After Coleoptera (beetles), Lepidoptera (butterflies and moths) and Hymenoptera (ants, bees, wasps) are the two most numerous orders, and together these three orders are responsible for half of all insect species.

Among Lepidoptera, in terms of species, moths outnumber butterflies by more than eight to one. Taxonomists attempt to group animals so that each category, such as family or genus, is monophyletic (includes all descendants of a single ancestor and nothing else). “Moths” is not a category as such, while butterflies are. Why? Because butterflies

(with their seven families) are an offshoot of moths that derived from a single ancestor, branching off moths’ evolutionary tree around 100 million years ago.

The approximately 150,000 species of moths are grouped in over 120 families, which in turn are divided into subfamilies and genera. This classification changes constantly with better understanding of the evolutionary history—morphological studies of the past 250 years are now supplemented by DNA analysis. While most of the larger moths, such as Saturniidae (saturniids or giant silk moths) and Sphingidae (sphingids, sphinx moths, or hawk moths) have been described, much work remains to describe the diversity of rapidly vanishing, smaller, tropical moths.

A moth family can be tiny or numerous. For instance, the family Endromidae to which the Kentish Glory (*Endromis versicolora*) belongs, contains only about 30 species, while the family Erebidae (erebids) includes tens of thousands of species belonging to diverse subfamilies such as tiger, lichen, and wasp moths (subfamily Arctiinae), underwing moths and their relatives (Erebinae), and tussock moths (Lymantriinae). Superficially, moths belonging to the same family can look very different from each other and can lead diverse lifestyles, but they are unified by more stable morphological characters, such as wing venation.

A SELECTION OF MOTH FAMILIES

Here we list and illustrate a few representatives of the most speciose families mentioned in the book—a more complete list of families can be found on page 281.

ACROLOPHIDAE

Tubeworm moths
(acrolophids)

ANTHELIDAE

Australian lappet moths
(anthelids)

BATRACHEDRIDAE

(batrachedrids)

BOMBYCIDAE

Silk moths (bombycoids)

BRAHMAEIDAE

Brahmin moths (brahmaeids)

COLEOPHORIDAE

Casebearer moths
(coleophorids)

COSMOPTERIGIDAE

(cosmopterigids)

COSSIDAE

Carpenter moths (cossids)

CRAMBIDAE →

Sky-pointing moths
(crambids)



DREPANIDAE

Hook-tip moths and casebearers (drepanids)

ELACHISTIDAE

Grass-miner moths (elachistids)

ENDROMIDAE

(endromids)

EREBIDAE ↓

Tiger, lichen, and wasp moths, underwing moths, tussock moths, owlet moths, woolly bears (erebids)

**GEOMETRIDAE** ↓

Inchworms, butterfly moths (geometrids)

**GRACILLARIIDAE**

Leaf blotch miner moths (gracillariids)

LASIOCAMPIDAE ↓

Lappet moths or eggars (lasiocampids)

**LIMACODIDAE**

Slug moths (limacodids)

MEGALOPYGIDAE ↓

Flannel moths (megalopygids)

**MIMALLONIDAE**

Sack-bearer moths (mimallonids)

NEPTICULIDAE

Leaf miners (nepticulids)

NOCTUIDAE ↓

Owlet moths (noctuids)

**NOLIDAE** ↓

Tuft moths (nolids)

**OECOPHORIDAE**

(oecophorids)

PLUTELLIDAE

(plutellids)

NOTODONTIDAE ↓

Prominent moths (notodontids)

**PRODOXIDAE**

Yucca moths (prodoxids)

PSYCHIDAE

(psychids)

PTEROLONCHIDAE

(pterolonchids)

PTEROPHORIDAE

Plume moths (pterophorids)

PYRALIDAE

(pyralids)

SATURNIIDAE ↓

Silk moths, oak worm moths, buck moths (saturniids)

**SCYTHRIDIDAE**

Flower moths (scythridids)

SESIIDAE

Clearwing moths (sesiids)

**SPHINGIDAE** ↓

Hawk moths (sphingids)

**STATHMOPODIDAE**

(stathmopodids)

TINEIDAE

Fungus moths (tineids)

TORTRICIDAE ↓

Carpenter moths (tortricids)

**URANIIDAE**

Sunset moths (uraniids)

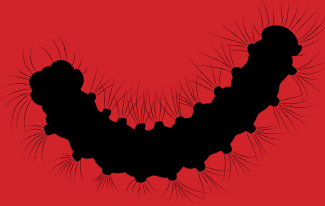
YPONOMEUTIDAE

Ermine moths (yponomeutids)

ZYGAENIDAE ↓

(zygaenids)





LIFE CYCLE

Eggs and oviposition

Moths may lay eggs (oviposition) singly or in batches of thousands, either glued to the host plant, inserted into it, or dropped from the air nearby by the adult female. Egg shapes can vary from a perfect sphere to something resembling a pancake, flying saucer, or football. They can be white, translucent, or colorful, but need to be inconspicuous, or have some way of repelling predators. The eggs must also withstand environmental pressures, from freezing cold and rain to intense heat, while protecting the delicate embryo of a future moth, often within the confines of a space a fraction of a millimeter in size.

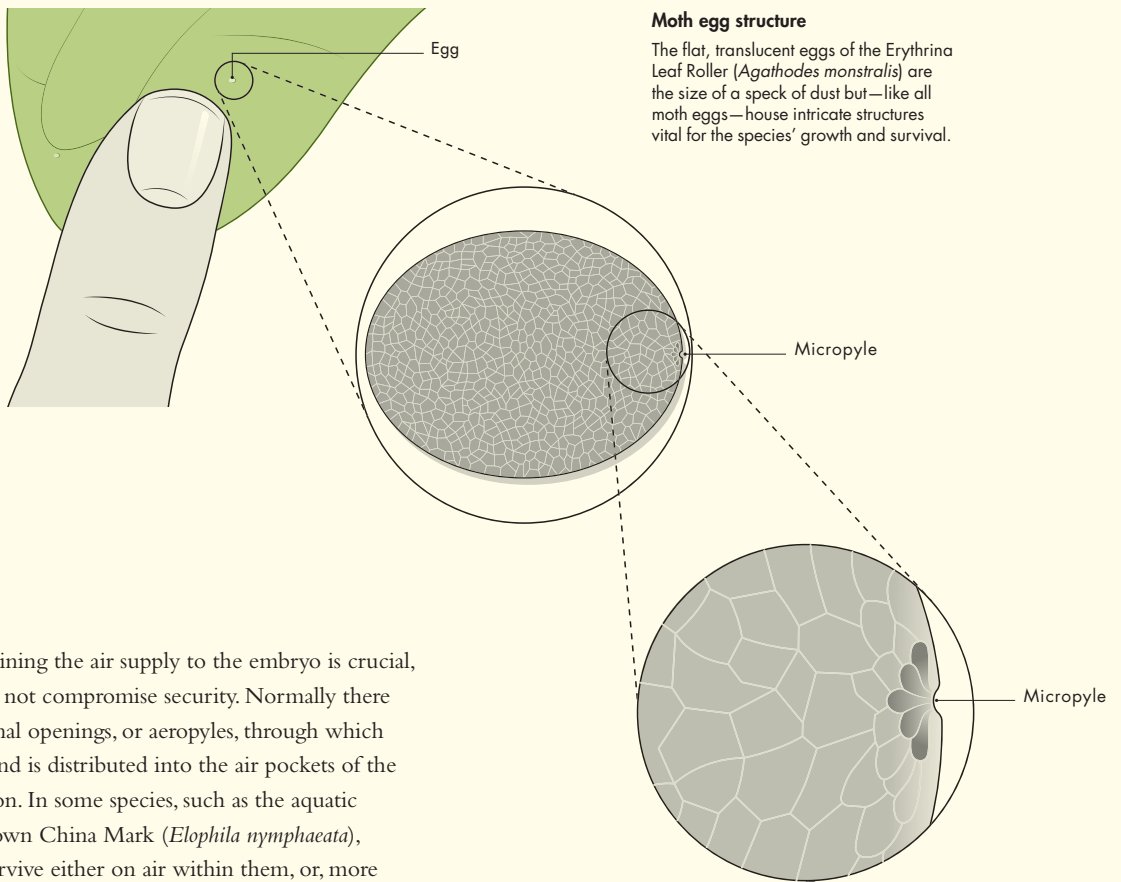


INGENIOUSLY CONSTRUCTED

While we may marvel at the Hagia Sophia and its unique dome and arches as examples of unsurpassed ancient architecture, moths have been masters of such construction techniques for more than 200 million years. When follicle cells within the female's ovaries produce the eggs, the proteins of the future shell are arranged into flattened spiral shapes called helicoids. As a result, the eggs have strong but light "struts and columns" of outer layer (exochorion) and airy structures of inner endochorion, which together form the shell.

Like birds' eggs, the moth egg contains a single egg cell that is fertilized just before laying by sperm which the female stores separately from the forming eggs in a special sac called a bursa copulatrix. Within the eggshell, the embryo is surrounded and protected by a membrane and a layer of wax. Similar to fish eggs, moth eggs have openings called micropyles through which sperm enters during fertilization.

← Females of the subfamily Plusiinae (Noctuidae) may lay hundreds of eggs in one batch—here on sweet clover.



Maintaining the air supply to the embryo is crucial, but it need not compromise security. Normally there are additional openings, or aeropyles, through which air enters and is distributed into the air pockets of the endochorion. In some species, such as the aquatic pyralid, Brown China Mark (*Elophila nymphaeata*), the eggs survive either on air within them, or, more likely, by absorbing oxygen from the air trapped in the mucous membrane that glues them to the plant surface underwater. If submerged, most terrestrial moth eggs can survive for some time by reducing their metabolic rate, living on the air supply stored in their air chambers, or on air trapped against their sculptured surfaces.

MOTH EGG SHAPES

Moth egg shapes vary from spherical to flat. Most are laid on a plant's surface, but some are inserted into plant tissue.





JUDICIOUS LAYING

Sometimes moth eggs are laid singly by a female aiming to distribute them widely among as many host plants as possible over a broad geographic area. This strategy spreads the risk of predation and other dangers, and provides more food for each offspring. Such behavior is more typical of butterflies, whose females fly by day and seek out host plants far and wide. Large, fast-flying hawk moths behave similarly—some species flying by day or at dusk, and covering large distances in search of suitable host plants. Eggs of hawk moths are spherical, camouflaged green (cryptic), and are glued to the surface of the leaf, usually on the underside. In another, mostly day-flying, group of clearwing moths (Sesiidae), eggs are also laid singly,

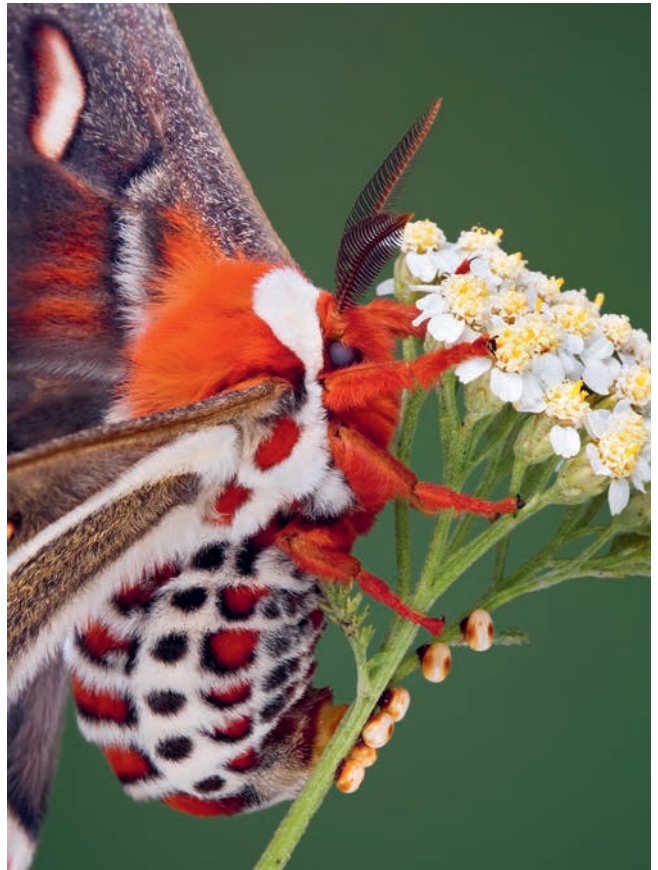
but are hidden in the crevices of the host plant or dropped on the ground near it. The young larvae must then burrow into the trunk or root where they develop. Some females, such as yucca moths of the Prodoxidae family, inject their eggs into the host plant tissue using an extended and sharpened tubular organ known as an ovipositor. Very frequently, however, eggs are laid in batches that are much more visible to predators and parasitoids (parasitic wasps and flies whose larvae develop inside immature moths). This may seem irrational, but saves females the energy deployed in flight, and minimizes the dangers they face from birds by day, and from bats by night. Caterpillars that result from eggs laid in batches frequently benefit from feeding in a group, which can more easily



↖ The Fall Webworm (*Hyphantria cunea*) first lays its round eggs in batches of several hundred, then covers them with hairs from the tip of its abdomen.

↑ Eggs with a flat base, such as these of the Buff-tip (*Phalera bucephala*) adhere better to a leaf's surface. The black dots (micropyles) are where the sperm entered the eggs.

↗ The Cecropia Moth (*Hyalophora cecropia*) lays large hard oval eggs in small batches on a variety of host plants from over 20 families.



overcome plant defenses. The Ornate Bella Moth (*Utetheisa ornatrix*) and Io Moth (*Automeris io*), for instance, both lay a total of more than 300 eggs in batches of 10 to 50. As chemically defended caterpillars grow, they may either disperse and feed individually, or stay as a group and gain additional protection by sending a stronger warning signal to predators. In some cases, gregarious (group-feeding) caterpillars, such as the Eastern Tent Caterpillar (*Malacosoma americanum*) or Fall Webworm (*Hyphantria cunea*), also make a communal nest for additional protection, and, in these species, eggs are laid in especially large clusters; the female Fall Webworm moth lays 400 to 1,000 eggs in a single batch and dies after oviposition.

→ The Gypsy Moth (*Lymantria dispar*) lays batches of 300–500 eggs in a mass on a tree trunk and covers them with hairs, which protect them from predators.

↓ Ground Lackey Moths (*Malacosoma castrense*) lay overwintering egg masses in circles around branches and protect them with a clear secretion that hardens around them like epoxy.



COLOR, HAIRS, AND CHEMICAL PROTECTION

To blend with their surroundings, eggs may be translucent or cryptically colored to resemble a part of the host plant, or fungi, detritus, bird droppings, or any other feature of the landscape where they are laid. Minute as they are, moth eggs are a highly desirable source of protein for smaller predators and parasitoids, such as various ants, wasps, and minute pirate and big-eyed bugs.

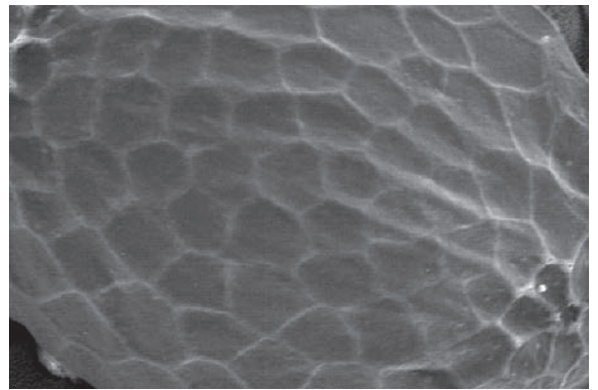
Some female moths, such as Gypsy Moths (*Lymantria dispar*), cover their batches of eggs with hairs for protection, while Eastern Tent Caterpillar moths (*Malacosoma americanum*) use varnish-like secretions that harden and provide a shield for the eggs. While bird predation of Gypsy Moth eggs can be as high as 80 percent, evidence suggests that the eggs are

unpalatable, as birds don't swallow them all at once, but eat them bit by bit, likely due to irritating hairs. The female Australian Processionary Caterpillar Moth (*Ochrogaster lunifer*) covers her egg masses with barbed tufts of hairs, while the South American silk moths in the genus *Hylesia* deposit urticant setae (irritant, hairlike bristles) over egg clusters that can cause allergic reactions in humans. Some tortricid moths, such as *Tortricodes alternella*, mask their eggs by using hardened structures on their abdomen to scrape dirt over the egg mass. Other species, such as the Ornate Bella Moth (*Utetheisa ornatrix*), lay brightly colored, poisonous eggs. A predator encountering them may taste one, but will leave the rest alone.

EGG SIZES AND INCUBATION TIMES

Partly as a result of different oviposition and survival strategies, but also depending on the adult size and species biology, the size of moth eggs can vary dramatically. This can be true even in very similar species of similar size: for instance, the Io Moth (*Automeris io*) and the Louisiana-eyed Silk Moth (*A. louisiana*), are so alike that they can form hybrids in captivity, but their egg size is significantly different. Among the largest moth eggs are those of the largest moths, such as the Asian Atlas Moth (*Attacus atlas*), whose eggs may measure $\frac{1}{8}$ in (2.7 mm) in diameter and weigh 6 mg, while the egg of a tiny Erythrina Leaf Miner (*Leucoptera erythrinella*, Lyonetiidae) is microscopic.

While most eggs hatch within 2 to 14 days, depending on the species and the temperature, in some cases, such as the widespread genus of underwing moths (*Catocala*), eggs have a built-in delay mechanism, known as diapause, which ensures they are dormant through the winter. Eggs at a diapausing stage can be deceptive, however, as it is not the egg, but the fully formed caterpillar inside it that is most frequently overwintering.



↑ The eggs of the Erythrina Leaf Miner (*Leucoptera erythrinella*) are among the tiniest—comparable in size to its host plant's leaf cells. While translucent when viewed under the light microscope (top), scanning electron microscopy reveals intricate details.

↓ Caterpillar of a Giant Owl Moth (*Brahmaea hearseyi*) hatching from an egg.



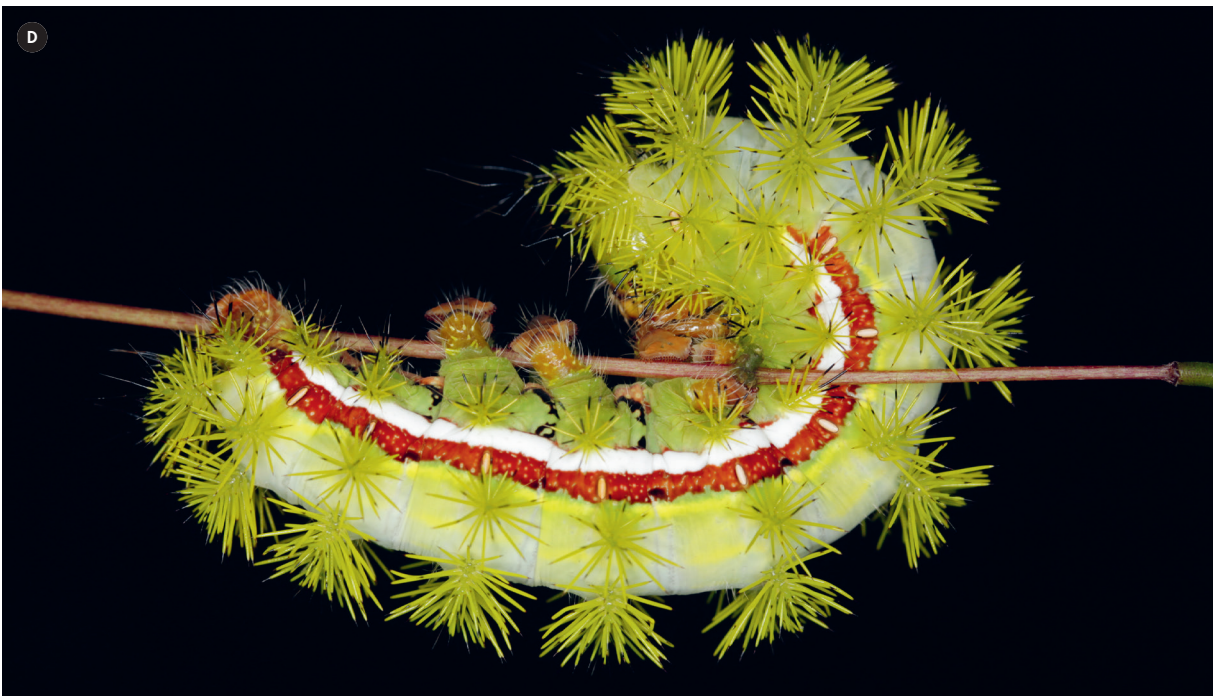
The ever-changing caterpillar

Moth larvae range in size from microscopic to 6 in (150 mm) or more in length and may be maggot-like, twiglike, leaflike, tentacled, hairy, spiky, or smooth—almost invariably more diverse than the stereotypical segmented grub with stubby legs of Alice in Wonderland or Eric Carle’s *The Very Hungry Caterpillar*.

What they all have in common is their appetite and growth rate. Most pass through at least five stages (instars), during which they change in both size and appearance. The caterpillar of the Cecropia Moth (*Hyalophora cecropia*) weighs just 3 mg at birth but 5,000 times more when it reaches its peak growth within less than a month. Imagine a human baby growing from 8 lb (3.5 kg) to 20 US tons in one month on a strictly vegetarian diet. From a cryptic, brown, twiglike grub about $\frac{1}{8}$ in (3 mm) in length, the Cecropia Moth caterpillar transforms into a green snakelike creature with yellow and blue protrusions along its body. The latter are not just decor: the spines help protect the larvae from vertebrate predators.

Io Moth (*Automeris io*) caterpillars undergo six instars as males and seven instars as females, and change greatly during their two-month-long development. Initially light brown (A), they soon acquire white stripes on a chocolate background, a coloration they maintain through the fourth instar (B), and become green or yellow in the fifth instar (C), when they disperse and feed solitarily until mature (D). Mature larvae display bright stripes, reminding predators of their venomous spines.



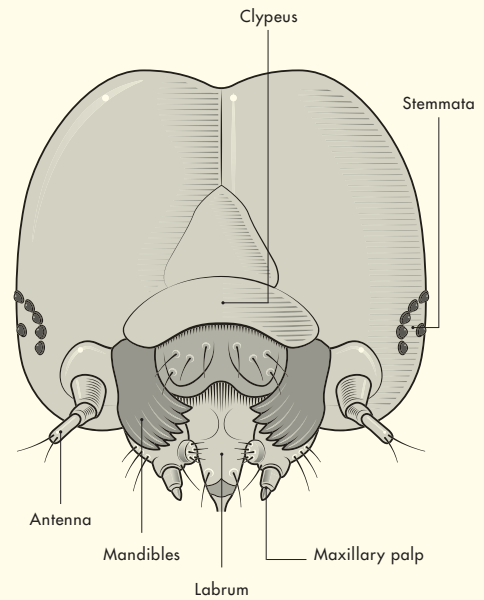


SENSING THEIR WORLD

Most caterpillars have six pairs of single-lens “eyes” (stemmata), but how well they see predators or other parts of their world is unclear. Rustic Sphinx (*Manduca rustica*) caterpillars, for example, will stop eating and “freeze” if they sense movement near them, but if someone approaching them stands still for a while, they will resume their feeding. Each stemma has a lens made of chitin (the same chemical from which the external skeleton of all insects is made), under which there is a crystalline cone. The stemmata also contain photoreceptors that transmit an external image to the optic lobe in the brain via seven axons—the nerve cell “wiring.” The structure is much less complex than the adult moth compound eye, and it is commonly believed that caterpillars have minimal sight. However, research into jumping spiders suggests that simple eyes may work in synergy to produce a better image than one eye could achieve alone—similar to the way single-lens elements combine to make up the compound lens of a cell phone camera.

Their 12 eyes and 2 antennae, which communicate with the brain, enable caterpillars to sense and navigate their environment. They also have some form of

HEAD OF A CATERPILLAR



Protective capsule

Akin to a camera in a waterproof case, the caterpillar head is enclosed in a protective chitinous capsule. This changes several times as the caterpillar grows and molts, exponentially increasing in size.



FINELY TUNED TASTE

A simple experiment, such as placing an Ornate Bella Moth (*Uteheisa ornatrix*) caterpillar in one corner of a large cage and a rattlebox (*Crotalaria* spp.) plant in the opposite corner, soon reveals how effectively it will find a host plant. Caterpillars have two antennae responsible for their sense of smell, but use their mouthparts (maxillae and labrum) to taste and make a final host-plant choice.

For the Ornate Bella Moth, this choice is essential to its survival, as consuming the plant's bitter toxic compounds arms it with potent defenses against predators. Many caterpillars have evolved a finely tuned biochemical mechanism to use toxic plant compounds for their benefit.

← Top: A *Uteheisa ornatrix* caterpillar feeding on a rattlebox pod is protected by its host plant's toxic chemicals from a carpenter ant attracted by the plant's extrafloral nectar. Left: A *U. ornatrix* caterpillar feeds on developing seeds.

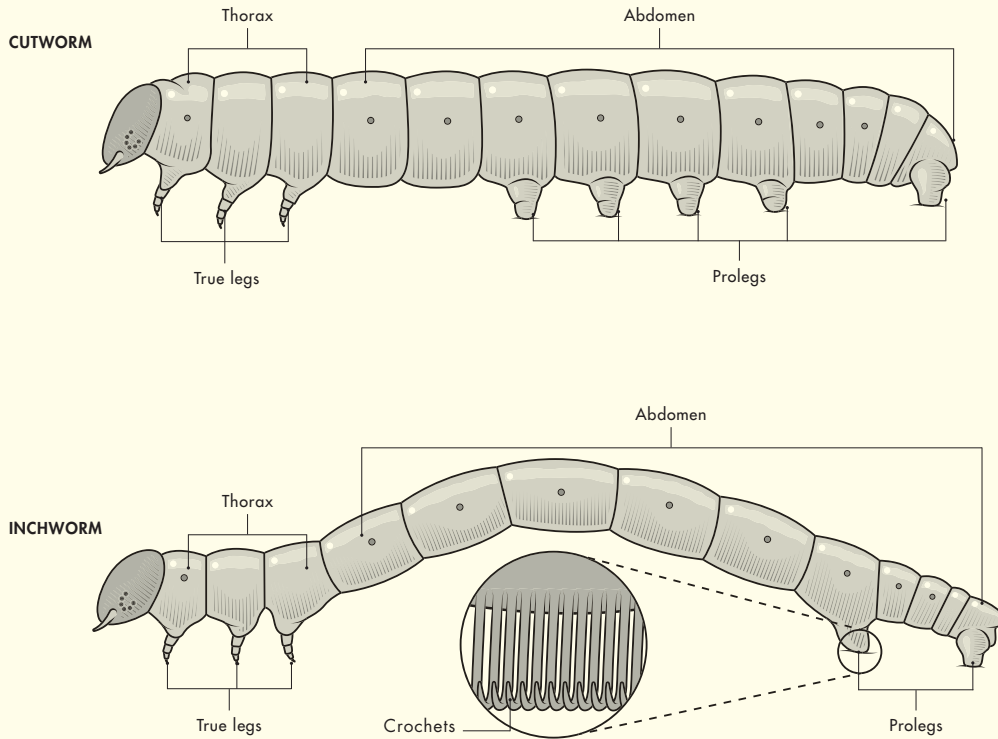


memory. Pavlov's dog-style experiments have proved that, by combining an odor with an electric shock, caterpillars of the Tobacco Hornworm (*Manduca sexta*) can be trained to avoid the odor and that memory persists through metamorphosis to the insect's adult stage. This suggests that whatever positive memories caterpillars acquire about their host plants may also pass to the adult moth, thus influencing the female's choices during oviposition. Like most insects, caterpillars are born with instincts that are quickly

modified by experience. For instance, when a polyphagous caterpillar (one that can develop on many host plant species) begins feeding and becomes accustomed to one host plant, it becomes less inclined to accept another.

↑ The spines of a mature Royal Walnut Moth caterpillar (*Citheronia regalis*) are a formidable defense against birds.

CATERPILLAR LEG ARRANGEMENT



MOVING AROUND

While caterpillars may appear multi-limbed, like all other insects, they have six true legs on the first three thoracic segments. In addition, however, they have a variable number of fleshy projections in the form of prolegs, which are equipped with crochets (sets of hooks) used for grabbing onto the host plant. Most caterpillars have five pairs of prolegs—four in the middle of the body and one at the end. However, the majority of inchworm (Geometridae) species have only two pairs on the last (tenth) and sixth abdominal segments; this helps distinguish the Horned Spanworm (*Nematocampa resistaria*) from the very similar-looking Curve-lined Owlet Moth (*Phyprosopus callitrichoides*),

Abdominal segments

Prolegs on a caterpillar's abdominal segments assist locomotion. Depending on the family, they can vary in number and location. A cutworm (Noctuidae) has them on the 3rd through 6th and last abdominal segments, while most inchworms (Geometridae) have only two pairs—on segments 6 and 10.

which has three pairs of prolegs, as both are found in the southern United States. Inchworms have an “inching” (earth-measuring) rather than a crawling gait, as do other caterpillars with a reduced number of prolegs, including the loopers, such as the Cabbage Looper (*Trichoplusia ni*).

In prominent moths (Notodontidae), such as the Puss Moth (*Cenura vinula*), found throughout Europe,

the anal prolegs may be reduced and modified, giving them a very characteristic posture, with a raised tail end. Other caterpillars that tend to have reduced prolegs are those that move little but, instead, tunnel through plant tissue, hollow stems, roots, or inside a single leaf (as leaf miners do). Limacodid larvae, so-called “slug” caterpillars, have no crochets, but may have pads and suction cups instead, which enable them to stick to smooth upper leaf surfaces without having to spin a silk pad, although the wet secretion from silk glands helps them adhere to the leaf.

Most caterpillars make silk, which they use in various ways: to drop from a host plant when escaping a predator and then hoist themselves back again, to build a shelter or a communal nest, to attach themselves to a plant during molting, and to make a cocoon for the pupa. Silk proteins flow from paired silk glands—long organs running on both sides of the gut—and are combined into silk inside the spinneret. Unlike spiders whose spinneret is at the tip of the abdomen, a caterpillar’s spinneret is on its head, protruding downward from between its labial palps.

↘ An inchworm, one of nearly 250 species in the genus *Eois*, navigating through the terrain in search of a place to pupate.



PARAGLIDING LARVAE

Some newly hatched (neonate) caterpillars crawl long distances, and Gypsy Moth (*Lymantria dispar*) neonates can also disperse by “ballooning.” Aided by a silk thread they produce and their fluffy morphology, they paraglide through the air, assisted by the wind. As a result, siblings from the same egg mass may end up feeding far from each other as mature caterpillars, spreading the population over available food sources. If a group of caterpillars of the Laurelcherry Smoky Moth (*Neoprocris floridana*) consumes all the leaves on one tree, they will, like trapeze artists, swing on the wind suspended on long silk threads until they land on another host tree.

← Caterpillars of the Laurelcherry Smoky Moth (*Neoprocris floridana*) will swing on a silk thread from a defoliated tree to find a new host plant.



☞ The Curve-lined Owlet Moth caterpillar (*Phyprosopus callitrichoides*) mimics a hanging dry leaf not only with appearance but also by swinging side to side imitating leaf movement with the wind.

☞ The Echo Moth caterpillar (*Seirarctia echo*) has a warning pattern similar to that of a coral snake.