CONTENTS

AMERICAN MOTH-BUTTERFLIES (HEDYLIDAE)

Hedylidae represent only about 0.1 percent of butterflies, but they deserve a mention in this book because they are very important for understanding the evolutionary connection between butterflies and moths. Despite their overall moth-like appearance, they share some 20 morphological characteristics with butterflies.

IDENTIFICATION THROUGH TRIANGULATION

Currently, all 35 species of Hedylidae are placed into a single genus, *Macrosoma*. The author of the first life history of a species in this genus (*M. heliconiaria* from Mexico) experienced one surprise after another as he reared the caterpillars he had found.

FROM DAY TO NIGHT AND BACK AGAIN

Butterflies are generally diurnal, with some exceptions, like the crepuscular (flying at dusk) owl butterflies and a few odd skippers that are active at dusk or at night. Hedylids and skippers are thought to have split from a common diurnal ancestor more than 100 Mya. From field observations, it seems that some *Macrosoma* have, over the course of evolution, partially reverted to a diurnal lifestyle, flying both by day and by night, while others have continued to be fully nocturnal.

Based on the morphology of the slender, hairless caterpillars with prominent head horns, the author thought he was rearing a satyrine butterfly, a member of the family Nymphalidae. When the caterpillars pupated, however, he became certain that the species was actually part of another butterfly family, as the chrysalides were typical of Pieridae. So, when the hedylid "moths" (as they were thought to be at the time) popped out of these chrysalides, he was flabbergasted. Imagine his surprise if he were to learn that today this species is classified as a butterfly.

CROSS-CHECKING WITH DNA

Since then, these nocturnal butterflies have been studied in great detail. DNA sequencing and analysis has confirmed their position as one of the most ancestral of butterfly lineages, together with swallowtails and skippers. Another exciting discovery was their ultrasonic "hearing" abilities—a result of special organs located on the wings that evolved to detect ultrasound in order to avoid bat predators.

← *Macrosoma hyacinthina* is in the only genus representing the family Hedylidae, in which the immatures resemble butterflies, but the adults look and behave like moths.

SKIPPERS (HESPERIIDAE)

According to the latest DNA-based evolutionary hypothesis, around 90 Mya, skippers and hedylids parted ways with swallowtails, with the first distinct skippers appearing 20 million years later. There are about 3,500 described skipper species today, grouped into 11 subfamilies, with new species being added every year.

AS FAST AS A FLASH

For ecologists and evolutionary biologists, skippers are a treasure trove, as they demonstrate tremendous versatility and a variety of unique adaptations. Their fast reflexes and quick, jumping flight make it difficult for birds to catch them. If one takes a photo of a perching skipper with the flash on, it frequently reacts to the pre-flash in the camera so quickly that the butterfly will be captured in flight every time.

AFRICAN GIANT SKIPPER

There are exceptions to the speedy escape strategy, even among skippers (see page 45). Caterpillars of the African Giant Skipper, *Pyrrhochalcia iphis,* for example, feed openly in groups—a sure sign that they have other means of protection. Indeed, they feed on toxic plant families, such as Anacardiaceae (to which cashews and poison ivy belong), which can endow them with chemical defenses.

As adults, these skippers are brightly colored, reach 4 in (10 cm) in wingspan, and fly relatively slowly. This species is part of the subfamily Coeliadinae, the most ancestral among the skippers. Thus, it is possible that the unique features of this butterfly reflect the earlier evolutionary traits of skippers, with younger skipper species evolving a more compact size and faster flight to compensate for their lack of chemical defense.

NYMPHS OF THE EVENING

The fast, erratic flight of skippers gained them their common name, but their Latin family name, Hesperiidae, is more poetic. "Hesperos" means "evening" in Greek and, in mythology, the "Hesperides" refers to the nymphs of the evening. Although skippers are generally active during the day, there are indeed many skipper species that are active late in the evening or even after sunset. Some groups of skippers in the Neotropics, such as the genus *Bungalotis*, are easier to observe by attracting them to light, as they are normally active right after dusk or before dawn. Some of these nocturnal skippers have been found sleeping in caves during the day—*Nascus paulliniae* from South America has even been observed actively feeding late at night.

ESCAPE MIMICRY

While most skippers are dark-colored and understated, some have iridescent colors on their upper wing surfaces, which they display readily when perching. In addition to functioning as signals to members of their own species, both male and female, the iridescent markings are thought to remind birds that their owners are too fast to be worth the chase.

Generally, toxic mimetic species fly slowly and signal to birds with their bright, conspicuous coloration: "Avoid eating me if you don't want an unpleasant taste in your mouth." In contrast, skippers engage in escape mimicry, conveying the message: "The last time you chased me, you wasted lots of time and energy and went hungry—it's not worth it." Mimicry among adult skippers results in their caterpillars differing from each other more than their adult forms do (see pages 44–45).

↓ A long proboscis allows skippers to reach nectar in deep flowers, but occasionally they will use it to feed on bird droppings, excreting some water to moisten their meal.

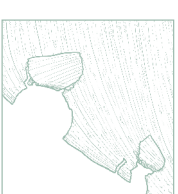
DIVERSITY OF SKIPPER CATERPILLARS

Skipper caterpillars frequently have eyespots on brightly colored heads or on the last abdominal segments. These spots and their body stripes can help scientists distinguish species that otherwise would be misleadingly similar. In fact, 10 different skipper species were once differentiated based on DNA and caterpillar morphology in Costa Rica, hiding under the same winged disguise.

UNIQUE DEFENSES

Skipper caterpillars are edible to a wide variety of predators and have hence developed a set of unique defenses. For example, they frequently build shelters, either by pulling together leaf margins or by cutting out parts of the leaf and using them as building material, making extensive use of silk thread. Yucca skippers of the genus *Megathymus* burrow into the roots of their host plants and create silk tunnels underground. The caterpillars of the Brazilian Skipper, *Calpodes ethlius*, which can be found from the United States to Argentina feeding on canna lilies and alligator-flag plants, have translucent skin, so that one can observe their internal organs at work—if you can spot the caterpillars!

↓ Skipper caterpillars, such as this Brazilian Skipper on an alligator flag plant (*Thalia*), make shelters by cutting and folding the leaves, which they secure with silk. To avoid predators, the caterpillars come out to feed at night.



→ (A) Brazilian Skipper, (B) African Giant Skipper, (C) Long-tailed Skipper. Among these species, only the caterpillars of the African Giant Skipper feed in the open during the day. They are colored aposematically and sometimes feed in groups, indicating that they are probably toxic to predators.

WHITES AND SULPHURS (PIERIDAE)

About 75 Mya, the lineages of white and sulphur butterflies began diversifying. Together with the highly mimetic Neotropical tribe of Dismorphini butterflies and a small genus *Pseudopontia* found in West Africa, they form the family Pieridae. Today, this family consists of over 1,000 species grouped into over 70 genera.

THE GREAT IMITATORS

When the 19th-century naturalist Henry Walter Bates (1825–1892) was exploring the Brazilian rainforest, he noticed a curious fact: some clearwing butterflies appeared to have three pairs of walking legs, while others only had two. This consternating observation was, in fact, an example of perfect mimicry between Dismorphini and the brush-footed butterflies of the tribe Ithomiini.

Dismorphini go to such lengths to copy ithomiines because they themselves are not toxic while ithomiines are memorably unpalatable to predators. This type of mimicry is known as "Batesian," in honor of the person who first described it.

↓ *Dismorphia theucharila* (left) is a nearly perfect mimic of *Ithomia arduinna*, even though it is a pierid.

While its ithomiine model has four walking legs, *Dismorphia* has six, giving its identity away to keen-eyed observers.

→ The Provence Orange-tip, *Anthocharis euphenoides*, is one of about two dozen orange-tip butterflies that feed on mustards throughout the Holarctic region, mostly in warmer climates. The caterpillars are well-adapted to consuming these cruciferous plants, which are rich in glucosinolates.

BRIMSTONES AND CABBAGE WHITES

The mimetic species of Pieridae described earlier in this chapter (see page 46) are more exceptions than the rule when it comes to this family. The typical shapes and colors of pierid butterflies are best exemplified by brimstones and cabbage whites.

LONG-LIVED BRIMSTONES

The caterpillar of the Common Brimstone, *Gonepteryx rhamni*, feeds on buckthorns (*Rhamnus*) and derives its Latin name from theirs. This butterfly has an interesting, well-researched biology: it overwinters as a reproductively inactive adult, then mates and lays eggs in the spring, which makes it one of the longest-lived species, with adults persisting for up to 10 months.

↓ The males of *Gonepteryx rhamni* are more lemon in color than the females, thanks to an additional pigment, and their wings reflect light in the UV spectrum that we cannot see.

SEQUENCING GENOMES

Sequencing whole genomes of animals, including butterflies, is becoming routine and can shed light on an organism's evolution and physiology. Doing so for the Small Cabbage White, *Pieris rapae*, demonstrated that its population in North America originated from a very small number of individuals. The same study also characterized the proteins responsible for directing plant defensive compounds into non-toxic chemicals during the metabolic process. Other proteins called pierisins are thought to help the immune system defend against wasp parasitoids, making some researchers think they could be potential candidates for anti-cancer drug research.

HIDDEN PATTERNS

Males and females of *Gonepteryx* sport different color patterns, a result of males having two color pigments and females, only one. The bright, lemon color of the males changes slightly depending on the angle of incidence and shows up as a different pattern under ultraviolet light. This scattering of UV light in males, which is absent in females, results in the male butterflies having a slight iridescence. Males of *G. cleopatra*, found around the Mediterranean, are further adorned with a bright orange patch. See page 68 and Chapter 9, pages 114–116 for more on sexual dimorphism.

YOUR TYPICAL WHITE BUTTERFLY

The genus *Pieris* represents the typical, pure white butterfly—dashing erratically through fields, briefly stopping at flowers, all but consulting a pocket watch. Under this guise hide nearly 40 different species, which include the Large Cabbage White (*Pieris brassicae*), common to Europe; the Small Cabbage White (*P. rapae*) that is now found worldwide; and the Great Southern White (*Ascia monuste*) from the American tropics.

CABBAGE AND PEA LOVERS

The pierid family has a long history of coevolution between host plants and butterflies. The subfamily Coliadinae, which includes clouded yellows (*Colias*), small grass yellows (*Eurema*), and larger sulphurs (for example, *Phoebis*), frequently feed on legumes.

Whites belong to the Pierinae subfamily, which often relies on cruciferous host plants, but there are many exceptions. It is the most recently derived among the four subfamilies, diversifying approximately 50 Mya, and is now represented by six tribes, such as orange tips (Anthocharini), wood whites (Leptosiaini), and, of course, the whites (Pierini).

MASS MIGRATIONS

There are some notable exceptions to the sulphurs' affinity for legumes. For example, the spectacular mass migrations of the Lyside Sulphur, *Kricogonia lyside*, which can be observed in subtropical scrub habitats from Texas to Latin America, are precipitated by their

SULPHURS AND LEGUMES

Sulphur butterflies favor legume host plants, which can be found from suburban backyards to freezing stone outcrops in the Himalayas. The Cloudless Sulphur, *Phoebis sennae*, migrates with the seasons along the southeastern coast of the United States, keeping its eye out for its caterpillars' favorite, the partridge pea. Some species favor senna and cassia plants for oviposition, while *Colias* feed on alfalfa, vetches, pea-shrubs, and goat-thorns, among others. During the brief summers in the mountains of the Caucasus and Central Asia, one can find endemic *Colias* species zooming around at great speeds among these plants at high elevations, where the weather is punishingly cold for most of the year.

FEEDING ON MISTLETOE

Butterflies can diversify and make themselves more robust through the tactical use of host plants, including switching to different ones when it suits them. There are some remarkable stories of host plant adaptation and resulting diversification in the Pierini tribe. For example, caterpillars in the genus *Delias* feed almost exclusively on mistletoe in Southeast Asia and the islands of the Pacific. Thanks to the chemical defense arsenal they have amassed from their mistletoe diet, the *Delias* butterflies have become quite successful and have radiated into over 200 very colorful species.

pursuit of lignum vitae (*Guaiacum officinale*), a shrubby plant in the caltrop family that's like mother's milk to their caterpillars.

Like the sulphurs, the Great Southern White, *Ascia monuste*, can travel high above the ground in such great assemblies that these mass migrations are easily detected by radar (see Chapter 8, pages 102–103 for more on migration). This species ranges from Florida to Argentina and is often lamented for being a frequent pest of cruciferous crops.

INTERTWINED WITH HUMANS

When humans migrate, they usually take their crops (and pests) with them. The history of the infamous Small Cabbage White, *Pieris rapae*, is quite interesting because it is closely tied to the spread and intermingling of human populations across the globe. Based on DNA analysis, *P. rapae* spread from its native range in the Mediterranean to northern Europe first. From there, it made its way to East Asia in the 18th century and then on to North America in the 19th century. By the first half of the 20th century, it had finally made it as far as Australia (via New Zealand).

↓ Caterpillars of the Small Cabbage White, *Pieris rapae,* derive defensive compounds from cabbage leaves called pinoresinols, which deters ants from attacking them.

BRUSH-FOOTED BUTTERFLIES (NYMPHALIDAE)

Nymphalidae, or "brush-footed" butterflies, form the largest and most diverse butterfly family, creating an umbrella for many unlikely relatives. They began to diversify 80 Mya, giving rise to very different subfamilies, such as the snout butterflies (Libytheinae) and milkweed and clearwing butterflies (Danainae). The snout butterflies form a very compact group of about a dozen species, some of which feed on sugarberry trees as caterpillars. As adults, they have uncharacteristically long palpi (for more about palpi, see Chapter 8, page 96), for which they received their common name.

TOXIC BEAUTIES

Milkweed butterflies (tribe Danaini) are characterized by their large size, slow flight, and affinity for milkweed host plants, such as *Asclepias* or *Cynanchum* (see Chapter 6, page 81). The smaller and more slender clearwing butterflies (tribe Ithomiini) often have partially or completely clear wings, making them almost invisible to predators. Others in this tribe have tiger-striped, orange-and-black wing patterns. These butterflies prefer to fly in the dark understory near their nightshade host plants and form mimicry rings throughout the Neotropics (see Chapter 9, page 117).

↓ A close-up of the head of the American Snout, *Libytheana carinenta* (left), versus that of the Painted Lady, *Vanessa cardui,* shows the long palpi for which the snouts got their name. Palpi have many sensilla and can detect the scent of ripe fruit.

→ The Neotropical Menapis Tigerwing, *Mechanitis menapis,* and the Southeast Asian Rice Paper Butterfly, *Idea leuconoe,* belong to the Danaine subfamily, in which bright colors serve as a reminder to predators of the butterflies' toxicity. Caterpillars also receive chemical protection from their host plants.

I SPOT AN EYESPOT

The most recently derived lineage of Nymphalidae is the subfamily Satyrinae, which today unifies groups that used to belong to several different families. Most of these butterflies are small- to medium-sized with eyespots and an erratic, jumping flight pattern. Some break-off lineages, like the subtribe Euptychiina, underwent a tremendous radiation in South America, with an estimated 500 species that occur very locally in association with endemic bamboos, grasses, and occasionally lower plants, like mosses.

ELUSIVE NYMPHS

Some of the species that fly in the dark understory of South American rainforests, such as species of *Haetera* and *Cithaerias* in the tribe Haeterini, no longer have much need for color. Over time, they underwent such a drastic reduction in the number of wing scales that their wings became mostly transparent, with only hindwing eyespots left for adornment. This pattern fools predators into attacking only the wing margins, deflecting attacks from the vital head region. As a result, even if these practically invisible butterflies are spotted by a keen-eyed predator, they still have a good chance of escaping largely unharmed, with just a bit of their wing missing.

A FONDNESS FOR FERMENTATION

Satyrines are frequently referred to as "wood-nymphs," because, unlike many of their other nymphalid relatives, they can be found inside forests, flitting around just above the forest floor. This peculiar behavior can be tied to the diet of the adult butterflies—while they do occasionally feed on flowers, they are very fond of fermented fruit (hence their being named after the bibulous companions of Bacchus). And what better place to find some rotting fruit than on the forest floor?

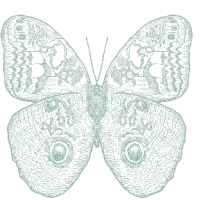
"DARWIN'S BUTTERFLIES"

In the West Indies, the genus *Calisto* radiated across different islands and separate mountain ranges into over 40 species, accounting for about 20 percent of Caribbean butterfly fauna. Why do so many similar species occur in one place? It is a similar phenomenon to that of Darwin's finches, the little birds in the Galapagos Islands that radiated into species with different diets and beak shapes. The rise and fall of sea levels caused populations of *Calisto* species to be separated for a long enough time to undergo speciation and to be reunited as non-interbreeding species. Over 30 million years, such processes led to a great diversity of closely related species utilizing different types of grasses as caterpillar food in close proximity but sometimes in vastly different habitats, from xeric lowlands to humid mountain bogs above 6,000 ft (2,000 m) of elevation (see Chapter 2, page 30).

OWL BUTTERFLIES

The Neotropical tribe Brassolini is comprised mostly of larger species that feed as caterpillars on the Zingiberales order of plants, from heliconias (such as wild plantains and lobster claws) to red ginger. Some of these species, such as the Forest Giant Owl, *Caligo eurilochus*, can even be a pest on cultivated bananas. The wing patterns of *Caligo* butterflies actually do resemble avian eyes, and it is widely believed that these patterns serve as a warning to predators.

↓ Owl butterflies have eyespots that resemble those of birds of prey, thus supposedly dissuading attacks by smaller birds.



There are 17 genera recognized as members of Brassolini, from the medium-sized *Bia* to the giant *Caligo*, which reach over 6 in (16 cm) in wingspan—all found in rainforests, from Mexico to Argentina. They have become a mainstay of live butterfly exhibits because they are easy to rear, large, and eye-catching.

THE GREAT RADIATION OF NYMPHALINAE

Between the time that the snout butterflies and danaines (see page 52) evolved some 75 Mya and the appearance of satyrines 20 to 30 million years later, brush-footed butterflies underwent a rapid radiation. As a result, the family today is comprised of a dozen subfamilies, one of them being Nymphalinae.

FAMILIAR GARDEN BUTTERFLIES

Some nymphalid butterflies, such as peacocks and tortoiseshells (*Aglais*), buckeyes (*Junonia*), admirals and painted ladies (*Vanessa*), and Mourning Cloaks (*Nymphalis antiopa*), may be very familiar to people in Europe and the United States, where the number of butterfly

FRUIT FLIES OF THE BUTTERFLY WORLD

Other members of the nymphalid family that frequently form nocturnal roosts and can be found in live butterfly exhibits are the longwing butterflies of the genus *Heliconius*. They fly slowly, are colorful, and are easy to propagate on passion vines. However, their fame does not end there: some 50 species of *Heliconius* frequently hybridize with each other, creating unexpected wing patterns. They are also adept at copying each other's appearance, often forming mimicry rings. In the last 50 years, the genus has gained a foothold as the new "fruit flies" for genetic studies and other research (see Chapter 9, pages 106–117), with many PhD degrees defended and articles published about them every year.

species per capita of butterfly enthusiasts is very low compared to more tropical countries. Other genera, such as daggerwings (*Marpesia*), which sport long hindwing tails and bright colors, are more familiar to people who live in South America or those visiting live butterfly exhibits, where these butterflies are frequently on display.

COMMUNAL SLUMBER

Like other animals, butterflies sometimes turn to "safety in numbers" as a strategy for survival. Nymphalids exhibit such clustering behavior, not only as eggs and caterpillars, but also as adults. For example, daggerwings and cracker butterflies (*Hamadryas*) form "roosts," aggregations of butterflies that come together to fold their wings up for the night. If one of the roosting butterflies is startled by a predator, they all fly up at once, allowing most of the participants to escape unscathed.

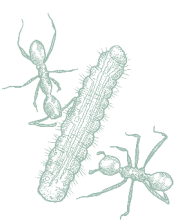
← The European Peacock, *Aglais io,* is one of the most beautiful and common butterflies found in Europe. These butterflies hibernate as adults and feed on nettles as caterpillars.

METALMARKS (RIODINIDAE)

Riodinidae is a family of small but very diverse butterflies that diverged over 70 Mya with their sister family Lycaenidae. They are mostly found in the Neotropics, with only a small representation in the Old World. The family is subdivided into seven tribes and around 130 genera, with more than ten times as many species.

FLEXIBLE GROUND PLAN

Riodinids are unified by similarities in wing veins and immature stages but are otherwise extremely variable. They range from species that have spectacular, shiny wings with long tails (like *Rhetus*) to amazingly accurate mimics of the clearwing butterflies (like *Stalachtis*). Some genera, such as *Calydna* or the numerous, far-ranging *Calephelis* are tiny—less than 3/4 in (2 cm) in wingspan—with a fluttering flight that makes them easy to confuse with small, day-flying moths. By contrast, metalmarks of the genus *Eurybia* in the New World or of the genus *Dodona* in Asia are larger, achieving a 2 1/2 in (6 cm) wingspan, and resemble miniature brush-footed butterflies in appearance and demeanor.



↙ Found in South America, the caterpillars of *Adelotypa annulifera* live on bamboo shoots and enjoy a symbiotic relationsip with ants that defend them in exchange for sugary secretions. The ants also don't attack visiting adult butterflies.

→ From the top: *Echydna punctata, Hyphilaria parthenis, Mesosemia loruhama.* These are just some examples of Neotropical riodinids. Male butterflies in this family frequently perch on leaves, monitoring their territory for females. This perching behavior, as well as the time of day at which it occurs, is species-specific.

FROM THE NEW WORLD AND BACK

There are two subfamilies of metalmarks recognized today: Riodininae and Nemeobiinae. They share a common evolutionary history, and both form mutualistic relationships with ants. Many riodinid caterpillars have special adaptations that allow them to signal to ants and reward them with sweet plant secretions. These ants, tamed by the caterpillars, remain aggressive toward other insects and vertebrates, thus providing these wily caterpillars with protection from predators.

OVER 90 PERCENT NEOTROPICAL

The riodinid family is thought to have originated in the Neotropics, and today over 1,300 species of riodinids can be found in the Latin American tropics, where they greatly diversified their shape, size, and natural history over millions of years. There are about 25 species that are found as far north as the United States, belonging mostly to the genera *Calephelis*, *Apodemia*, and *Emesis*. These species tend to have more conventional life histories than their jungle relatives.

SWEETENING THE DEAL

In the Neotropics, *Adelotypa* caterpillars feed on bamboo shoots, prompting the production of extrafloral nectar that draws ants and butterflies to these sweet droplets (see page 58). The ants do not display any aggression toward the butterflies, indicating that there must be some chemical and/or visual cues by which the ants accept them. On the other hand, *Pachythone xanthe* caterpillars, which feed on scale insects tended by Azteca ant shepherds, do not rely on the good graces of the ants. Instead, the caterpillars have developed a shield-like carapace for protection, and for added security, they also make use of sugar-secreting organs to bribe the ants.

TIMING IS EVERYTHING

The reproductive rituals of metalmark butterflies have attracted the attention of researchers, since these butterflies mate during very specific hours of the day. Usually, the coupling is preceded by territorial displays, in which males perch at deliberately chosen locations. Males sometimes congregate (a behavior known as "lekking") and engage in contest flights and other interactions, which can even involve non-violent contact that has been compared to Sumo wrestling. Mating occurs shortly after a female enters the lekking territory (see Chapter 7, page 90 and Chapter 8, page 105). The primary reasons for lekking in Riodinidae, as in most other insects, is thought to be attracting females to the area.

OLD WORLD RIODINIDS

The other subfamily of metalmarks that is recognized today, Nemeobiinae, has a more complicated origin: it is mostly found in the Old World, where it diversified further by spreading to Asia, Africa, and Madagascar. Species like the spectacularly colored Malay Red Harlequin, *Paralaxita damajanti*, can be found from Borneo, Java, and the Malay Peninsula to southern Vietnam. The four species of the genus *Saribia* are found exclusively on Madagascar and sport intricate "false-head" patterns (see page 65 and Chapter 12, page 150). There is only one European member of the family, the Duke of Burgundy, *Hamearis lucina*, which looks like a miniature fritillary but has a caterpillar typical of riodinids that feeds on primulas. On the other side of the world, *Styx infernalis*, a highland species from Peru, resembles a pierid butterfly and, along with the Costa Rican Metalmark, *Corrachia leucoplaga*, is thought to have resulted from dispersal of an Old-World lineage to the Americas.

↓ *Styx infernalis* was at some point considered its own family of Lepidoptera but turned out to be a New World species of the mostly Old World subfamily of Nemeobiinae.

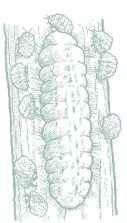
GOSSAMER-WINGED BUTTERFLIES (LYCAENIDAE)

The family Lycaenidae encompasses eight subfamilies. Among these are hairstreaks (Theclinae), blues (Polyommatinae), and coppers (Lycaeninae), which are more common across Europe, more numerous, and more recently evolved. The two ancestral lineages, comprising sunbeams (Curetinae) and harvesters and woolly legs (Miletinae), are mostly found in Southeast Asia, Indomalaya, Australia, and the Afrotropics.

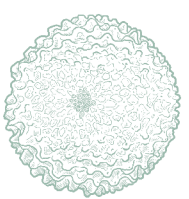
A CATERPILLAR IN APHID'S CLOTHING

The subfamily Miletinae is less known than blues, hairstreaks, or coppers, but its species have remarkable life histories. For example, the caterpillar of the Harvester Butterfly, *Feniseca tarquinius*, the only miletine butterfly in North America, feeds not on plants but on woolly aphids, sometimes using their remains as camouflage. The evolution of this unusual behavior may be explained by the adult butterfly's affinity for the sweet secretions of these aphids and the major benefit gained through carnivory: transition from egg to pupa in just over a week.

↓ Carnivorous Harvester caterpillars feed on woolly aphids, which allows them to develop rapidly.



↓ The eggs of Lycaenidae, such as this one of the Common Blue, *Polyommatus icarus*, are sturdy and finely sculpted.



→ Blue butterflies in the genus *Polyommatus* include over 200 species whose males have bright upper-side coloration while the females are dark. They feed as caterpillars on various members of the pea family, such as the bird's-foot trefoil (*Lotus corniculatus*), vetches (*Vicia*), and crownvetches (*Securigera varia*).

MASTERS OF ILLUSION

The subfamily Theclinae includes many butterflies that have a "false head": a pattern that converges on a spot at the tip of the hindwings, frequently accompanied by a little "tail." By moving their hindwings back and forth in a scissor-like motion, the butterfly gives the impression that the hindwing spot is its head and the wing tails are antennae. As a result, small ambush predators, such as jumping spiders and crab spiders, which lie in wait on flowers, attack these appendages, allowing the butterfly to get off lightly!

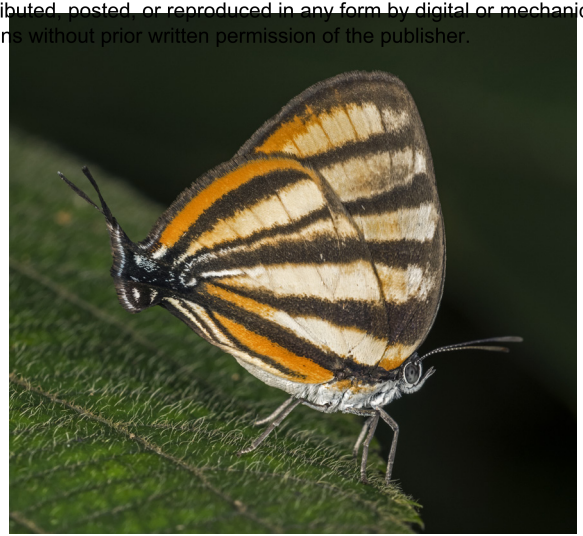
CONVERGENT EVOLUTION OF "FALSE HEADS"

The false-head pattern of Theclinae, beautifully exemplified by members of the genera *Arawacus*, *Thecla*, *Favonius*, *Atlides*, *Semanga*, and *Iraota*, can also be found in other families of Lepidoptera. It must have proven an extremely effective strategy for surviving lethal attacks by predators, as it has repeatedly evolved separately in families as diverse as swallowtails, nymphalids, skippers, and geometrid moths.

The same strategy is found in other groups of insects and even in vertebrates. For example, some fish, like the red drum (*Sciaenops ocellatus*) in the United States or the tailspot blenny (*Ecsenius stigmatura*) in the Western Pacific, have prominent eyespots on their tails to deflect predator attacks. But no group of animals has perfected this illusion better than the theclines!

TOXIC OFFSHOOTS

Some Theclinae species developed alternative defense strategies against predators by adopting toxic host plants. The Great Purple Hairstreak, *Atlides halesus*, supplements its false-head pattern with a penchant for feeding on mistletoe and a warning coloration to remind predators of this fact. Others, such as the Atala Butterfly from Florida and the Caribbean, as well as its Latin American relatives in the genus *Eumaeus*, sequester cycasin from their host plants, a compound that is highly toxic to vertebrates.



↑ *Arawacus separata*, Colombia. Lines converging on a tail and a spot attract even more attention to the "false head," which can be lost without harm to a fooled predator.

ENGINEERING ON SMALL SCALES

Many Eurasian theclines, like species in the genus *Chrysozephyrus*, have a spectacular iridescent coloration that is the result of nanostructures on the wing scales (see Chapter 9, page 110). Their eggs, which serve as the overwintering stage, must withstand harsh, cold conditions and inundations with water. The result is an elegant engineering solution executed on the microscale: spiky domes resembling coral but with a mathematical regularity in structure.

BUTTERFLIES ON FIRE

The subfamily Lycaeninae are colloquially known as "coppers" in English, while in other languages their common name connotes "fire." Indeed, these butterflies look like ephemeral sparks flying across the verdant backdrop of meadows, appearing and disappearing as their wings open and close. This behavior signals to their mates and rivals and may also help to evade predators. Some coppers, such as *Athamantia* species in Central Asia, have little "tails" on their hindwings, creating false-head patterns like those of Theclinae.

COMMON COPPERS

The typical appearance of Lycaeninae is exemplified by the Scarce Copper, *Lycaena virgaureae* (once upon a time common in Europe), whose males have shiny, orange-red upper wing surfaces adorned with elegant black margins. Females have further adornment in the

UNDERSTANDING COLOR

Observing the fiery sheen of Lycaeninae wings as the sunlight bounces off them in the split-second between wing flaps, one can't help but wonder what kind of trickery creates such brilliant metallic colors. Researchers are able to probe this question with a combination of reflectance spectroscopy and scanning electron microscopy. With these two techniques, they can quantify how light-scattering behavior changes with miniscule alterations to the nanostructural patterns of the wing. The results can be surprising: a dull brown wing can be transformed into an iridescent metallic red simply by halving the distance between the crossbars that connect the main ridges in the wing scales.

form of black spots that stand out on this fiery orange backdrop. Another well-known member of the genus *Lycaena* (which includes over 80 species) is the Small Copper, *L. phlaeas*. This red-and-black butterfly is among the most widespread species in the world, ranging from Eurasia to northern Africa to North America.

CHEWING ON SORREL

Like many other members of the genus *Lycaena*, the caterpillars of the Small Copper feed on docks or sorrels (*Rumex*), with the eggs serving as the overwintering stage. Despite the fact that coppers feed on a relatively common host plant, their survival is not always guaranteed. The Large Copper, *L. dispar*, became extinct in the British Isles in the middle of the 19th century, when the damp habitats favored by the butterflies were converted to agricultural land.

← A Large Copper, Poland. This species is widely distributed throughout Europe, but unfortunately the subspecies native to Britain became extinct in the mid-19th century.

BLUES AREN'T ALWAYS BLUE

The subfamily Polyommatinae, colloquially known as "blues," comprises a number of common species whose males display sky-blue, sometimes iridescent, patterns on the upper surface of their wings. Female blues tend to be more modestly colored. In the European Adonis Blue, *Lysandra bellargus*, for example, they are a muted brown with orange spots.

SEXUAL DIMORPHISM AND SPECIATION

Rapidly evolving coloration and the stark difference between male and female wing patterns in this subfamily suggests that coloration plays a big role in sexual selection. Studies on the over 200 species in the genus *Polyommatus* found that the most closely related species actually had the largest variation in color. This suggests that these nuances in color are for the benefit of the female of the species, which relies on hues to recognize potential mates.

ENDANGERED MYRMECOPHILES

The endangered Miami Blue Butterfly, a subspecies of *Cyclargus thomasi,* feeds on nicker beans along the coast of the Florida Keys. This tiny butterfly has a non-obligatory association with ants, such as the Florida carpenter ant (pictured), which receive a sweet secretion from the caterpillars and in exchange do not attack them as they would otherwise. The Large Blue Butterfly, *Phengaris arion,* now rare in Europe, is not so sweet: its caterpillars parasitize *Myrmica* ant nests by chemically mimicking the ant queen, thereby tricking worker ants into feeding them at the expense of the ant colony.

CHROMOSOME EVOLUTION

Scientists who study the evolution of chromosomes are finding some butterfly genera to be especially fruitful groups for investigation, as there are many intriguing phenomena. Larger taxonomic groups, such as butterfly families, generally have similar numbers of chromosomes, but there are often sudden, unexplained deviations. The blues in the genus *Polyommatus* are such an exception, and hold the title for having the most chromosomes in all non-polyploid (i.e., without duplication of chromosomes) animal species. In *P. atlanticus*, its nuclear DNA is "packaged" into a staggering 452 separate chromosomes!

VENTRAL WING PATTERNS

When blues are not in flight or mating, these butterflies tend to keep their wings closed, showing the world their less brilliant underside patterns, which often feature a series of concentric circles. Spotted patterns are helpful in visually disrupting the shape of a butterfly, assisting in camouflage. At close range, the marginal spots serve as deflectors of attacks from the head to the wing margin. Zebra blues (*Leptotes*), which include around 30 species predominantly found in Africa, sport not only spots but also little hindwing tails and a single bright spot, amplifying the "false-head" pattern similar to that of hairstreaks (see page 64).

CRYPTIC CATERPILLARS

Polyommatinae are mostly associated with herbaceous host plants, especially favoring nitrogen-rich legumes. Females frequently lay their eggs in the flowers themselves and on hatching, the caterpillars start their lives munching on succulent blooms, gaining both shelter and nutrition. As the caterpillars grow and pupate, they remain cryptic, camouflaged among petals and leaves. Since it's not possible to elude ants even with the best camouflage, these caterpillars produce sweet secretions to bribe these soldiers.

FOUR LIVES IN ONE

Metamorphosis is, in essence, about the division of labor. There are many benefits to having a complete cycle of metamorphosis with four stages of development: the embryo-housing eggs, the fast-growing caterpillar, the shape-shifting pupa, and the mate-seeking and egg-producing and -dispersing adult. This strategy gives an organism flexibility and grants each individual, population, and species a higher chance of survival.

ANY STAGE CAN DIAPAUSE

The egg can serve as a simple embryo incubator that endures no more than a week, or it can be an overwintering bunker that protects the fragile organism from harsh external conditions. In fact, any stage of development can enter diapause (a physiologically inactive stage) to deal with adverse circumstances, including the butterfly itself. The adult is usually only on the wing for a couple of weeks but can live up to 10 months, when necessary.

Every species has its own strategy. The Brown Hairstreak, *Thecla betulae*, glues its eggs to bird cherry twigs to see out the harsh winter. In many satyrines, such as the North American Common Wood-nymph, *Cercyonis pegala*, it is the newborn caterpillars that are the diapausing stage. In the Hungarian Glider, *Neptis rivularis*, the older caterpillar builds a winter shelter out of the host plant leaf. The Common Brimstone, *Gonepteryx rhamni*, and the European Peacock, *Aglais io*, slumber through the winter as mostly inactive adults, though the Peacock will show off its eyespots if disturbed, in an attempt to ward off predators.

↓ The Tawny Emperor, *Asterocampa clyton*, widespread through eastern North America, is attracted to tree sap and fermented fruit.

(continued...)

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