CONTENTS

EXTINCTION

ABOVE | The only known specimen of the Mauritius Snout *Libythea cinyras*, in the Natural History Museum, London. The head and abdomen are missing, but its distinctiveness is supported by its unique wing pattern.

In *On the Origin of Species*, Charles Darwin recognized extinction as part of natural selection: "species and groups of species gradually disappear, one after another, first from one spot, then from another, and finally from the world." Indeed, we know that some butterflies have become extinct. Some of these are represented by a handful of fossils or specimens held in museum collections, while others are known only from illustrations.

Three of the many species of butterflies listed as Extinct on the IUCN Red List are *Libythea cinyras* (Nymphalidae), *Lepidochrysops hypopolia*, and *Deloneura immaculata* (both Lycaenidae). One of these, the Mauritius Snout *L. cinyras*, is known from a single specimen collected in Moka, Mauritius, in 1865. Roland Trimen published the description of this butterfly in 1866 and implied that there was another specimen in the "South African Museum," but this specimen has never been located. The single known specimen is held at the Natural History Museum in London. Two African lycaenids were also last recorded in the late 1800s and are considered not to have been rediscovered since, although more research is needed to clarify the identities of these hairstreaks. It is important to emphasize that most tropical butterflies need their status assessed.

Fossil records and amber inclusions of butterflies (i.e., trapped in resin) are limited compared with other fossilized insects, and about

LEFT | *Prodryas persephone* is a well-preserved fossil of a nymphalid butterfly from the Eocene. The species was described by Samuel Scudder based on this fossil specimen and represents type specimen no. 1 at the Museum of Comparative Zoology (Cambridge, USA).

BELOW | Jan Sepp's illustration of an enigmatic skipper *Papilio flavomarginatus*. While it is currently classified in a skipper genus *Salatis*, it is difficult to narrow down its origin and identity without any known specimen.

30 are known. Among these fossils, the nymphalid *Prodryas persephone* from the Eocene Florissant shale beds in Colorado is the best-preserved butterfly fossil. These fossils connect us to ancient life, as well as providing insights into the evolutionary history of butterflies.

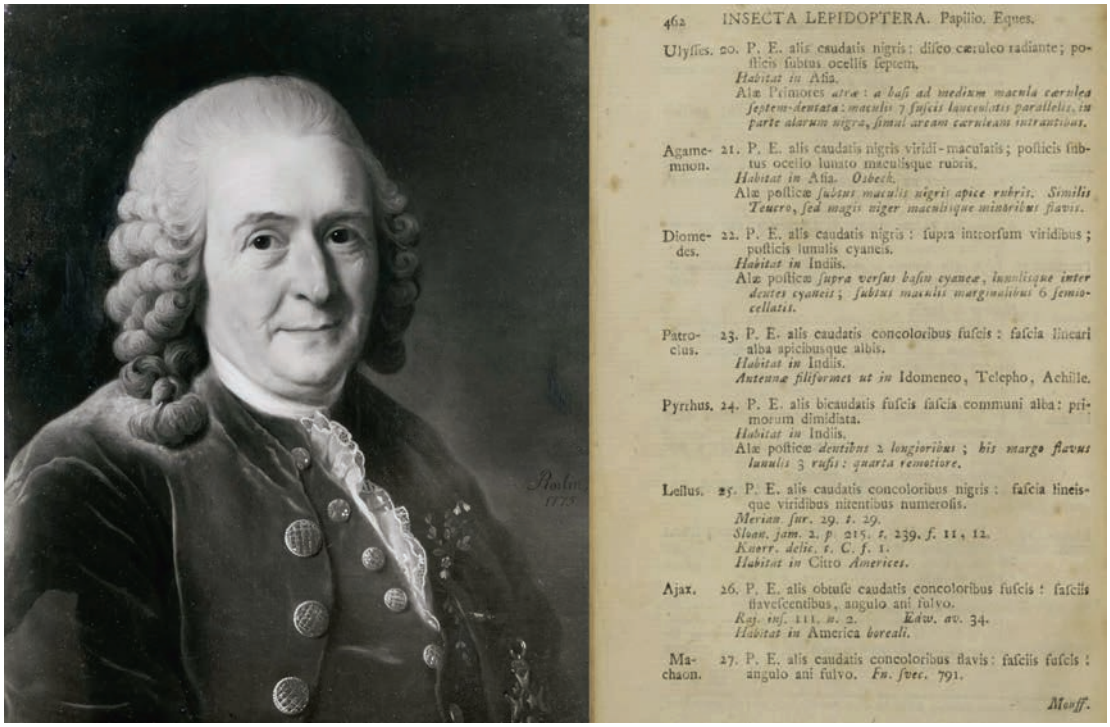
In reality, there are many butterflies, especially in the tropics, that we do not know much about and are unidentified. These enigmatic butterflies are known only from illustrations, often accompanying the original description, while the specimens used to prepare the description by the author (type material) have been lost. An example is the Neotropical skipper *Papilio flavomarginatus* (Hesperiidae), which was named in the mid-1800s by Dutch entomologist Jan Sepp, who described many butterflies from Suriname based on observation and drawings made by a naturalist, H. J. Scheller. Scheller traveled to Suriname in the late 1700s and made life history notes and illustrations by directly observing immatures as well as adults. Sepp later acquired Scheller's field notes and drawings, made modifications, and added text to describe taxa he considered new to science, presumably without having physical specimens. At this point, we do not know of any skipper specimen that matches Scheller or Sepp's drawings. Another enigmatic specimen was described by Johan Christian Fabricius as *Hesperia busiris* in 1793 based on a drawing prepared by William Jones. No specimen was known and for more than two centuries this species was classified as a skipper of an unknown origin. Recently, a noctuid moth, presumably from western Africa, described in 1854 was concluded as conspecific with *H. busiris* based on a single known specimen, which might have been used to name both "butterfly" and moth.

HISTORY OF STUDYING BUTTERFLIES

Humans and butterflies presumably had close interactions when we developed agriculture about 12,000 years ago and transitioned into a more sedentary lifestyle from a nomadic way of life. As we had to grow and produce our own food, identifying and understanding pests and non-pests would have been a critical part of the farming lifestyle. We had to classify beneficial, neutral, and harmful insects to survive. This attempt to classify insects, which undoubtedly included butterflies, can be considered as an embryonic phase of taxonomy (the science of naming and classifying organisms); it is important to emphasize that we have been classifying objects since the beginning of humanity, and we will continue to classify them until we disappear from this planet. One of the first attempts to systematically classify organisms was made by Aristotle. He divided organisms into groups, one of which, termed *Entoma*, included insects, which he further classified based on the presence or absence of wings and mouthpart characters. A translated version of Aristotle's *Historia Animalium* suggests he examined butterflies (possibly the Cabbage White *Pieris rapae*) and observed the immature stages.

A notable figure in the study of butterflies is Maria Sibylla Merian (see p. 19). She was born in

BELOW AND LEFT | Portrait of Maria Sibylla Merian in her later years, and her painting of the Menelaus Blue Morpho *Morpho menelaus* and the Pomegranate Tree *Punica granatum* (Lythraceae). The caterpillar depicted is a Banded Sphinx Moth *Eumorpha fasciatus*, not a Menelaus Blue Morpho.



462 INSECTA LEPIDOPTERA. Papilio. Eques.

Ulyſſes. 20. P. E. alis caudatis nigris: diſco cæruleo radiante; poſticis ſubtus ocellis ſeptem.
Habitat in Aſia.
Alæ Primores *atræ: a baſi ad medium macula cærulea ſeptem-dentata: maculis 7 ſuſcis lanceolatis parallelis, in parte alarum nigra, ſimul aream cæruleam intrantibus.*

Agamemnon. 21. P. E. alis caudatis nigris viridi-maculatis; poſticis ſubtus ocello lunato maculisque rubris.
Habitat in Aſia. *Osbeck.*
Alæ poſticæ *ſubtus maculis nigris apice rubris. Similis Teucro, ſed magis niger maculisque minoribus flavis.*

Diomedes. 22. P. E. alis caudatis nigris: ſupra intorſum viridibus; poſticis lunulis cyaneis.
Habitat in Indiis.
Alæ poſticæ *ſupra verſus baſin cyaneæ, lunulisque inter dentes cyaneis; ſubtus maculis marginalibus 6 ſemiocellatis.*

Patroclus. 23. P. E. alis caudatis concoloribus ſuſcis: faſcia lineari alba apicibusque albis.
Habitat in Indiis.
Antennæ filiformes ut in Idomeneo, Telepho, Achille.

Pyrrhus. 24. P. E. alis bicaudatis ſuſcis faſcia communi alba: primorum dimidiata.
Habitat in Indiis.
Alæ poſticæ *dentibus 2 longioribus; his margo flavus lunulis 3 rufis: quarta remotiore.*

Leſſus. 25. P. E. alis caudatis concoloribus nigris: faſcia lineisque viridibus nitentibus numeroſis.
Merian. ſur. 29. t. 29.
Sloan. jam. 2. p. 215. t. 239. f. 11, 12.
Knorr. delic. t. C. f. 1.
Habitat in Citro *Americes.*

Ajax. 26. P. E. alis obtuſe caudatis concoloribus ſuſcis: faſciis flavefcentibus, angulo ani fulvo.
Raj. inſ. 111. n. 2. Edw. av. 34.
Habitat in America *boreali.*

Machaon. 27. P. E. alis caudatis concoloribus flavis: faſciis ſuſcis: angulo ani fulvo. *Fn. ſuec. 791.*

Muſſ.

ABOVE | Portrait of Carl Linnaeus and a page from the 10th edition of his *Systema Naturae*. It is deemed to have been published on January 1, 1758, which is the arbitrary starting date of zoological nomenclature.

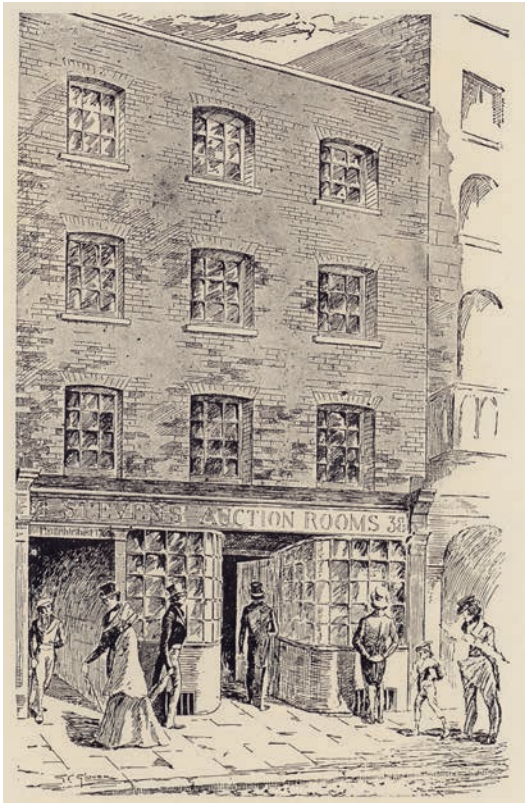
Germany in the mid-seventeenth century and grew up raising butterflies and moths. She dedicated herself to practicing her watercolor painting skills by meticulously documenting plants and their interactions with butterflies, caterpillars, and other insects. Her commitment and engagement in painting the metamorphosis of caterpillars led her to travel to the then Dutch colony of Suriname. Merian spent two years capturing the lifecycle of tropical butterflies with their host plants (as well as other creatures) through engravings and watercolors, which led to the production of her monumental work *Metamorphosis Insectorum Surinamensium*. Her attention to detail coupled with her artistic talents means that her work is prized for its aesthetic values as well as its scientific merit. Like the butterflies she painted, Merian and her work sit at the intersection of art and science. Because of its dual nature, her work was far-reaching and provided evidence of metamorphosis (although she was not the first to document it) at a time when many people believed in spontaneous generation.

Merian's work influenced Carl Linnaeus's *Systema Naturae*, in which binomial nomenclature was adopted (tenth edition, 1758), and where all known butterflies, from swallowtails to skippers, were classified under the generic name *Papilio*. Over 300 species of butterflies were described by Linnaeus, including several misidentified moths, such as *Urania*. Linnaeus' work significantly advanced our understanding of butterflies and other organisms by assigning a binomial to each of them as well as producing order by grouping

them into nested hierarchies (class > order > genus > species). Subsequently, Linnaeus's student Johan Christian Fabricius established the genus *Hesperia* to accommodate those species known today as skippers. Fabricius was a prolific Danish entomologist known for naming about 10,000 new species of insects, including over 1,600 butterflies and moths. Fabricius further motivated Pierre André Latreille to publish his *Précis des caractères génériques des insectes*, *disposes dans un ordre naturel* (*Summary of generic characteristics of insects*, *arranged in a natural order*) in 1796 where he introduced the concept of family and tribe. Two butterfly families, Papilionidae and Hesperiidae, are attributed to Latreille and the root for other butterfly families accepted today can be traced back to around this era. Latreille's colleague at the museum in Paris, André Marie Constant Duméril introduced the term *Rhopalocera* (as *Ropalocéres*) in 1823, which was used to scientifically refer to butterflies by many subsequent authors. *Rhopalocera* means "clubbed antennae," and, in contrast, moths were termed *Heterocera*, meaning "variable antennae," reinforcing the classic distinction between butterflies and moths based on antennae shape. Similarly, the terms *Diurini* and *Nocturini* were also used for butterflies and moths respectively.

The Victorian era saw serious interest from the public in natural history specimens, and exotic tropical bird and butterfly specimens, especially, received special attention and commanded good prices at auction houses. The so-called Stevens Auction Rooms at 38 King St., Covent Garden, in London was where various items such as plants, butterflies, and elephants were sold, including specimens collected by Alfred Russel Wallace and Henry Walter Bates. Their work was financially supported by Samuel Stevens who was partially in charge of the auction room. Here, *Agrias claudina godmani* (Nymphalidae) from Brazil reached a record price for an insect. Evidently, there was a market that could support Wallace and Bates's expeditions. Similarly, many other naturalists in Europe or America embarked on journeys to tropical rainforests and brought back specimens.

In the second half of the nineteenth and the early twentieth century, there was an explosion of interest in naming and describing new butterfly species, especially from European explorers and naturalists, mostly from the UK or Germany. Our understanding of butterfly species diversity improved significantly during this time. German



LEFT | Stevens Auction Rooms at 38 King Street, London. From Emily Allingham's *A Romance of the Rostrum*, published in 1924.

Preis-Liste No. XA

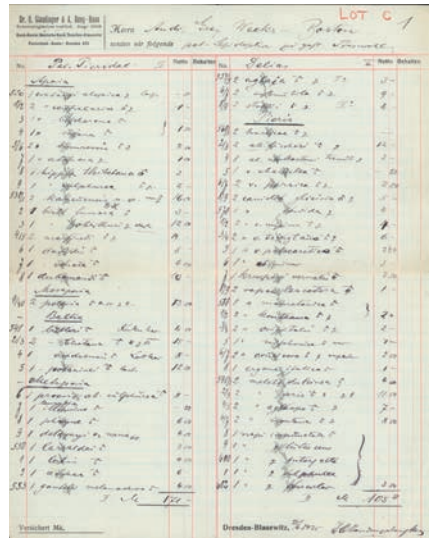
über

gespannte Lepidopteren

von

H. Fruhstorfer, Berlin NW.,

Thurmstrasse 37.



LOT C

entomologist Hans Fruhstorfer was one of the most prolific authors, publishing descriptions of new butterfly taxa. Fruhstorfer traveled around the globe and supported himself by selling insect specimens and shells. The Dresden-based insect trading company Staudinger & Bang-Haas also issued catalogs and price lists for butterfly specimens and supported scientific endeavors. Otto Staudinger and Andreas and Otto Bang-Hass (father and son) were all accomplished Lepidoptera taxonomists and influential dealers of their time. Commercial venture and science seem to have been two sides of the same coin during this period. Walter Rothschild wrote in the preface of Emily Allingham's *A Romance of the Rostrum* (a story about the Stevens Auction Rooms), "I have always felt … the rooms at 38 King Street … were among the greatest aids and inducements to the study of Systematic Zoology." Like Stevens, Rothschild funded naturalists, including Albert Stewart Meek, who shot a Queen Alexandra's Birdwing *Ornithoptera alexandrae*. The Victorian era was the time when science was not yet institutionalized, so many studies of butterflies were self-funded by naturalists who had a single-minded desire and enthusiasm to better understand butterflies, mainly by amassing specimens.

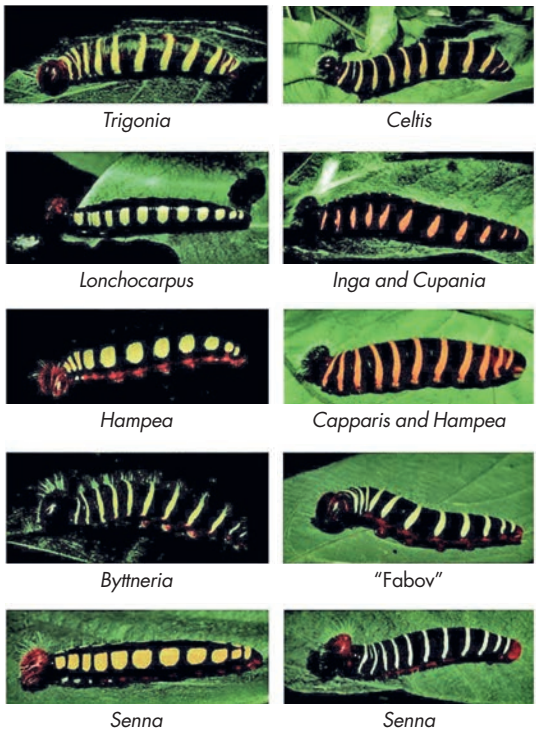
ABOVE | Examples of price lists for butterfly specimens sold through the firms Hans Fruhstorfer (left) and Staudinger & Bang-Haas (right). The latter list was compiled and sent specifically to a Boston-based butterfly collector, Andrew Weeks.

While the Victorian era cannot be experienced directly, the energy and enthusiasm of early naturalists can be felt through literature and archival records. The history of the study of butterflies has established the achievements of a diverse group of people, who contributed toward our understanding of these beautiful creatures, an understanding based on their innate motivation to explore the natural world.

STUDYING BUTTERFLIES TODAY

One major advancement in our understanding of butterflies has been achieving a certain degree of stability in classification owing to the DNA revolution. Seven families are recognized and their relationships seem well resolved at a higher classification level. The Darwinian era saw many scholars who influenced classification by promoting "tree-thinking" or "evolutionary thinking," such as Ernst Haeckel, building upon the groundwork of Latreille and Fabricius. The late twentieth century saw the foundation of Hennigian phylogenetics, which was followed by the introduction and subsequent rise of molecular techniques and computational power over the past few decades, elucidating the evolutionary history of butterflies. Consequently, we have now arrived at a more natural classification of butterflies, based on relatedness rather than resemblance. The more recent placement of the families Hedylidae and Hesperiidae in butterflies was supported by reconstruction of the phylogeny based on DNA sequence data. At the species level, genetic data have contributed particularly toward the discovery and description of cryptic butterfly species that were previously overlooked by experts.

In 2004, a group of researchers combined DNA data with caterpillar morphology and host plant records at a site in Costa Rica to show that skipper *Astraptes fulgerator* (Hesperiidae), previously thought to be a single common and variable species ranging from southern USA to northern Argentina is, in fact, a complex of at least ten species just in Costa Rica. DNA data also revealed that two satyrine species from South America, *Caeruleuptychia helios* and *Magneuptychia keltoumae* (both Nymphalidae), were in fact the male and female of the same species, morphologically distinctive due to sexual dimorphism. It has even been possible to extract and sequence DNA from museum specimens collected from the 1700s onward, so butterfly specimens housed at natural history museums and in private collections, all around the world, are now highly sought for DNA sequencing analysis. A whole new area of research has developed, termed *museomics*, meaning genomics dedicated to museum materials.



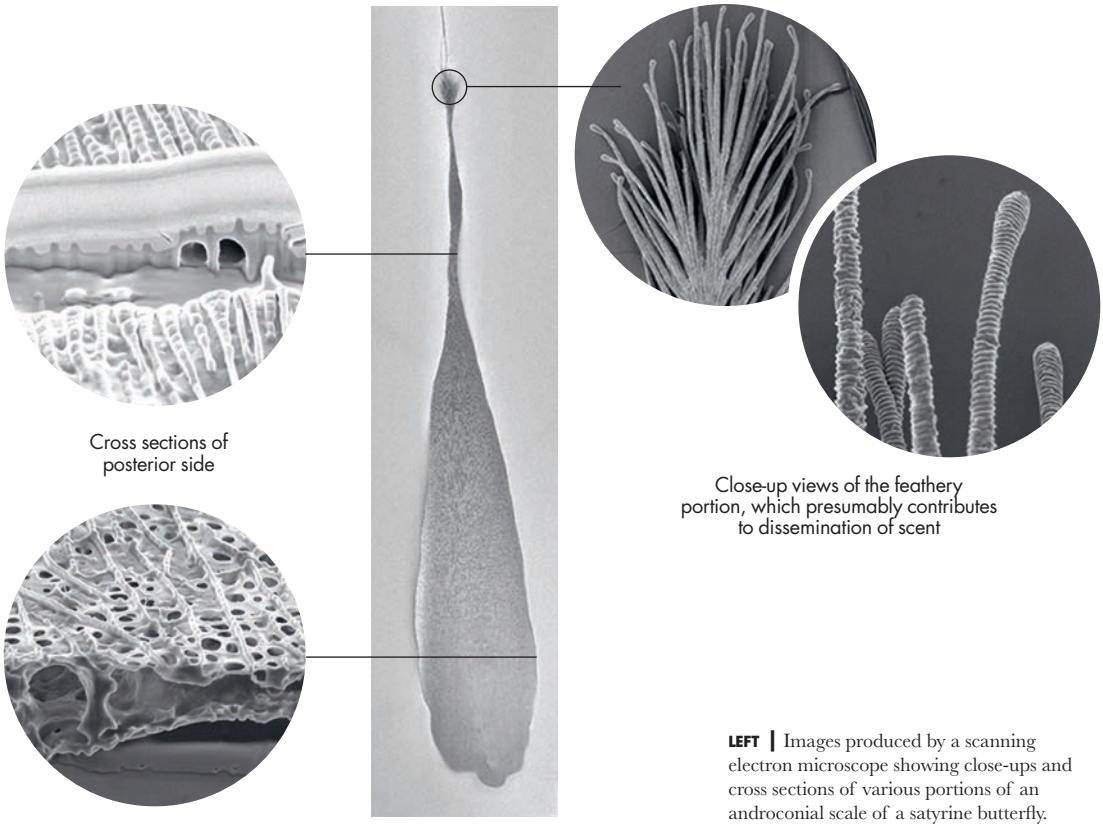
LEFT | Diversity in caterpillar patterns that partly supported "ten species in one" in a study in Costa Rica of the skipper *Astraptes fulgerator* (Hesperiidae). Each name indicates the different plants that the caterpillars feed on.

Accumulation of butterfly specimens collected over centuries in natural history museums has allowed innumerable research projects to answer questions related to climate change, macroecology, evolution, and conservation. These existing specimens and their label data are being digitized and databased, and gradually being made accessible to the outside world, which will be used to answer some of society's pressing questions. At the Natural History Museum in London, the details of over 180,000 specimens of British butterflies collected over 200 years have been individually digitized. An international group of researchers used these data to assess the impact of climate change on the body size of British butterflies by investigating the relationship between body size and temperature. Their research suggests that adult butterfly body size increases with temperature during the late stages of larval development, providing insights into how butterflies can respond to climate change.

This type of research using large data sets coupled with international collaboration is typical of butterfly research conducted at academic institutions today. Further, with advancement of various technologies, we are able to look at certain aspects of butterflies in-depth. Scanning electron microscopy (SEM) is used for examining the ultrastructures of butterfly scales (see p. 15). A computed tomography (CT) scanning technique is an imaging procedure that can be used to capture internal structures. Researchers used CT scans to monitor the process of a butterfly pupa developing into an adult butterfly while still alive inside (Maria Sibylla Merian would have loved to have seen that!). With the development of artificial intelligence and machine learning, researchers have been able to systematically study evolutionary patterns in species diversity and compare males with females in some species, including birdwings.

ABOVE | These two specimens (upper- and undersides) were previously thought to represent two different species until DNA revealed that these are the male (top) and the female (bottom) of the same nymphalid butterfly, *Caeruleuptychia helios*.

ANDROCONIAL SCALE

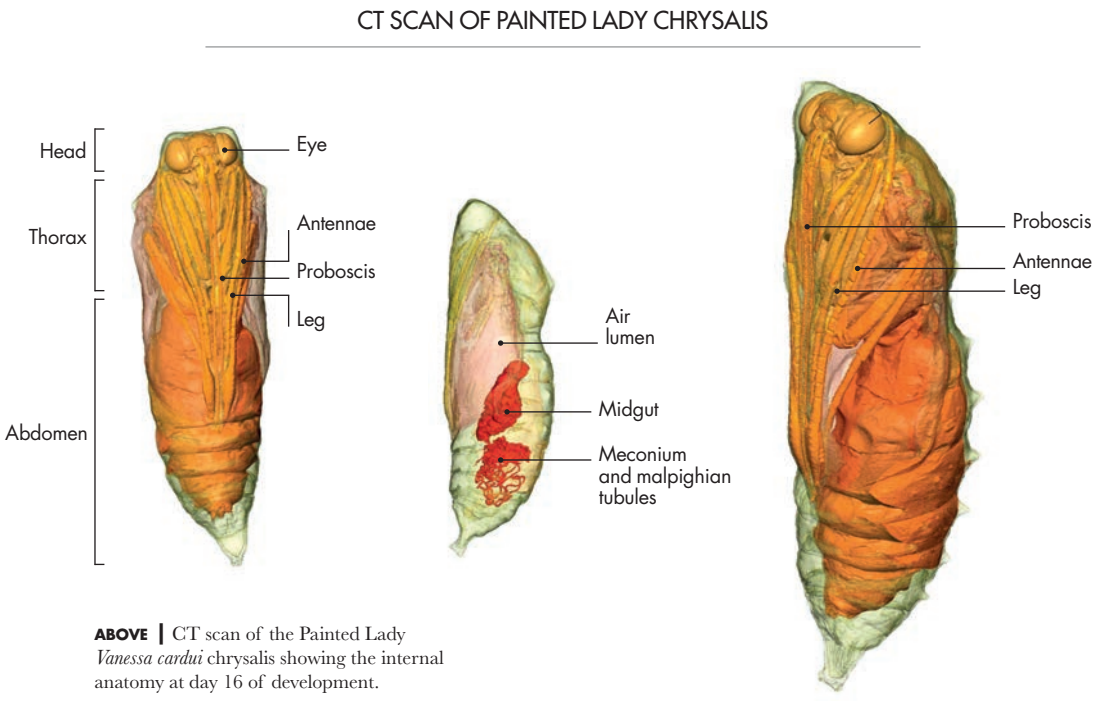


LEFT | Images produced by a scanning electron microscope showing close-ups and cross sections of various portions of an androconial scale of a satyrine butterfly.

We live in a world where we rely heavily on the internet for obtaining information and for researching collaboratively. Additionally, many parts of the world can now be reached within a few hours or days. This can be advantageous for butterfly research, but if we care about the butterflies on the planet today we need regulations to prevent chaos. The Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) is an intergovernmental agreement to ensure that international wildlife trading does not jeopardize existing populations of threatened species. Four butterfly species are considered endangered and receive the top level of protection under CITES Appendix 1 (swallowtails *Papilio chikae*, *Parides burchellanus*; Homerus Swallowtail *Pterourus* (*Papilio*) *homerus*; and the Queen Alexandra's Birdwing *Ornithoptera alexandrae*) along with rhinos, elephants, and gorillas. Specimens of these four species collected after July 1, 1975—dead or alive—are prohibited for international trade. Other species of butterflies are listed in CITES but under categories with fewer limitations. This does not mean that people can freely collect and study butterflies that are not listed under CITES. Many countries require collecting permits, even for studying common butterflies, in addition to export permits to take specimens out of their original country. Further, if the study involves DNA analysis, the Nagoya Protocol on Access and Benefit Sharing can come into play. This is an international

agreement that came into force in 2014 and ensures that the benefits arising from the utilization of genetic resources are shared in a fair and equitable way (known as *access and benefit sharing*). The rationale behind this agreement is that genetic resources originating from a country must be shared equally with that country, particularly if they are used for commercial purposes.

The study of butterflies, especially natural history and taxonomic work, was undertaken by few museums and societies in Europe in the nineteenth century and relied considerably on the efforts of individual naturalists, such as Bates, Wallace, Rothschild, and Fountaine, to name only a few. However, nowadays it is becoming less simple for nonprofessional entomologists and naturalists to contribute to butterfly research due to the bar being raised and research depending on the use of molecular data and other advanced techniques that are not readily available to amateur entomologists. While they can continue to enhance current knowledge of butterflies, the limits to the types of work they can undertake and separation from professional entomology has its disadvantages. Modern science, founded on the study of the genome is based largely at institutions, but contributions from amateur naturalists and citizen scientists is crucial for a better understanding of the biology, ecology, and conservation of butterflies. Several online initiatives—including eButterfly and photography platforms such as iFoundButterflies, iNaturalist, Butterfly Catalogs, Butterflies and Moths of North America (BAMONA), and Flickr, and also social media platforms—show that there is a huge enthusiasm for butterflies. Since butterfly diversity is concentrated in tropical countries in the Global South, it is important to encourage and facilitate the inclusion of amateurs and researchers from various backgrounds in butterfly research.



ABOVE | CT scan of the Painted Lady *Vanessa cardui* chrysalis showing the internal anatomy at day 16 of development.

BUTTERFLY NOMENCLATURE

SCIENTIFIC NAME VERSUS COMMON NAME

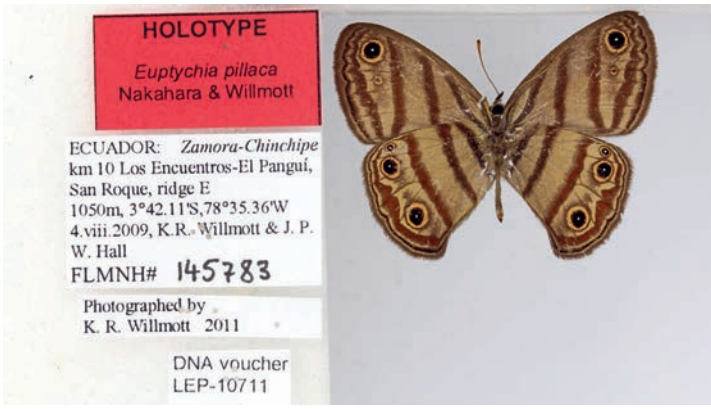
A butterfly represented by the scientific name *Papilio glaucus* is also known by the common English name Eastern Tiger Swallowtail, and both names refer to the same swallowtail, found in the eastern USA. Current taxonomy uses Linnaeus's method of naming species, called *binomial nomenclature*, whereby each species has a unique combination of two names, consisting of the genus name and the specific epithet. An advantage of this naming system is its inherent clarity—each taxon is known internationally by the same name—which is essential when fostering international communication about relationships among taxa. Hence, we can assume that *Papilio glaucus* is closer to other species in *Papilio* than to butterflies in other genera.

Common names vary according to language and even locally, which can lead to confusion. Common names can be informative and engaging if understood by the audience, but scientific communication is often between people who do not share the same language, so an accepted scientific name can be more useful. Most tropical butterflies do not have widely accepted common names. Conversely, some species have multiple common names, even in the same language. For instance, the butterfly known as the Mourning Cloak in North America and the Camberwell Beauty in the UK has one scientific name: *Nymphalis antiope*. Scientific names are meant to overcome this problem. Ideally, every species should be represented by a unique and universally accepted scientific name, although collisions do occur, where two different scientific names have been applied to the same butterfly or two different butterflies have been given the same name. The International Commission on Zoological Nomenclature (ICZN) published a set of rules for treatment and use of names to resolve such nomenclatural issues and many potential causes of confusion. These rules should be

TAXONOMIC NAMES

Category	Latin suffix (example)	Latinized suffix common name (example)	English common name
Order	-ptera	Lepidoptera	Butterflies and moths
Superfamily	-oidea	Papilionoidea (papilionoids)	Butterflies
Family	-idae	Papilionidae (papilionids)	Swallowtails, Apollo, and festoons
Subfamily	-inae	Papilioninae (papilionins)	
Tribe	-ini	Papilionini (papilionines)	Swallowtails

Genus and species names form a unique combination, for example, *Papilio alexanor*.
For subspecies a third name is added, for example, *Papilio alexanor destelensis*.



LEFT | A type specimen usually bears a red label indicating that it serves as the standard for the species.

consulted before a name is selected for an undescribed new butterfly. Authors may name undescribed butterfly species after a characteristic feature of the insect, a place of origin, a person (or people), or in reference to an in-joke; ideally, it should sound euphonious. While not specified by the rule book, it is not recommended that you name a new species after yourself!

SUBSPECIES

Subspecies is the taxonomic rank below species. There are many subspecies recognized for butterflies. The subspecific name is added as a trinomen at the end of a binomen, and typically reflects a geographical variation in species occupying a wide range, although other naming criteria can be applied. Subspecies can be raised to species level and species can be downgraded to subspecies depending on the available scientific evidence. For example, in the Philippines, the Luzon Peacock Swallowtail *Papilio chikae chikae* is known from Luzon and another subspecies, *P. chikae hermeli*, from northern Mindoro. *Papilio chikae hermeli* was originally described as its own species, *P. hermeli*, but evidence suggests that it is conspecific with *P. chikae*, but represents a geographic variation. The Large Copper that became extinct in the UK in the 1850s is, in fact, the nominotypical subspecies *Lycaena dispar dispar* (Lycaenidae), while two other subspecies of *L. dispar* are extant in Europe and Asia.

TYPE SPECIMEN

Every new species described should have an objective standard. The specimen serving as this standard should represent the main characteristics that separate the newly named species from others. The objective standard, which shows these characters, is called the type specimen, and it is designated by the original author(s) or by subsequent designation. Modern descriptions include the designation of a holotype (one specimen), while in the past the concept of a species was typically based on a series of specimens (syntypes). The type specimen is a reference that can be checked if there is doubt about the identity of a species; thus it is important to mention in the paper describing it which institution holds the specimen so other researchers can locate and inspect it. A red or brightly colored label is frequently attached to type specimens to indicate their unique status. As science progresses, the interpretation and the concept of species can change, but the type specimen will remain as long as the specimen exists.

DISCOVERING NEW SPECIES

Discovering a new butterfly species is exciting. There are hundreds of butterflies still waiting to be discovered, described, and named by science. So where will these new butterfly species be found? Remote, unexplored areas mostly in the tropics are certainly good places to find new species. However, new species can be hiding in plain sight. Sometimes we just need to study our local butterfly fauna in-depth. For example, as recently as 2014, a new species, Intricate Satyr *Hermeuptychia intricata*, was found in the southern USA. Scientists often find new species when sorting out drawers in museum collections, where specimens collected at different times and from many different locations are stored.

So, what happens when someone thinks they might have found a new butterfly species?

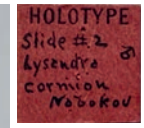
The first step to check is the identity of the butterfly and that it has not been named previously. Typically, this is done by reviewing published literature and, if there is any doubt, checking type specimens and other specimens of related species to assess whether there are wing pattern or other variations. It is important to exclude the possibility of the butterfly representing merely a variation, a form, or an

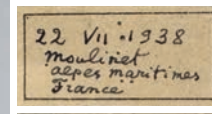
BELOW | Intricate Satyr *Hermeuptychia intricata* resting on a leaf. The recent discovery of this species probably represents a proverbial "tip of the iceberg" of cryptic species hiding in plain sight.

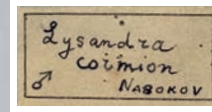
aberration, of a known species. Discussion with butterfly taxonomists can also be beneficial. To characterize the species, the genitalia should be inspected for both sexes if available and/or the DNA sequenced to find which taxa it is closely related to and which genus it should be placed in.

Once the name has been chosen for the new butterfly, a paper fully describing it must be written and published in an appropriate journal to introduce it to the scientific community and to the world. The article should include figures illustrating notable features, especially the genitalia, as well as the body and wing patterns, habitats, host plants, and all the other information the authors have. The paper must be peer-reviewed by fellow specialists to be published in a scientific journal, fulfilling requirements of the ICZN. Once published, the name of the new butterfly species can be used officially to communicate about that butterfly.

BELOW | Vladimir Nabokov is known as a novelist and poet, but he also studied butterflies (especially Lycaenidae) at the Museum of Comparative Zoology (Cambridge, USA). As a taxonomist as well as a poet, he expressed his passion for naming new species in a poem "On Discovering a Butterfly".







BUTTERFLIES AND SOCIETY

The first butterflies emerged around 100 mya, while humans have been on the planet for just a few hundred thousand years. The earliest humans would have lived in a very different environment from ours today: closer to nature, sensitive to the changes in seasons, and closer to plants and animals, including butterflies.

Human attitudes to insects might not always be positive, but butterflies often stand apart. Most insects are seen as "creepy crawlies," with little favorable public attention. Insects are often thought of in terms of pest control to protect crops or reduce the transmission of diseases such as malaria. This was not always the case, though; insects in past cultures were revered (e.g., by the Egyptians and Mayans), but with increasingly intensive agriculture and an awareness of their pathogenic associations, they are often considered negatively (though their importance as pollinators is becoming more widely understood). Butterflies are an exception, although some species can be pests of crops, being among the few insects that bring joy to people, due to their beautiful colors, delicate nature, and elegance.

Among insects, butterflies are one of the more conspicuous and charismatic groups, engaging the public's sympathy and interest. Butterflies attract attention as symbols of sunny days, freedom, and purity, and may also indicate a healthy environment. Some ancient cultures considered them to be the souls of the dead flying to heaven. Their day-flying habit and size make them relatively easy to observe, photograph, and paint, and they can also be bred relatively easily by amateur naturalists. Perhaps for all these reasons, the relationship between humans and butterflies is long and deep, and pervades science, art, and broader culture. Artistic interest emerged

BELOW | Early butterflies (and birds) depicted in an ancient Egyptian wall painting in the Tomb of Nakht, Thebes, Eighteenth Dynasty.

LEFT | Mural in Colombia of Literature Nobel prize winner Gabriel Garcia Márquez, author of *One Hundred Years of Solitude*. In the novel, the yellow butterflies swarm constantly around the main character, Mauricio Babilonia, as a symbol of magical realism.

BELOW LEFT | *Still Life with Flowers in a Decorative Vase*, c. 1670–1675, painted by Maria van Oosterwyck.

independently in various ancient human cultures. Some of the oldest depictions of butterflies can be seen in geometric designs in Scottish Neolithic stone carvings (c. 3000–5000 BCE). Truly identifiable butterflies appear in Egyptian times, with examples in tomb drawings, amulets, and jewelry from the Old Kingdom period (c. 2686–2181 BCE) onward. The tomb of the high-ranking official Nebamun (1350 BCE), in particular, contains vivid illustrations of butterflies in a hunting scene, providing evidence of the presence of various species at a particular location at this time. They feature in gold ornaments from pre-Columbian cultures of South America too.

In the Renaissance, classical, and modern art periods, butterflies were included in paintings as symbols of beauty, nature, freedom, resurrection, transformation, and life. They are found in many

LEFT | Pre-Columbian gold ornament depicting a butterfly, which was used as a nose ornament by Indigenous people, now cast as a pendant by Colombian artist Claudia Amaya.

artworks from these eras, especially where scenes are set in nature. The Dutch Golden Age painter Maria van Oosterwyck went further, using butterflies as the focus of her paintings.

Butterfly motifs are now widespread in art and jewelry and on clothing. They are frequently depicted on stamps, coins, and notes, with endemic or local species often depicted.

Butterflies have also been used as metaphors in literature. In Shakespeare's *King Lear*, the protagonist reminisces about butterflies. J. R. R. Tolkien describes an interaction with colorful butterflies as they fly in the sun in a treetop in *The Hobbit*, contrasting them with the lost explorers' experiences in the dark forest below. *Alice's Adventures in Wonderland* features a talking caterpillar, who later metamorphoses. In a poignant moment in the anti-war classic *All Quiet on the Western Front*, the butterflies in no-man's land contrast with surrounding desolation. And in *One Hundred Years of Solitude*, by Gabriel García Márquez, a virtuous character is followed by yellow butterflies wherever he walks. Márquez, who went on to win the Nobel Prize for Literature following this work, hails from Colombia, the world's most biodiverse country for butterflies. In movie adaptations of all these books, and in other feature films such as *Encanto*, *The Butterfly Effect*, *Papillon*, *Bambi*, *Mary Poppins*, and more, butterflies often depict joy, color, and the innocence of nature.

The contemporary artist Damien Hirst has used butterflies in new ways. *In and Out of Love*, exhibited in 1991, featured live butterflies, which emerge from chrysalises, fly, feed, and die within the exhibit. In *I am Become Death*, *Shatterer of Worlds*, Hirst used 3,000 sets of butterfly wings in a kaleidoscopic image that has the appearance of stained glass.

Although most interactions between butterflies and people are positive, there are exceptions. Some caterpillars are pests. For instance, *Pieris rapae* (known as the Cabbage White in North America and Small White in Europe) can decimate crops of cabbage, broccoli, and brussels sprouts. The current rate of destruction of primary forests, where butterflies are most diverse, and increasing intensification of agriculture are now resulting in

a so-called "Insect Armageddon", with butterflies affected just as badly as other groups. Fortunately, though, butterflies have increasingly become a focus for insect conservation.

The rise of ecotourism has increasingly involved butterflies. With the decline of nature in many areas of human habitation, butterflies can now be brought to the people in butterfly houses, spaces controlled for temperature, light, and humidity, allowing colorful and larger tropical species to be bred in the middle of cities and then to fly around fascinated visitors. Butterfly houses are largely commercial ventures, but as they become more popular in tropical countries, efforts are made to host local species, and so these initiatives are contributing to our knowledge of butterfly life histories, as well as raising awareness of conservation issues and bringing ecotourism income to local communities. Visitors to the Amazon or other tropical regions marvel at the diversity of butterflies, which are often a focus for photographers. A small but increasing number of butterfly tour operators take clients to see or photograph butterflies or to witness events such as the Monarch migration in Mexico. These initiatives bring increasing work opportunities for local butterfly experts and citizen scientists, and encourage local people to protect their natural resources.

Of all the insects, butterflies have, therefore, gained particularly prominent societal recognition.

BELOW | A live butterflies house in the Botanical Gardens in Quindio, Colombia, where the public can connect and engage with nature and its conservation.

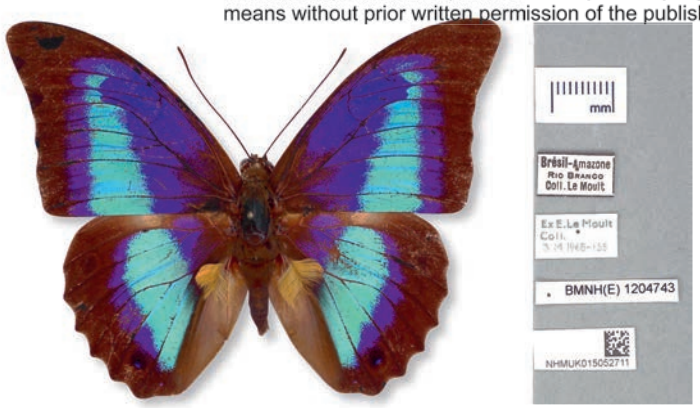
BUTTERFLY CLASSIFICATION

The true butterflies, or Papilionoidea, are a superfamily (another formal rank in the taxonomic hierarchy) within the order Lepidoptera, which also includes moths. Traits that all the Lepidoptera share include scaled wings as adults, and the lifecycle of egg, caterpillar (larva), chrysalis (pupa), and adult (imago). Butterflies are a relatively recent grouping, and the monophyly of the superfamily, meaning that they descend from a common ancestor, has been widely accepted. The diurnal butterflies are currently arranged into seven families as listed on pages 10–11. There are 41 subfamilies in total, reflecting the vast array of guilds but also close relationships. Some of these are long-recognized and have always been considered as "butterflies."

Papilionidae (swallowtails) are a striking group of generally large butterflies, often with tail streamers. The Lycaenidae (blues, coppers, and hairstreaks) have an incredible diversity, not only in taxa but also in their lifecycles, which for many taxa are linked to ants (see pp. 159 and 161). Two groups that have been less studied are the Pieridae (whites and yellows) and the metalmarks in the Riodinidae family, a diverse group of small butterflies distributed around the world, though most are tropical.

The most species-diverse group is the Nymphalidae (brush-foots). These include various well-defined groups that are sometimes recognized at family and subfamily level, and sometimes recognized at the tribe level, including the Satyrini (ringlets), Morphini (morphos), and the Brassolini (owls); they also include some of the most familiar butterflies, such as the Peacock, Monarch, and fritillaries. Until recently two groups were excluded.

ABOVE | The Papilionidae family includes some of the most spectacular and large butterflies, for example, the Queen Alexandra's Birdwing *Ornithoptera alexandrae*.



Hesperiidae, the skippers, were often considered to be "sisters" to the butterflies and placed alongside them, or alternatively as a subgroup of moths. Molecular studies have shown the skippers to be part of the butterfly phylogeny. Finally, members of the Hedylidae are small and dull colored and were considered moths until

TOP | Museums around the world facilitate access to millions of specimens collected over hundreds of years, helping the study of butterfly classification.

ABOVE | Despite the fact that butterfly classification started more than 250 years ago, some remote areas still have species to be discovered. Recently, this new species, the Yariguies Ringlet *Idioneurula donegani*, was found on an isolated mountain in Colombia.

ABOVE | The Blue Morpho *Morpho helenor peleides*, a beautiful butterfly found from Mexico south to Argentina.

very recently, but are now classified as a small group of butterflies.

The total number of species of butterflies is uncertain as, with new research, technology, and communication tools available, new species are regularly described from the most diverse areas of the planet, especially the tropics. Disagreements among taxonomists and the rapid changes in nomenclature make it almost impossible to provide an accurate figure. There are approximately 20,000 species recognized and certainly some hundreds yet to be named. With the current unprecedented rate of extinctions of species on the planet during the Anthropocene, organizing and naming species has become urgent, in order to understand the relationships among organisms and to become aware of the existence of species that are not yet known but are at risk.

HOW TO USE THIS BOOK AND INTRODUCTION TO TAXON PROFILES

This book provides an overview of the currently recognized families, subfamilies, and tribes of the true butterflies of the superfamily Papilionoidea. The order in which the families are presented is intended to reflect their time on the planet, starting with the most ancient and oldest extant lineages. At subfamily and tribe levels, the arrangements generally follow the same structure, with those placed together being those with the closest relationships. However, some subfamilies and tribes are grouped under one profile, either because they are newly classified and we have less information about them, or for reasons of space. The number of pages devoted to each profile is determined partly by how much or how little is known about the group being described, and partly by the number of species in the group.

The classification and taxonomic arrangement presented here reflects an attempt at an up-to-date consensus, and reflects the most recently published taxonomic works and phylogenies. Most, if not all, of the arrangements are supported by molecular analysis of genetic material (DNA). We have then incorporated our experience gained over decades of studying butterflies in the field and in large museum collections around the world. Advances in detailed morphological and molecular analysis will doubtless continue, bringing further dynamic changes in classifications across the higher taxa. Current technology has accelerated the rate of discovery of new species, and the understanding of the relationships among them; this will inevitably cause changes to the number of species and genera recognized here.

Each profile begins with the current taxonomic status of the group being described; representative English names of the group are given. The main text then gives a summary of the group and how it is made up, an impression of the numbers within the group, and its main characteristics. Interesting features and key species are picked out, and some information about caterpillars and pupae may be given.

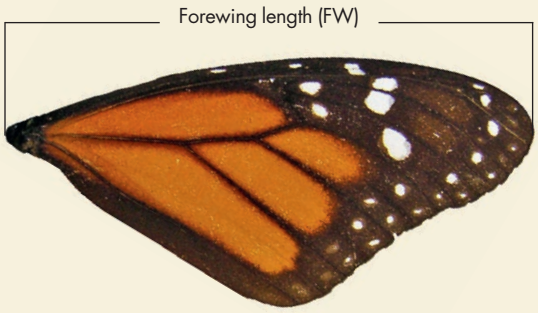
Each information panel begins with a range map, which is generic and provisional; the maps are based largely on distributional records found in the literature and some of the websites listed on page 234, as well as from museum collections. The distribution of each group is also summarized in the information panel.

The genera listed in the information panel are comprehensive for most groups; however, for those groups with the highest diversity, only a few representative genera are listed.

To give an idea of the size of the species in each group, the average forewing lengths (see below) are arranged into three categories: large (1½–4 in/40–100 mm), medium (¾–1½in/20–39 mm), and small (<¾ in/<20 mm).

The "Host Plant Families" section includes some of the known plant families on which caterpillars of each group feed.

Photos have been chosen to show features typical of each group and give a flavor of the extraordinary diversity of wing patterns that butterflies display.



ABOVE | Forewing length as given in this book is measured as the longest straight-line distance from the wing base to the wingtip.

OPPOSITE | A pair of swallowtail butterflies in the genus *Papilio* mating.

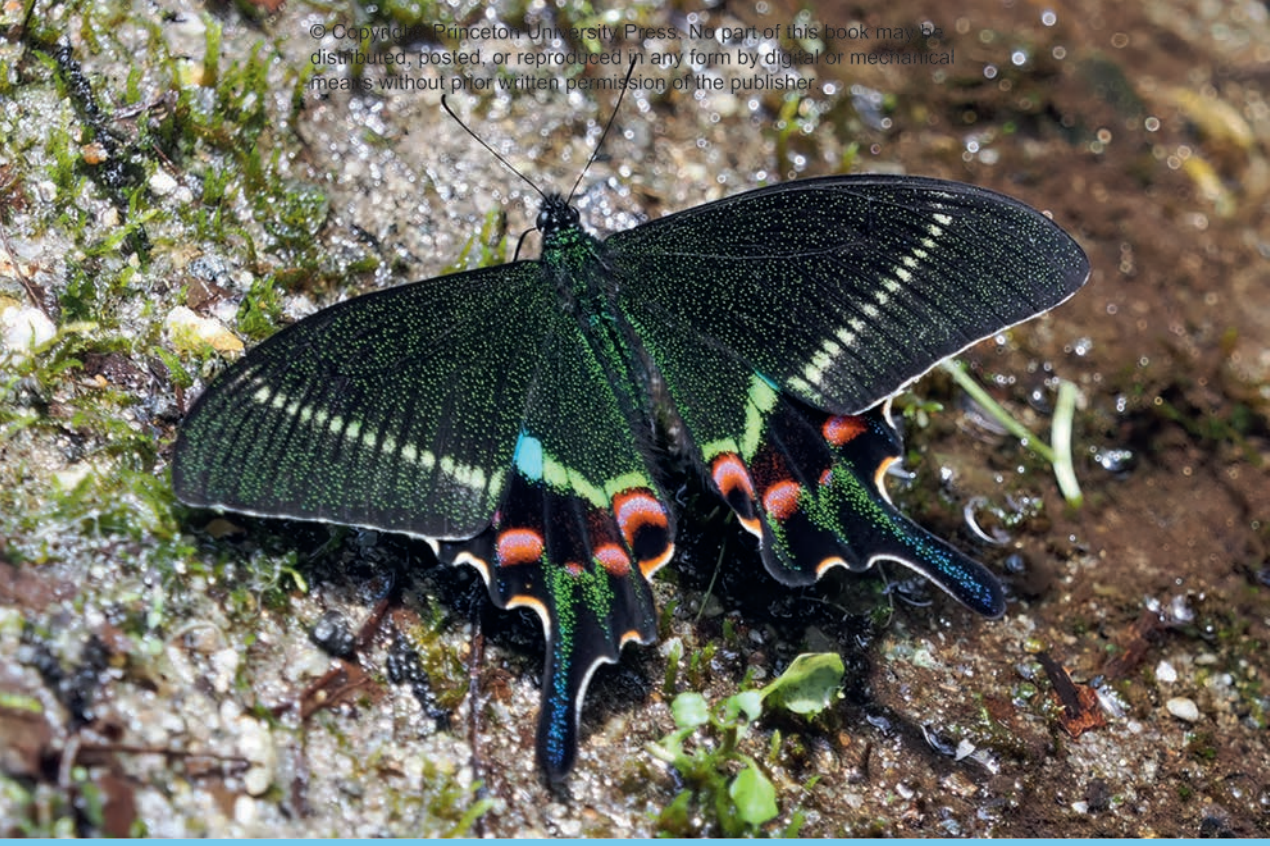
PAPILIONIDAE
SWALLOWTAILS, APOLLOS, AND FESTOONS

The family Papilionidae includes butterflies that are often large and colorful, and, despite having around 614 species, more than 2,086 subspecies, and 31 genera, it is the least species-diverse group of true butterflies after the moth-like family Hedylidae. Extant species are arranged in three subfamilies: Baroniinae, Parnassiinae, and Papilioninae. Members of a further subfamily, Praepapilioninae, are known only from fossils. Size, color, and habitats vary considerably in this cosmopolitan family, which can be found virtually everywhere from forest to deserts and from mountains to gardens. Extensively studied by scientists, Papilionidae is the best taxonomically documented group of butterflies, and probably of Lepidoptera; the whole family has benefited from being the only one fully assessed for threat in the IUCN Red List. The charismatic appearance of species in this group has encouraged the attention of amateurs and collectors over time, resulting in very large numbers of individuals stored in private and scientific collections around the world. This family is the most ancient group of butterflies, some of which were present on the planet millions of years before humans, even including some species that became extinct long ago. Recent molecular studies suggest that the subfamily Baroniinae is so ancient that it might one day be recognized in a separate family of its own.

ABOVE | A female Great Mormon *Papilio memnon* (right) feeding on nectar from flowers and sharing with another species of swallowtail butterfly.

Adults can be recognized from a combination of characters that can be identified by the amateur: the first (front) pair of legs are large and fully operational in both males and females and have well-developed claws; the antennae are relatively close at the base; and the hindwings often have projections like "tails" with their inner margins containing modified scales in males. However, these wing characters are not universal: they are absent in some species and can also be present in some species in other families. To the specialist eye, the arrangement of the veins, including a transverse nervure in the forewings, is key to distinguishing them from other butterfly groups.

Eggs are spherical and most do not have many patterns on the surface. The first instar caterpillars have long spines and later develop a retractile and bifurcated organ with a gland (osmeterium) that emits foul odors in response to disturbance. The pupa or chrysalis is angular and held upright by the cremaster, supported by tail hooks.



ABOVE | A spectacular Krishna Peacock *Papilio krishna*, a species found in forests in South and Southeast Asia.

Parasites, natural enemies (predators), microclimate, and availability of the caterpillars' host plants are the primary factors that regulate populations of swallowtails. Practices affecting their host plants, such as destruction, conversion, and reduction of natural habitats because of deforestation, logging, crops, cattle grazing, and urbanization, are the biggest threats to all butterflies. However, iconic species have been instrumental in the development of a conservation culture, from butterfly houses engaging the public and educating them about tropical species and threatened tropical forests, to teaching children to appreciate insects. Some Papilionidae have become flagship or keystone species, envoys of campaigns for the protection of habitats and other less charismatic organisms, raising local, national, regional, and even international awareness. Species in the family Papilionidae have been fundamental study models for understanding evolution, genetics, mimicry, biochemical analyses, and, more recently, climate change.

THE LIVING FOSSIL BUTTERFLY

ABOVE | The Mexican endemic *Baronia brevicornis* is an enigmatic butterfly that has long lived on the planet but is currently under threat because of the loss of its habitats.

The most primitive species—and the oldest extant lineage of the true butterflies—evolved 80–90 mya and has a subfamily of its own. It is represented by a single genus and species, *Baronia brevicornis*, endemic (not found elsewhere in the planet) to dry forests in Mexico. Two subspecies are currently recognized: the nominate *brevicornis*, which was described in 1893, and the subspecies

GENERA
Baronia

DISTRIBUTION
Neotropical; endemic to southern Mexico

HABITATS
Local in deciduous scrub forests dominated by acacia-like trees at 1,600–4,500 ft (500–1,400 m) elevations in southern Mexico; seasonally dry tropical biome

SIZE
Small to medium: up to 1⅓ in (35 mm)

HOST PLANTS
Thorny bush *Vachellia campechiana* (Fabaceae) (synonym *Acacia cochliacantha*)

CONSERVATION
Categorized as Endangered on the IUCN Red List because of the fragmentation of habitats where the butterfly and host plant are found. Mature acacia trees are associated with grazing systems, and some habitats where *Baronia brevicornis* is found

rufodiscalis, named over a century later. These "living fossils" have a very distinctive appearance among Papilionidae, with dark, tail-less wings and scales colored yellow, orange, and brown. However, there are several forms (polymorphism) in both males and females, with around 25 "forms" named. Females can be larger, paler, and rounder winged than males. Males display strong territorial behavior.

The ecology of this species was unknown for over a hundred years until Mexican researchers pioneered detailed studies of its lifecycle and monitoring of the species populations. Eggs are laid individually, well-separated on the underside of leaves of bushy host plants, hatching after five days. Chalcid wasps can parasitize them. Caterpillars develop five different instars in one month and build tubular structures from the leaves of the host plant. Apparently, this behavior reduces predation, as does the strongly odored substance secreted from a specialized structure called the osmeterium. The pupa develops underground, emerging as an adult after almost 11 months. Peak rainfall periods and humidity are environmental factors known to determine the emergence of both adult butterfly and the leaves in the host plant. Although adults may be found in various patches of forest, reproduction occurs only in areas with good availability of the host plant, where it comprises at least 70 percent of vegetation cover.

have been degraded by 40 percent due to agriculture, including cattle grazing, and timber extraction. Despite its localized distribution and IUCN status, this species is not listed by CITES. The EDGE program for species that are "evolutionarily distinct and globally endangered" does not include butterflies; however, this iconic species would be a prime candidate for listing

TOP LEFT | A male of *Baronia brevicornis* resting on plants. Its antennae are relatively short compared with other butterflies in the family.

TOP RIGHT | Females of *Baronia brevicornis* are distinctive and display different forms and colors.

PARNASSIANS, APOLLOS, AND FESTOONS

BELOW | The striking Spanish Festoon *Zerynthia rumina* can be found in rocky habitats and warm, dry areas in the Iberian Peninsula, southeastern France, and northern Africa.

The Parnassiinae subfamily includes medium- to large-sized butterflies with striking patterns in their wings. They have a remarkable distribution, flying in some of the most remote and highest elevation spots of the planet, such as the Himalayas. There are eight genera, almost 80 species, and over 350 subspecies recognized,

GENERA
Archon, *Hypermnestra*, *Parnassius*, *Allancastria*, *Sericinus*, *Zerynthia*, *Luehdorfia*, and *Bhutanitis*

DISTRIBUTION
Palearctic region in Europe and North Asia; Middle East, North Africa, Southeast Asia, and western North America

HABITATS
In Northern Hemisphere, most species in mountain habitats often at high elevations and sometimes even up to 16,000 ft (5,000 m). *Hypermnestra* is found in arid deserts, *Luehdorfia* in humid forests, and *Zerynthia* in lowland meadows and mountains

SIZE
Large to very large: 1¾–4¾ in (45–120 mm)

HOST PLANT FAMILIES
Aristolochiaceae (*Archon*, *Allancastria*, *Sericinus*, *Zerynthia*, *Luehdorfia*, *Bhutanitis*),

arranged in two tribes, although some authorities recognize three tribes with the addition of the Luehdorfiini. Butterflies in Parnassiinae have a single anal vein in the hindwings, and the pretarsal claws of males are asymmetrical. Species in the genera *Parnassius* and *Zerynthia* show spectacular geographical variation that can be confusing; in the *Parnassius* genus alone, around 280 subspecies have been described and many more "forms." Members of these genera have been subdivided by some into

Zygophyllaceae (*Hypermnestra*), and Crassulaceae (*Parnassius*)

CONSERVATION

Bhutanitis ludlowi is currently categorized as Endangered on the IUCN Red List and listed in CITES Appendix II, along with other species in the genus: *B. lidderdalii*, *B. thaidina*, and *B. mansfieldi*. *Parnassius apollo* and many of its subspecies are also CITES listed

TOP | The Apollo butterfly *Parnassius apollo* is a good flyer over long distances. It shows variation in the eyespots and marks on its wings that can vary in size and number and also in color between individuals, but also between populations from different regions.

ABOVE | Some populations of the Apollo butterfly *Parnassius apollo* occupy small areas, including isolated mountains. The loss of habitat is undoubtedly the biggest threat for the long-term survival of the Apollo butterfly.

innumerable variations and forms, causing taxonomic inflation and confusion. Researchers using molecular characters have suggested that species in *Parnassius* occurring in remote areas of Central and Western Asia show morphological evolution, involving processes of loss and reappearance of characters such as red spots in the wings.

Because butterflies are ectotherms, regulating their body temperature using external sources, they are highly sensitive to their environment. Some species that fly at high elevations and species endemic to mountains have been excellent study organisms for climate

(continued...)

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