INTRODUCTION

What Are Butterflies?

Butterflies are members of the order Lepidoptera that belong to the superfamilies Papilionoidea and Hesperioidea. All other members of the order Lepidoptera are called moths by default. Usually butterflies are contrasted with moths, as shown in table 1. Every one of these generalizations about the differences between butterflies and moths has many exceptions, even in our own fauna. Although the most butterflylike moth family (Castniidae) has no representatives here, we have plenty of diurnal, brightly colored moths, some of which have somewhat-clubbed antennae (they taper to a club, rather than being abruptly clubbed). Most people take them for butterflies, just as many people call *Pieris rapae* a Cabbage Moth because a plain white animal just doesn't register as a "butterfly" to them. The Papilionoidea (true butterflies) and Hesperioidea (skippers) are defined technically on anatomical grounds that need not trouble most users of this book. In recent years a small family of dull-colored "moths" from the New World tropics (Hedylidae) has been found to be nocturnal butterflies after all. (Go figure!)

If you are new to butterfly study, simply familiarize yourself with the look of the various families and read the introductory matter about each. Different books divvy up the families differently—the Heliconiidae may be a family of their own or a subfamily of the Nymphalidae, for example. Don't worry too much about this. The evolutionary (ancestor-descendant) relationships among the groups are real, but the rankings we assign to them are human constructs applied for our convenience. There seems to be no evidence that the butterflies themselves care what we call them.

However you define them, butterflies have been perceived as charismatic by many cultures, past and present. In Hindu tradition, Brahma watched the metamorphosis of a butterfly and was filled with great peace as he looked forward to his own reincarnation and perfection. The ancient Greeks objectified the soul as a butterfly. Associations of the soul with butterflies can be found in folklore from Germany and the Balkans to New Zealand and Assam. Butterflies are prominent in pre-Columbian Mesoamerican art (usually swallowtails!). The Pima Indians say the Creator, Chiowotmalki, flew over the world as a butterfly, looking for the

TABLE 1 Key Differences between Butterflies and Moths

BUTTERFLIES	MOTHS
Active by day	Active by night
Brightly colored	Dull colored
Clubbed antennae	Simple or feathery antennae
Relatively small body	Relatively large body
Rest with wings held over back	Rest with wings open, or rooflike at sides

right place to put mankind. Although butterfly life histories were known to peasants around the world, the first scientific descriptions of them date only to the seventeenth century. Extremely accurate portrayals of adult butterflies can be found in many late Medieval and Renaissance illuminated manuscripts. They are somewhat mysterious, insofar as the butterfly net had not yet been invented—where did the models come from?

It is surprising but true that we have no record of butterfly study or collection in California before the Gold Rush. At that time a Frenchman, Pierre Joseph Michel Lorquin, collected extensively and sent material to the distinguished French entomologist J. B. A. de Boisduval who, in turn, named and described many of our species (see the sidebar "California's First Lepidopterist"). Although California has produced many butterfly workers since, the early efforts were mostly taxonomic. In fact, the first really *biological* treatments of California butterflies only appeared in the middle decades of the twentieth century. The first butterfly book in the California Natural History Guides series was *Butterflies of the San Francisco Bay Region* by J. W. Tilden (1965), followed by Garth and Tilden's *California Butterflies* (1986). We have learned a lot since then, and the emphases in field guides have changed—away from collecting and toward nonconsumptive activities and conservation.

Richard Vane-Wright, a distinguished lepidopterist at the British Museum (Natural History), has written that scientists should devote themselves to studying the origins and dynamics of life in all its manifestations, in the hope that this understanding will help us to "coexist with nature in an intelligent way." That's the slant of this book.

Regional Butterfly Geography

This book covers the traditional 10 Bay Area counties (Marin, Sonoma, Napa, Solano, Contra Costa, Alameda, Santa Cruz, Santa Clara, San Mateo, and San Francisco), the Sacramento–San Joaquin Delta (including part of San Joaquin County), and the Sacramento Valley portions of nine more counties (Sacramento, Yolo, Sutter, Butte, Colusa, Glenn, Tehama, Shasta, and Placer). This only *seems* odd.

The Bay Area is defined rather arbitrarily. It incorporates very diverse landscapes, vegetation, and climates. In fact, no similar-sized chunk of real estate anywhere else in the United States commands such diversity. The Sacramento Valley and the Delta occupy a larger chunk of real estate but are much more uniform physiographically, climatically, and ecologically. In fact, the butterfly fauna of Turtle Bay near Redding is pretty much identical to that along the American River Bikeway in Sacramento, 165 miles away.

Anyone who has driven Interstate 80 between Sacramento and the Bay Area knows that drawing a line between the Sacra-

CALIFORNIA'S FIRST LEPIDOPTERIST

The first known butterfly collector in California, Pierre Joseph Michel Lorquin (1800?–1877), was a French forty-niner. Unsuccessful in the gold fields, he nonetheless remained in California into the 1860s, collecting insects for entomologists in Europe and the eastern United States. His most famous patron was Jean Baptiste Alphonse D. de Boisduval (1799–1879), the most distinguished French lepidopterist of the time. Boisduval published a series of papers naming and describing the species Lorquin sent him, producing the first monograph of the Californian fauna. A great many common California butterflies were thus named by Boisduval. Unfortunately none of Lorquin's correspondence or field notes seems to have survived, so what we know of his travels is largely at second hand, through references in Boisduval's works. We know he ascended the Sacramento and Feather Rivers and was frequently in the Bay Area, where he befriended the early San Francisco lepidopterist Herman Behr. Boisduval praised his courage in "braving the tooth of the bear [grizzlies were still abundant] and the fang of the rattlesnake." He mento Valley and the Bay Area is an arbitrary exercise. Putting aside purely human artifacts (county lines, zones for automobile insurance rates, the limits of irrigation districts, or Catholic dioceses), one can draw lines based on various natural criteria that may not agree among themselves. The eastern edge of the Inner Coast Range can be used as a natural boundary. But the Coast Range breaks between Vacaville and Fairfield and doesn't reappear until Antioch—while the east-west trend of the Potrero Hills further clouds the picture. Vegetation is largely a function of climate, with significant effects of soil type. Many of you already know that the cold California Current is responsible for the clammy gray summers of the coastal fog belt, and that the Central Valley is clear and blazing hot in the summer. Heating inland causes the air to rise and the barometric pressure to fall. This draws in cold, dense marine air ("nature abhors a vacuum") which rushes inland through the gap at the Carquinez Straits. This is the "Delta wind" or "sea breeze" that makes the area near the Delta so much more livable than areas farther north or south. The Delta and Suisun Marsh are cooled substantially but see little coastal fog or low cloudiness. They thus form a climatic transition between the Bay Area and the Sacramento Valley. In summer, Vaca-

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said Lorquin reached "the glaciers of the Sierra Nevada," but this is doubtful, and there are no alpine species among the material he sent back.

Because it is important to fix the type-localities of Boisduval's names, J. F. and T. C. Emmel and S. O. Mattoon (1998), after carefully reviewing everything that was known about Lorquin and his travels, examined the extant type-specimens and compared them to recent material from throughout the species ranges. On this basis they designated type-localities they believe to be good matches. According to them, quite a few common, widespread California butterflies were probably described from specimens Lorquin collected in or near San Francisco or Sacramento.

Lorquin also traveled widely in the Orient, collecting as he went, and was about to leave for the Philippines when he died in 1877.

Until someone invents a time machine, or Lorquin's diary turns up in an attic somewhere, there is no way to prove the inferences by the Emmels and Mattoon to be true. But isn't it fun to imagine what it would be like to be a French-speaking butterfly collector in the rough-and-tumble days of Gold Rush California?

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ville is usually about 5 degrees C (10 degrees F) warmer in the afternoon than downtown Fairfield, and 8 degrees C (15 degrees F) warmer than Cordelia. The pivot point is typically at Lagoon Valley.

The same gap produces a precipitation anomaly in the Vaca Hills just west of Vacaville, where winter storms are amplified as moist air rises upslope on the *east* side of the range. This is reflected in the vegetation and in butterfly distributions. Many unusual butterfly distributions reflect such local situations. For well-informed lepidopterists, it's great fun to search them out. In this case, the Tailed Copper *(Lycaena arota)* and the Crown Fritillary *(Speyeria coronis)* are beneficiaries of the anomaly.

However, you do not need to go that far inland to find dramatic climatic gradients. The cold, gray marine layer is usually less than 600 m (2,000 ft) thick, which means the higher hills in the Bay Area poke well above it and into the hot sunshine. Slight topographic features can have dramatic effects on microclimate, as every San Franciscan knows. Every San Francisco neighborhood has one or more microclimates all its own. For critters the size of butterflies—*cold-blooded* critters—that kind of variation can mean a lot. (See Harold Gilliam's *Weather of the San Francisco Bay Region* [2002] in the California Natural History Guides series.)

So what butterflies should you expect to see where?

Butterflies are heavily dependent on plants—as adult food sources and as larval hosts. The mere fact that a species' host plant occurs in a place does not guarantee that the butterfly will—but if the plant is *absent,* the butterfly will surely be (except as a stray). Butterflies are also responsive to vegetation structure (layering, shade, distribution and geometry of light gaps—remember that these move during the day) and to the overall landscape. It is a truism that to know the butterflies of an area, you should learn the plants. Experienced butterfly workers can often go to a place they have never been before, perhaps even in the dead of winter, and successfully predict what species will be found there. But life is full of surprises. Things that "should be" in a place may *not* be because of some past catastrophe, such as fire. If sources of colonists are available, the species may eventually return. But it takes time—years, decades, perhaps even centuries.

Because of its complex geography, the Bay Area has many—at least 20—major types of plant communities. (Plant communities are classified for our convenience, and most grade into others along their borders, but it is often useful to act as if they are "real.") They are classified in two ways—based on species composition (floristics) or growth form (physiognomy)—and all of this gets to be a bit much for users of this book. Relatively few of our butterflies are tied rigidly to one or only a few communities. The ecological determinants of what occurs where can be simultaneously both coarser and more subtle than plant community classification. Rather than review the vegetation in depth, I encourage you to use this book in conjunction with the plant community information in *Introduction to California Plant Life,* by Robert Ornduff et al. (2003) in the California Natural History Guides series. In this book I have tried to be as precise as possible in defining vegetational association species by species, rather than using standard classificational formulas. In many cases the physiognomy is more informative than community species composition. Usually both factors come into play.

About Serpentine

You will find frequent references to serpentine in this book. Aside from being California's state rock, serpentine (really serpentinite) has fascinated ecologists for decades because its unusual chemistry selects for unusual floras and plant communities. Species found only on serpentine are called serpentine endemics (leather oak *[Quercus durata]* is a good example). Some species occur on serpentine and other unusual soils, but not on "normal" soils; MacNab cypress *(Cupressus macnabiana),* which also occurs on gabbro, is an example. The native herbaceous genus *Streptanthus,* collectively known as jewel flowers (in the mustard family [Brassicaceae]) has speciated dramatically on serpentine soils; several species have very restricted ranges. In general, serpentine vegetation tends to be open, with much bare soil (hence, serpentine sites are often referred to as barrens); tree oaks are excluded; and community boundaries can be razor-sharp where the serpentine contacts other rock/soil types. Serpentine is common in the Coast Ranges and occurs within the city of San Francisco. It has a characteristic butterfly fauna. Two species (John Muir's Hairstreak *[Mitoura gryneus muiri]* and the Sleepy Duskywing *[Erynnis brizo lacustra]*) are serpentine endemic in our region, and about six more species occur preferentially on serpentine. (See *California Serpentines* by Arthur R. Kruckeberg

[1984] and *Introduction to California Soils and Plants,* also by Kruckeberg, both in the California Natural History Guides series.) There is no serpentine in the Sacramento Valley.

The Sutter Buttes

There is one big chunk of bedrock smack in the middle of the Sacramento Valley: the volcanic Sutter Buttes, sometimes called "the world's smallest mountain range." The Buttes are mostly privately owned. Public access, including guided tours, is provided through the Middle Mountain Foundation in Chico. The natural history of the Buttes is documented in the book *Inland Island* by Walt Anderson (2004). This book includes a preliminary butterfly list, but it is probably far from complete. The Middle Mountain Foundation is interested in having more butterfly work done in the Buttes. As might be expected, the fauna of the Buttes is more a (depauperate) foothill fauna than one characteristic of the Sacramento Valley floor.

To Be Continued

Several dozen unusual or unique botanical sites are within the area covered by this book. Some have special soils; others, special microclimates; some have both. Any area that has endemic and/or relict plants is of interest. Although they are well known to native plant enthusiasts, most of these areas have never been surveyed for butterflies. Every one of them could easily become a pet project for a reader of this book—or even a senior honors thesis or master's thesis for a student. Some 150 years after Lorquin first collected in the Bay Area, our ignorance is a sad and shameful state of affairs.

We know the isolated Antioch dunes have a special butterfly—Lange's Metalmark *(Apodemia mormo langei)*. But what about the isolated sandhills at Bonny Doon in the Santa Cruz Mountains, home of various rare plants including the endemic Bonny Doon manzanita *(Arctostaphylos silvicola)?* We know John Muir's Hairstreak has followed its host, Sargent cypress *(Cupressus sargentii),* to Cedar Mountain Ridge near Livermore in southeastern Alameda County. But what other serpentine "goodies" are there? When will someone do a butterfly fauna of Ring Mountain?

Talk to your California Native Plant Society chapter. Scrutinize the geologic maps of your area. Not all ecological "islands" will bear fruit lepidopterologically, but you never know until you try. When Bruce Gervais and I looked for edaphic-endemic butterflies in the Sierra foothills, we were successful beyond our wildest dreams. On the other hand, vernal pools, with their fleeting and unpredictable seasonality, never have special butterflies.

Don't just sit there. *Do It.* (Good luck!)

Where Are Our Butterflies From?

The science of historical biogeography tries to interpret the origins and evolution of floras and faunas in geographic context. The species found in a given area may be derived from very different sources and can be assigned to geographic "elements" reflecting the historical influences affecting that area. The butterflies covered in this book reflect a long and complex history of geologic and climatic change. The climatic preferences shown by the species today may be clues to their origins in the distant past. California has been getting drier for millions of years, but the mediterranean climate we have now, in which nearly all the precipitation falls in the winter, is relatively young. Most, if not all, of our butterflies evolved in climates with summer rain. Adapting to present-day California meant adapting to that long, hot, dry summer.

Before the Pleistocene ice ages (roughly two million to 15,000 years ago), during the Tertiary Period, rich and diverse forest floras dominated the midlatitudes of the Northern Hemisphere. Tectonic (mountain-building) activity combined with climatic change to fragment this flora, leaving species that had once grown side by side eventually isolated in widely different parts of the globe. A substantial part of our butterfly fauna belongs to genera or species groups whose contemporary distributions strongly suggest that they were involved in this process. (We have abundant plant fossils, but very few of butterflies—none from California.)

Our California Tortoiseshell *(Nymphalis californica)*, for example, is very closely related to two Old World species, the Large Tortoiseshell *(N. polychloros)* and Yellow-legged Tortoiseshell

(N. xanthomelas). Our Gray-veined White *(Pieris "napi")* belongs to a very complex group of populations found all around the Northern Hemisphere in cool, moist, mostly forested habitats; no one is sure how many biological species there are. (The true *P. napi* is European.) Our orange-tips are related to species on the East Coast and in Europe, the Middle East, and the Far East. Our Anise Swallowtail *(Papilio zelicaon)* and the skippers of the genus *Ochlodes* have very close Old World kin. Our tailed blues are outliers of a Eurasian group, and so on.

A few species are found naturally (not by human intervention, as far as we know) in both Eurasia and North America. The Arctic Skipper *(Carterocephalus palaemon)* is one. The Painted Lady *(Vanessa cardui),* Red Admiral *(V. atalanta),* and Mourning Cloak *(Nymphalis antiopa)* are others. In the nineteenth century the great naturalist Louis Agassiz, the "father of the Ice Age," suggested (on religious grounds!) that the last three must have been accidentally introduced in commerce in the early days of European colonization. No hard evidence exists pro or con, but most biologists today assume the distributions of these migratory butterflies are natural.

The Cabbage White *(Pieris rapae),* was, however, introduced to North America from Europe in the mid-nineteenth century. The great American lepidopterist Samuel H. Scudder, who had been a student of Agassiz, mapped its spread over the continent from its point of introduction in southern Canada. As discussed in its species account, there remains a possibility that it was introduced even earlier in California, perhaps by the Spanish during the Mission Period.

The history of our biota also involves a tropical element. During the earlier Tertiary, climates were moist and warm, and vegetation characteristic of Central America extended up into our area. As the climate dried, these plants and communities disappeared. We have two native butterflies, the Great Purple Hairstreak *(Atlides halesus)* and the Pipevine Swallowtail *(Battus philenor),* of unambiguously tropical origin, but neither is likely to have persisted through millions of years of climate change. I explain below why the Pipevine Swallowtail is almost certainly a recent arrival. We have one more tropical species, the Gulf Fritillary *(Agraulis vanillae),* in the Bay Area, but it is an extremely recent arrival and probably an introduction.

The Mormon Metalmark *(Apodemia mormo)* represents a faunal element derived from Mexico. Many plants characteristic of California chaparral and oak or pine-oak woodland entered our area from Mexico, where they evolved in a climate with cool, dry winters and warm, wet summers. The plants appear to have made the transition to the mediterranean climate spectacularly well, while Mexican butterflies by and large have not. The butterflies of our Southwest deserts, which enter southeastern California, are still dependent on the summer monsoonal rains. One of them, the Marine Blue *(Leptotes marina)*, is a frequent visitor to our area but at present does not persist. Its own lineage goes back much further, rooted in the Old World tropics.

One of our strangest butterflies is the Golden Hairstreak *(Habrodais grunus)*. It belongs to an Old World group and is not closely related to our other hairstreaks. This may seem surprising, since it is so well adapted to our summer drought, but it seems historically akin to the Eurasian element, not the Mexican. Our Pine White *(Neophasia menapia)* is not closely related to our other whites. It has one living congener in northwestern Mexico and southeastern Arizona. The genus *Neophasia* is related to pierid genera in the New World tropics and to the genus *Delias* from the Indo-Australian region. It is a real enigma in our fauna.

Molecular Keys to the Past

A scientific breakthrough that is helping us work out the history of our butterfly fauna is called molecular phylogeography. This is the study of gene distributions among populations in space. Relatively easy and inexpensive DNA sequencing now allows us to do precise, quantitative genetic comparisons among populations and species. Sometimes we can use a technique called the polymerase chain reaction to obtain usable amounts of DNA from dead, dry museum specimens—we might even sequence the DNA of extinct species! These data are then analyzed using computerized procedures that reconstruct ancestor-descendant relationships and historical movements. For example, if we found a population of a foothill butterfly isolated in the Sutter Buttes, it might be possible to tell whether it got there from the Coast Ranges or the Sierra Nevada, even with no morphological evidence.

In the case of the Pipevine Swallowtail, phylogeographic studies over its entire range reveal that our populations have very little genetic variation, compared to those from the southeastern United States and especially Florida. We infer that our populations went through a genetic "bottleneck," probably due to their having been founded relatively recently by only a few individuals. We believe that the Pipevine Swallowtail had an Ice Age refuge in or near Florida and spread out after deglaciation, attaining its current range only recently. The genetic evidence strongly contradicts the hypothesis that it is an ancient relict from the Tertiary Californian tropical biota. Its host plant, the endemic California pipevine *(Aristolochia californica),* belongs to a genus found in both the Old and New World tropics. We still don't know if the plant is old or new in our biota. One of the curious facts about the Pipevine Swallowtail is that, as a poisonous and warningly colored species, it has mimics everywhere else in its range, but not in California where it is actually most abundant. This also suggests it hasn't been here very long. (See the sidebar "Mimicry" later in this introduction.)

Molecular phylogeography is being applied to more and more groups of butterflies and promises to make testable many ideas that have generated much heat and little light in biogeography for decades.

Regional Affinities of Our Fauna

In 1890 the Bay Area lepidopterist H.H. Behr pointed out that the butterfly fauna of the coast from the Bay Area north was largely a subset of that of the Sierra Nevada. The same is true of the flora. The summer fog markedly reduces the physiological stress imposed by the rainless regime. Without it there would be no redwoods, no Douglas fir *(Pseudotsuga menziesii)*, and no "montane" element in the Bay Area butterfly fauna—species such as the Great Arctic *(Oeneis nevadensis),* Blue Copper *(Lycaena heteronea),* Two-banded Skipper *(Pyrgus ruralis),* Arctic Skipper *(Carterocephalus palaemon),* and the now-extinct Strohbeen's Parnassian *(Parnassius clodius strohbeeni)* from the Santa Cruz Mountains. Many of these are hanging on in very special microclimates. We have abundant fossil plant evidence that shows repeated exchange between the Coast Ranges and Sierra Nevada during the Quaternary (Pleistocene plus Holocene). However, such exchange should not be taken for granted. For example, molecular phylogeography shows that Coast Range (including the Bay Area) and Sierra Nevada populations of the Colorado Skipper *(Hesperia colorado)* are distinct and perhaps not all that recently separated. It would be very interesting to compare molecules from populations of, say, the Two-banded Skipper at sea level in the Bay Area and at tree line in the central Sierra, since we think we know the time frame in which their distribution developed.

Taking a L-O-N-G View

Butterflies first appear in the fossil record in the early Tertiary, some 60 million years ago. By the Oligocene, in the mid-Tertiary (about 35 million years ago), we find most of the extant families—and some modern genera, for example, the painted ladies. It seems strange to think of such delicate creatures preserved in stone, and indeed butterfly fossils are rare—too rare to be very useful in reconstructing historical biogeography, though they can and do present us with astonishing surprises. Because plant fossils are much more numerous (both macrofossils such as leaves and cones, and microfossils—pollen grains, which can often be identified under a strong microscope), we can reconstruct ancient vegetation and then ask ourselves what butterflies might have inhabited it. To do this we have to assume that host-plant and community associations have been stable over the time frame involved—a risky assumption, as we will see. But it is a stimulating intellectual exercise. The great Berkeley paleobotanist Ralph Chaney showed, for example, that a redwood forest similar to Muir Woods grew in the Miocene (some 20 million years ago) in an area of central Oregon that supports sagebrush steppe today. Imagine how different its butterfly fauna must have been then!

Butterfly Life Histories

Metamorphosis

Like all Lepidoptera, butterflies are holometabolous—that is, they have a life cycle encompassing four distinct stages: egg, larva (caterpillar), pupa (chrysalis), and adult. Another term for such a life cycle is "complete metamorphosis."

Metamorphosis is regulated by the endocrine system. Several glands and hormones are involved, forming a "chain of command" with built-in checks and balances (feedback loops). Stretch receptors in the caterpillar tell the nervous system to secrete eclosion hormone, which then stimulates the prothoracic gland to produce ecdysone, or molting hormone. Another hormone, juvenile hormone (JH), is produced by structures in the head called corpora allata. So long as circulating JH is high, each molt leads to another larval stage. As the caterpillar matures, JH levels drop off while ecdysone levels do not. This situation triggers the critical events of metamorphosis. As the adult forms, JH production may resume, stimulating reproductive maturation. In butterflies with seasonal reproductive diapause, or dormancy, JH production is triggered by changing day length or other environmental stimuli and causes ovulation and sexual behavior to begin. Sperm production (spermatogenesis) begins in the late larval stages and seems to be independent of JH. Much of the research on the physiology of metamorphosis has been done with moths, but the principles seem to apply broadly to butterflies as well.

Most people are familiar with a number of butterfly species, but far fewer know their early stages. In fact, the early stages of some of our butterflies have still not been described scientifically. The characteristics of the early stages are just as specific as those of the adult and can be used in classification. Field guides to American caterpillars are just beginning to appear; perhaps one for California is in the cards.

Eggs

Butterfly eggs may be spindle or milk-bottle shaped (Pieridae and Danainae), turban shaped (Lycaenidae), or more or less hemispherical or dome shaped (Hesperiidae and Papilionidae; some Nymphalidae). They are usually white, yellow, or pale green, but those of sulphurs and several whites and orange-tips whose larvae feed on flowers and fruit of the host plant are red or orange. Eggs of the Pipevine Swallowtail *(Battus philenor)* are also rusty red. Seen under an electron microscope, butterfly eggs display intricate patterns of sculpturing or meshwork in the shell, or chorion. Often they have vertical "ribs," which may be connected by thinner horizontal ones. The ribs converge to the upper end of the egg where there are openings, called micropyles, through which sperm enter to achieve fertilization. The micropyles are often surrounded by a rosette of "cells" resembling the petals of a flower. Some butterfly eggs are modified to admit and hold air (through holes called aeropyles), functioning like little diving bells when the host plant is submerged in water or buried in snow. We rarely find empty butterfly eggshells; most larvae eat them immediately after hatching. In species that lay masses of eggs, the first larvae to hatch often nibble at the chorion of nearby eggs, accelerating their hatching in the process.

Larvae

Butterfly larvae undergo a number of molts. At each molt the caterpillar sheds its old skin, which is then often eaten to recycle the nutrients it contains. The head capsule, which is heavily reinforced with a material called sclerotin, is completely inelastic as well as inedible. When rearing larvae, one may collect the head capsules to determine reliably how many molts (usually five) occur. A few butterfly larvae actually molt once inside the eggshell before hatching! The number of molts is usually fixed but may vary in some species, especially those with larval dormancy. The period between molts is called an instar, and larvae can conveniently be classified by instar using the abbreviations L_1, L_2, and so forth. A turn-of-the-century entomologist named Harrison G. Dyar discovered that the sizes of successive head capsules of the same larva are related in a nearly constant ratio, each being about 1.2 to 1.3 times the previous one. This is known as Dyar's law.

Some larvae change their appearance dramatically during development. The Anise Swallowtail *(Papilio zelicaon),* for example, looks like a bird dropping as a first or second instar but then develops a characteristic green ground color with black rings on each segment, incorporating yellow or orange spots. Anise Swallowtail larvae are blacker in cool and humid environments; a few are nearly all black. In hot, dry environments they have much more light green.

The Pipevine Swallowtail larva is normally purplish black with soft red "horns," but development in intensely sunny, hot conditions induces mostly red or all red coloration. Some lycaenid larvae may, to a degree, match the color of their host. Many larvae change color prior to pupating. The green larvae of