BEETLES of Western North America

Arthur V. Evans

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Arthur V. Evans

Princeton University Press Princeton and Oxford

DEDICATION

This book is dedicated to my parents, Ed and Lois Evans, who instilled in me a love for nature and the West; my high school biology teachers Bob Brister and Mike Hanlon, who fueled my passion for field biology; Bob Duff, who first exposed me to the incredible diversity of beetles in western North America; Charlie Hogue, who introduced me to the power of macro photography to illustrate and educate; Elbert Sleeper, for providing me with the academic foundation for all my future studies of the Coleoptera; Chuck Bellamy, who accompanied me on so many field trips throughout the West and beyond; and to my wife, Paula Evans, whose unwavering love and support, combined with her insatiable curiosity for all things beetle, made this book possible.

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PREFACE

The companion volume for this book. Beetles of Eastern North America, began as an exploration of the beetle fauna that inhabited my newly adopted home state, Virginia. However, Beetles of Western North America is more of a homecoming. Its seeds were first sown more than five decades ago during week-long summer camping trips with my family in California on the Central Coast and along the entire length of the Sierra Nevada. Throughout the rest of the year, my parents, Lois and Ed Evans, took my sister Alice and me on weekend excursions to explore the natural wonders and historical sites throughout the Mojave Desert. My parents actively encouraged my interest in insects from a very early age. Later, while on a 4-H field trip to the Entomology Department at the Natural History Museum of Los Angeles County, I learned of the Lorguin Entomological Society that held its monthly meetings at the museum. For several years afterward, my parents made the three-hour round-trip drive numerous times so that I could attend these incredibly influential meetings.

It was during one of my early museum visits that I met Bob Duff, who later invited me to my first insect collecting trip to southeastern Arizona. For several summers, we searched for beetles in the canyons and surrounding environs of the Sky Islands, an archipelago of isolated mountain ranges that connect the southern reaches of the Rockies to the northernmost extent of Mexico's Sierra Madre Occidental. Our trips usually began with brief forays through the mountains and lower desert of southern California, before heading east to cross the Colorado River. On one of these trips, we explored southern New Mexico and drove as far east as western Texas. These expeditions, coupled with Bob's vast entomological knowledge and generous spirit, inspired me to focus my entomological interests on beetles, especially scarabs.

During the summer of 1973, between my sophomore and junior years at Palmdale High School, I enrolled in Field

Biology, a class taught by Bob Brister and Mike Hanlon that, to this day, stands as one of my favorite courses ever. In particular, I recall an overnight camping trip in a white fir forest high in the San Gabriel Mountains where we set up lights to attract nocturnal insects, including many beetles whose identities were yet unknown to me, most of which appear in this book.

Upon graduating high school in 1975, I was hired as student worker in the Entomology Department at the Natural History Museum. There I worked with Charlie Hogue, Julian Donahue, Roy Snelling, and Fred Truxal, all of whom instilled in me the importance of fieldwork, maintaining meticulous records, and keeping a well-curated insect collection. Charlie was particularly influential during my early days in entomology and was instrumental in developing my nascent interest in macro photography and writing for a popular audience.

In spring of 1978, I enrolled in the entomology program at California State University, Long Beach (CSULB), for the express purpose of studying beetles with Elbert Sleeper, a noted authority on weevils. Just weeks before the start of the fall semester, I found myself once again in southeastern Arizona. One evening, while I was tending my blacklight sheet in Bog Springs Campground in Madera Canyon, Chuck Bellamy walked out from the shadows and introduced himself. He was enrolled as a graduate student at CSULB with Sleeper as his advisor, and was pursuing a graduate research project on buprestids. This chance meeting marked the beginning of a friendship and numerous field trips together on two continents over a period of 35 years.

My family, along with these friends and mentors, most of whom are now passed, all had a deep and sustained influence on me both personally and professionally. Their collective support and passion for the natural world helped to propel me on a lifelong path of discovery and scholarship in Coleoptera.

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Once again, I thank Robert Kirk, publisher at Princeton University Press, for the opportunity to write this book. His continued support, guidance, and, most importantly, patience, were instrumental in its completion. I also appreciate the dedication, expertise, and support of his colleagues including Mark Bellis, Bob Bettendorf, Wanda España, Abigail Johnson, Dimitri Karetnikov, Caitlyn Robson, Steve Sears, Matthew Taylor, and Lucinda Treadwell, as well as David Price-Goodfellow at D & N Publishing.

In addition to my own field experiences and those of others, the information in this book was drawn largely from primary sources, located either in my personal library or through digital libraries, particularly the Biodiversity Heritage Library (BHL) and Journal Storage (JSTOR). These most precious resources have long been invaluable to me for this and countless other research projects. Special thanks to the Boatwright Memorial Library at the University of Richmond in Richmond, Virginia, for providing access to JSTOR and various online journals. Many pertinent publications were generously made available by their authors at ResearchGate.

The taxonomic scope and aesthetic appeal of this book would have been impossible to achieve were it not for the excellent beetle images supplied by talented and dedicated photographers. I am forever grateful to the following photographers for their generosity and support of Beetles of Western North America: Alice Abela, Bob Allen, Dave Almquist, Gary Alpert, Bob Anderson, Thomas Atkinson, Paul Bedell, Christoph Benisch, Tom Bentley, Brendon Boudinot, Margarethe Brummermann, Emily Butler, Gary Campbell, Mike Caterino, Patrick Coin, Jillian Cowles, Alan Cressler, Rob Curtis, John Davis, Wendy Duncan, Josef Dvořák, Werner Eigelsreiter, Charley Eiseman, Lynette Elliott, Mike Ferro, Kara Froese, Judy Gallagher, Kevin Gielen, Lucie and Matt Gimmel, Matt Goff, Nicolas Gompel, Henri Goulet, Margy Green, Don Griffiths, Gary Griswold, Joyce Gross, Jeff Gruber, Dennis Haines, Jim Hammond, Guy Hanley, Charles "Chip" Hedgcock, Karl Hillig, Don Hodel, Charlie Hogue (deceased), Jim Hogue, Anna Holden, Tony Iwane, Andrew Johnston, Chris Joll, Scott Justis, Kojun Kanda, Jay Keller, Stanislav Krejčík, Louis LaPierre, Cedric Lee, Mike Lewis, René Limoges, Steve Lingafelter, Ed Lisowski, Nathan Lord, Stephen Luk, Ted MacRae, David Maddison, Crystal Maier, Kirill Makarov, Chris Mallory, Steve Marshall, Kerry Matz, Sean McCann, Gary McDonald,

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Jennifer Read expertly prepared all 1,500+ images used in this work. She converted JPEGs into TIFFs when needed and, only when absolutely necessary, cropped, sharpened, adjusted exposure, repaired or replaced the occasional missing or damaged appendage, and removed dust and stray hairs so that the subject of each and every image looks its absolute best. Jennifer also rendered the illustrations accompanying the key to families.

The following family, friends, and colleagues afforded invaluable assistance to me in terms of providing logistical support for fieldwork, accompanying me in the field, organizing research and collecting permits, furnishing specimen identifications, sorting out taxonomic issues, providing pertinent literature and images, collecting live specimens to photograph, supplying unpublished biological and locality data, or reviewing portions of the manuscript: Rolf Aalbu, Melissa Aja, Ron Alten, Bob Anderson, Sandy Anderson, Salvador Anzaldo, Allan Ashworth, Brad Barnd, Cheryl Barr and Bill Shepard, Ben Beal, Paul Bedell, Chuck (deceased) and Rose Bellamy, Robert Beiriger, Vassili Belov, Larry Bezark, Pat Bouchard, Allison Boyer, Jeff Brown, Margarethe Brummermann and Randy Kaul, Alan Burke, Susan Burke, Dave Carlson, Chris Carlton, Mike Caterino, Don Chandler, Joe Cicero, Andy Cline, Rich Cunningham, Susan Doniger, Hume Douglas, Eric Eaton, Ilya Enuschenko, Terry Erwin (deceased), Alice Evans, Ed and Lois Evans (both deceased), Paula Evans, Bryan Eva, Zack Falin, Vini Ferreira, Linda Ford, Cristina Francois and John Kraft, Nico Franz, Dave Furth, Steve Gaimari, Rosser Garrison and Natalia van Ellenreider, Michael Geiser, François Geniér, Matt and Lucie Gimmel, Lisa Gonzalez,

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Starting in 2010, I undertook six trips to collect and photograph beetles for this book and drove more than 8,000 miles across Washington, Oregon, California, Nevada, and Arizona. I am most grateful to the following individuals and their agencies or institutions for the warm hospitality and numerous kindnesses extended to me during these excursions: Brian Brown (Natural History

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I thank Dan Young (University of Wisconsin, Madison), whose thorough review and constructive criticism of *Beetles* of *Eastern North America* proved incredibly useful during the compilation of this volume.

Lastly, I owe a debt of gratitude to the taxonomists, both present and past, many of whom are listed above. For it was their dogged pursuit of describing and diagnosing species that made it possible for others to identify beetles housed in their collections and in the fine images that appear on the following pages. Perhaps this distillation of their dedication and hard work will inspire a new generation of talented and energetic taxonomists. In a world of evershrinking natural habitat and financial support for taxonomic research, we need taxonomists now more than ever to help document and conserve beetles.

As with all my previous books, I share the success of this work with all the aforementioned individuals, but the responsibility for any and all of its shortcomings, misrepresentations, inaccuracies, and omissions falls squarely on my shoulders.

UPDATES TO BEETLES OF EASTERN NORTH AMERICA

The companion volume to this book, *Beetles of Eastern North America* (Princeton University Press, 2014) covers 1,409 species in all 115 families known to occur east of the Mississippi River. Numerous taxonomic changes that have occurred since its publication, along with corrections for errors of identification, are listed below.

p. 71. *Cylindera unipunctata* (Fabricius) is now known as *Apterodela unipunctata* (Fabricius).

p. 75. Species figured is not Rusty Rib-headed Beetle, *Schizogenius ferrugineus* Putzeys, but is the Pale Sloperumped Beetle, *Clivina pallida* Say.

p. 106. *Helophoris grandis* Illiger is now in the family Helophoridae. *Hydrochus squamifer* LeConte is now in the family Hydrochidae.

- p. 141. Species figured is not *Platydracus maculosus* (Gravenhorst), but likely *P. mysticus* (Erichson).
- p. 144. *Platycerus virescens* (Fabricius) is now known as *P. quercus* (Weber).

p. 162. *Maladera castanea* is now known as *Maladera formosae* (Brenske).

p. 180. *Cyphon collaris* (Guérin-Ménèville) is now known as *Nyholmia collaris* (Guérin-Ménèville).

- p. 181. Cyphon padi (Linnaeus) is now known as
- Contacyphon neopadi Klausnitzer.
- p. 182. Species figured is not *Prionocyphon discoideus* (Say), but is *P. limbatus* LeConte.
- p. 221. *Limonius griseus* (Palisot de Beauvois) is now known as *Gambrinus griseus* (Palisot de Beauvois).
- p. 221. *Limonius stigma* (Herbst) is now known as *Gambrinus stigma* (Herbst).
- p. 228. Cardiophorus cardisce (Say) is now known as *Paracardiophorus cardisce* (Say).
- p. 230. *Dictyoptera munda* (Say) is now known as *Punicealis munda* (Say).

p. 241. Silis bidentatus (Say) should be Ditemnus bidentatus (Say).

p. 260. *Grynocharis quadrilineata* (Melsheimer) and *Lycoptis americana* (Motschulsky) are now in the family Lophocateridae. *Peltis septentrionalis* (Randall) is now in the family Peltidae.

p. 261. *Thymalus marginatus* Chevrolat is now in the family Thymalidae.

p. 272. Species figured is not *Collops quadrimaculatus* (Fabricius), but *C. balteatus* LeConte.

p. 284. *Henotiderus obesulus* (Casey) is now known as *H. centromaculatus* Reitter.

p. 284. Species figured is not *Caenoscelis basalis* Casey, but *C. ferruginea* (Sahlberg).

p. 307. *Hypodacne punctata* LeConte is now in the family Euxestidae.

p. 307. *Murmidius ovalis* (Beck) is now in the family Murmidiidae.

p. 328. Species figured is not *Eustrophopsis bicolor* (Fabricius), but *Synstrophus repandus* (Horn),

p. 349. *Helops aereus* Germar is now known as *Nalassus aereus* (Germar).

p. 363. Asclera puncticollis Say is now known as Ischnomera puncticollis (Say).

p. 364. Asclera ruficollis Say is now known as Ischnomera ruficollis (Say).

p. 384. Image is *Elonus gruberi* Gompel, not *E. basalis* (LeConte).

p. 390. *Tragosoma depsarius* (Linnaeus) in North America is now known as *T. harrisii* (LeConte).

p. 446. Species figured is not *Kuschelina gibbitarsa* (Say), but *K. thoracica* (Fabricius).

p. 492. *Larinus planus* (Fabricius) is now known as *L. carlinae* (Olivier).

GEOGRAPHIC COVERAGE AND CLASSIFICATION

Beetles of Western North America covers 1,428 species in 131 families that occur in Canada and the United States west of the Continental Divide (see map below). The classification presented is that proposed by John Lawrence in the revised edition of Beutel and Leschen (2016), supplemented by Gimmel et al. (2019), Kundrata et al. (2014), and Shin et al. (2017). See the Appendix for Selected References (p. 590) and Classification of the *Beetles of Western North America* (p. 564) for complete bibliographic information and the tribal and subfamilial placement of the species that appear in this book, respectively.



Western North America with inset illustrating major landforms, natural regions, and provincial and state boundaries.

HOW TO USE THIS BOOK

To get the most out of this book, read its introductory sections before venturing out into the field. Once you have become familiar with the lives and bodies of beetles, when and where to look, and the basics of how to collect them, move on to the *family* diagnoses. Learn the diagnostic features that characterize each family, then peruse the individual accounts to get an idea of where and when to look for specific species. Equipped with this information, you will be much better prepared to locate and observe beetles and recognize the specific characteristics that are required for their identification.

ILLUSTRATED KEY TO THE COMMON BEETLE FAMILIES

To assist with the identification of the most commonly encountered beetle families in western North America, a dichotomous key is presented (pp.67–73) consisting of a series of "either-or" choices based on the quality of physical features possessed by a specimen. As with a road map, the reader is directed through a series of junctions called *couplets* that, through a process of elimination, will lead to a smaller and more manageable subset of beetle families. Cross-referenced families in **bold face** are the most likely options, while those in plain text should also be consulted if the bold-faced options don't agree with the specimen in hand.

FAMILY TREATMENTS

Each family treatment includes the family name and its pronunciation, followed by the accepted common name, pronunciation of the scientific family name, a brief overview of the natural history of the species in the family, and a family diagnosis. The *Family Diagnosis* consists of external morphological features that will help to confirm the familial placement of a beetle, including shape, and features of the head, *thorax*, *abdomen*, and appendages. *Similar Families* provides a list of beetle families with species that are superficially similar in appearance, followed by their distinguishing characters. *Fauna* includes the number of species and genera for each family in Canada and the United States as presented in Marske and Ivie (2003). Updated counts are given, if readily available.

With regard to the pronunciation of family names. I have used Edmund C. Jaeger's The Biologist's Handbook of Pronunciations (1960) as a guide. A primer on the proper pronunciation of Latin and Latinized scientific names that addresses the well-known vagaries between North American speakers seldom trained in Latin versus European speakers fluent in one or more Romance languages (and who are generally better versed in Latin), is well beyond the scope of this book. It is understood that Latin is not English, and as Jaeger notes, "It should ever be remembered that while there are formal rules of pronunciation they have not always been observed. Long usage has in certain cases established other ways of sounding some letters, especially vowels, and of placing accents. It is also well to keep in mind that words, especially derived ones, may be pronounced differently by phonetic experts and reputable biologists residing in different countries. The individual preferences are indeed many." In North America, vowels in beetle family names traditionally retain their English sounds, as do consonants, except that "ch" is pronounced "k." It is my hope that readers unfamiliar with beetle family names will find here a foundation on which to learn to pronounce them with a modicum of confidence in the company of North American coleopterists. Following Jaeger, the pronunciations presented in the family diagnoses are indicated by their division into parts (but not necessarily syllables) with hyphens, accents, and diacritical marks pronounced as follows:

â as in far
ā as in bay
ē as in be
ê as in her
ī as in line
ō as in bone
ô as in bore
ū as in blue
û as in urge

SPECIES ACCOUNTS

The species accounts provide the accepted common name (if any), scientific name and authority, length in millimeters, overall form, and color of living beetles. The bright colors (pink, red, orange, yellow, green) of some living beetles frequently fade after death, while metallic colors and iridescence are usually permanent, except in some tortoise beetles (Chrvsomelidae). Read the species accounts carefully to discern species-specific features that may not be evident in the photo. As good as the photographs are in this book, they sometimes do not adequately highlight the subtle characters necessary for accurate species identification. Snap judgments based solely on overall appearance and color may result in misidentifications. Information on distinguishing males and females is presented for many species in which the sexes differ markedly from one another externally. Brief notes on seasonality, habitat, food preferences (for adults and occasionally larvae), and distribution are provided and are based, in part, on published accounts and my own field observations. Exotic or adventive species, either purposely or accidentally introduced, are indicated when appropriate. Every effort has been made to ferret out published distributional records and augment them with

unpublished data gleaned from websites, local lists, records provided by avocational coleopterists, and specimens examined in select museums. Still, the actual distributions of many species are very likely broader than indicated in this book. When known to me, the total number of species in the genus known to occur west of the Continental Divide is included in parentheses at the end of the account. An accurate count of western taxa within speciose genera was sometimes impractical. In these genera, the number of species is followed by NA to indicate the total number of species in Canada and the United States. These numbers are intended to convey the diversity of the genus and thus alert the reader to the possibility of additional species that are similar in appearance that occur in the region.

IDENTIFICATION

Identifying beetles to genus and species can be challenging. Although many conspicuous species are easily identified by direct comparison with a good photograph, most beetles are small, and the characters necessary for their accurate identification simply cannot be examined without having the specimen in hand. Ideally, it is best to capture and properly prepare a short series of specimens so that



HOW TO USE THIS BOOK | IDENTIFICATION

they are available for detailed microscopic examination. Although 10x or 20x hand lenses are very useful for this purpose, a stereoscopic dissecting microscope with good lighting is ideal. Using a hand lens or microscope to examine specimens takes a bit of practice at first, but once you have mastered these indispensable tools, you will never again waste time by straining your unaided eyes to count tarsomeres and antennomeres or examine genitalia.

Many beetles are positively identified to species only through examination of the male reproductive organs and comparison with detailed illustrations and photos in monographs, or comparison with authoritatively identified specimens that were determined by experts.

Although providing detailed drawings of thousands of beetle reproductive organs is well beyond the scope of this book, it is useful to get into the habit of extracting the male genitalia while the specimen is still fresh and pliable so they can be easily examined by a specialist or compared with literature that depicts the genital structures of closely related species. You can extract the genitalia from the posterior opening of the abdomen by gently pulling them out with fine-tipped forceps or with the aid of a fish-hooked insect pin. Removing genitalia from dried specimens requires that the specimen first be softened in a relaxing chamber, or placed in boiling water with a few drops of dish soap added as a wetting agent. Once the genitalia are extracted, you can leave them attached to the tip of the abdomen by their own tissue, where they will dry in place, or remove them entirely and glue to an insect mounting point placed on the pin between the mounted beetle and its locality label for later examination. Some beetles, especially very small species, require specialized techniques for extracting and preserving their genitalia. Consult the pertinent literature or a specialist before undertaking the dissection of these specimens.

Readers requiring accurate species identification, especially for control of horticultural, agricultural, and forest pests, are encouraged to consult coleopterists affiliated with cooperative extension offices or the entomology department of a museum or university for verification.

INTRODUCTION TO BEETLES

BEETLE MORPHOLOGY

Although colors and patterns are sometimes useful, beetles are classified and more reliably identified based on their morphological features. Therefore, a basic understanding of beetle morphology (Fig. 1) is essential for better understanding of not only their evolutionary relationships, but also the terminology used in the family diagnoses and species accounts that appear in this book.





EXOSKELETON

Adult beetles are protected by a highly modified *exoskeleton* that functions as both skeleton and skin. Internally, the exoskeleton serves as a foundation for powerful muscles and organ systems, while externally providing a platform for important sensory structures that connect beetles to their surrounding environment. The exoskeleton is light, yet durable, and composed of a multilayered structure comprising the polysaccharide *chitin* and the protein *sclerotin*.

The exoskeleton is subdivided into *segments*, some of which are composed of smaller plates, or *sclerites*. The segments are joined into functional units that form three body regions (head, thorax, abdomen) and appendages (mouthparts, antennae, legs). Segments are joined together by membranes of pure chitin or separated by narrow furrows called *sutures*. The division of the exoskeleton into body regions and appendages affords flexibility to beetle bodies, much the way the joints and plates of armor allowed knights to maneuver in battle.

BODY SHAPE

When viewed from above, the basic body shape (Fig. 2) of a beetle is variously described as elongate, oval, triangular, or antlike, among other descriptors. Parallel-sided refers to the straight and parallel sides of the body. Terms like *convex*, *hemispherical*, flat, and flattened are also useful for describing the upper or *dorsal* surface. These descriptors are best determined when beetles are viewed from the side. Lady beetles (Coccinellidae) and some leaf beetles (Chrysomelidae) are sometimes referred to as "hemispherical" because their dorsal surfaces are very convex, while the *ventral* surface or underside is relatively flat. *Cylindrical* is usually applied to elongate, parallelsided species with convex dorsal and ventral surfaces and suggests that they would appear almost circular in cross section.

SURFACE SCULPTURING

The nature of the outer surface of beetle exoskeletons, or surface sculpturing, is very useful in species identification. Surfaces can be shiny like patent leather or dulled (*alutaceous*) by a minute network of fine cracks resembling those of human skin. The surfaces of the head and legs,

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Figure 2. Body shapes.

a. elongate, Zopheridae; b. elongate, Passandridae; c. elliptical, Ptinidae; d. elongate-oval, Byturidae; e. elongate-oval, Cerylonidae; f. elongate-oval, Staphylinidae; g. oval, Trogidae; h. oval, Endomychidae; i. broadly oval, Coccinellidae; j. broadly oval, Brentidae; k. obovate, Tetratomidae; l. triangular, Staphylinidae; m. limuloid, Staphylinidae; n. antlike, Staphylinidae.

especially in burrowing species, are sometimes dulled by normal abrasion as the beetle burrows through soil or wood. Sometimes the surface is *glaucous*, or coated with a grayish or bluish coating of waterproof wax secreted by epidermal glands underlying the exoskeleton. This coating is easily rubbed off or dissolved in chemical preservatives and is usually evident only in freshly emerged individuals. Shiny or not, many beetle bodies are typically covered to varying degrees with small pits called *punctures*. Punctures range from very small (*finely punctate*) to large (*coarsely punctate*) and may be shallow or deep. The density or distance of punctures from one another is often reported in terms of the degree of separation in relation to the puncture's diameter. *Contiguous* or nearly contiguous punctures are

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those with their rims in contact with one another, or nearly so. *Cribrate* surfaces are those where irregular punctures are so closely spaced that the surface appears perforated, while *rugose* (rough) surfaces have raised areas formed by small wrinkles, distinct ridges, tubercles, or fingerprint-like whorls. *Granulate* surfaces consist of many small, distinct, and rounded tubercles, like the pebbled surface of a basketball. An *impunctate* surface lacks punctures altogether.

Punctures sometimes bear a single hairlike *seta* (pl. *setae*). Setae are fine or bristly, stand straight up (*erect*), nearly straight (*suberect*), or lie nearly flat on the surface (*recumbent*). Flattened setae, or *scales*, range in outline from nearly round, to *oval* (egg-shaped), *obovate* (pear-shaped), *lanceolate* (spear-shaped) to *linear* (long and slender). Densely setose or scaled surfaces may be partially or completely obscured from view, while the complete absence of setae or scales altogether is referred to as *glabrous*.

HEAD AND ITS APPENDAGES

The capsule-shaped head (Fig. 3) is attached to the thorax by a flexible, membranous neck that is sometimes visible from above (e.g., Meloidae) but usually hidden, along with part of the head, within the first thoracic *segment*, or *prothorax*. In the fireflies (Lampyridae), some hooded beetles (Corylophidae), and other beetle families, the head is completely hidden from above by a hoodlike extension of the dorsal *sclerite* of the prothorax, or *pronotum*.

The compound eyes are usually conspicuous and composed of dozens or hundreds of individual facets or lenses. Awash in light, the lenses of day-active (*diurnal*) beetles are relatively small and flat, while nocturnal species have more convex lenses adapted for gathering all available light. Flightless, cave-dwelling, and subterranean species often have small compound eyes with only a few lenses or may lack eyes altogether. Compound eyes are typically round, or oval to kidney-shaped in outline. The front margins of kidney-shaped eyes may be weakly to strongly notched, or *emarginate*; the antennae of some species may originate within or near the emargination. The eyes are sometimes partially divided in front by a narrow ridge of cuticle, called the *canthus*. In whirligigs (Gyrinidae) and some throscids (Throscidae) and longhorn beetles (Cerambycidae), the canthus completely divides the eye. Some skin beetles (Dermestidae) and omaline rove beetles (Staphylinidae) also possess a simple eye, or *ocellus*, comprising a single lens located on the front of the head between the compound eyes.

The males of several species of Geotrupidae and Scarabaeidae have horns on their heads modified into spikes and scooped blades that are used in mostly "bloodless" battles with other males of the same species over resources that will attract females. The variation of horn size in males of the same species is of particular interest to scientists who study sexual selection. Environmental factors, especially larval nutrition, may play a more important role in horn development than genetic factors. Although outgunned in battle, less endowed males are still fully capable of mating with females and fertilizing their eggs when the opportunity arises.

The mouthparts of all beetles follow the same basic plan: an upper lip (labrum), a pair of mandibles and maxillae, and a lower lip (labium). Although the mandibles of beetles are variously modified to cut and tear flesh (e.g., Carabidae), grind leaves (e.g., Chrysomelidae), or strain fluids (some Scarabaeidae), they also serve other purposes. The outsized mandibles of male Lucanus mazama (Lucanidae) and Archodontes melanopus aridus (Cerambycidae) are not used for feeding at all, but likely have a role in sexual selection. The relatively short and powerful mandibles of the California Prionus, Prionus californicus (Cerambycidae), are used as weapons for defense. Male tiger beetles (Carabidae) use their mandibles to firmly grasp the female during copulation. Attached to the maxilla and labium are delicate, flexible, fingerlike structures, or palps, that assist beetles in the manipulation of food. The long and conspicuous maxillary palps of water scavengers (Hydrophilidae) are easily mistaken for antennae. Each palp is divided into articles called palpomeres. Protecting



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Figure 4. Mouthpart orientation.

a. prognathous head, *Trichocnemis* (Cerambycidae); b. hypognathous mouthparts are directed downward, perpendicular to the long axis of the body, *Chrysochus* (Chrysomelidae); c. rostrate mouthparts are directed downward and are typical of most plant feeding beetles, *Curculio* (Curculionidae); d. maxillae form elongate sucking tube extending posteriorly under body, *Nemognatha* (Meloidae).

the mouthparts from above in most beetles is a broad plate of cuticle formed by the leading edge of the head, or *clypeus*. Underneath the head of most beetles is a sclerite analogous with a lower lip called the *labium*. At the base of the labium are two more sclerites: *mentum* and *gula*.

The mouthparts of beetles vary in terms of their orientation related to the long axis of the body (Fig. 4a–d). For example, the mouthparts of predatory and some wood-boring beetles are typically *prognathous*, and are directed forward and aligned with the long axis of the body. *Hypognathous* mouthparts are directed downward and typical of most plant-feeding beetles, including chafers (Scarabaeidae), some longhorn beetles (Cerambycidae), leaf beetles (Chrysomelidae), and weevils (Curculionidae). The hypognathous mouthparts of some net-winged beetles (Lycidae) and narrow-waisted beetles (Salpingidae), and many weevils (Curculionidae) and their relatives are drawn out into a relatively short or elongate *rostrum*. For most beetles, the primary organs of smell and touch are the *antennae*. These structures are usually attached to the front or sides of the head, often between the eyes and the bases of the



mandibles. Although the antennae exhibit an incredible diversity of sizes and shapes, they all consist of three basic parts: *scape*, *pedicel*, and *flagellum* (Fig. 5). Insect morphologists note that only the scape and pedicel have their own internal musculature and thus are the only true antennal segments, while the remaining articles of the flagellum lack any intrinsic musculature and are called *flagellomeres*. Distinguishing segments and flagellomeres to communicate information about the number of antennal

Figure 6. Basic antennal types of beetles. a. filiform, *Callidium* (Cerambycidae); b. moniliform, *Cucujus* (Cucujidae); c. serrate, *Chalcolepidius* (Elateridae); d. pectinate, *Emelinus* (Aderidae); e. pectinate, *Euthysanius* (Elateridae); f. bipectinate, *Zarhipis* (Phengodidae); g. flabellate, *Ptilophorus* (Ripiphoridae); h. clavate, *Eurymycter* (Anthribidae); i. capitate, *Bactridium* (Monotomidae); j. lamellate, *Polyphylla* (Scarabaeidae); k. geniculate, *Cactophagus* (Curculionidae).



















articles is unwieldy. For the sake of morphological correctness and clarity, all visible antennal articles are referred to as *antennomeres*. The scape is antennomere 1 and the pedicel is antennomere 2. Antennomeres 3–11 refer to the articles of the flagellum. The typical number of antennomeres in beetles is 11, but 10 or fewer are common in some families, while 12 or more occur only rarely.

Beetle antennae are generally shorter than the body and somewhat similar in both sexes. In longhorn beetles (Cerambycidae), males are often distinguished by antennae that reach or exceed the elytral apices, while those of the female are distinctly shorter. For example, male pine sawyers in the genus *Monochamus* have long, threadlike antennae up to three times the length of the body, while those of the female are only slightly longer than the body. In other species, the expanded surfaces of ornate antennal modifications possessed by male *Polyphylla*, *Sandalus*, *Zarhipis*, and *Euthysanius* are packed with sensory pits capable of tracking pheromones released by distant or secretive females.

The principal forms of beetle antennae (Fig. 6) include the following:

- filiform, or threadlike, with antennomeres uniformly cylindrical, or nearly so
- moniliform, or beadlike, with round antennomeres of uniform size
- serrate, or saw-toothed, with flattened, triangular antennomeres

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- pectinate, or comblike, with short antennomeres each bearing a prolonged extension (ramus)
- bipectinate, or comblike, with short antennomeres each bearing two prolonged extensions (rami)
- flabellate, or fanlike, with antennomeres bearing long extensions (rami) that fit together like a fan
- plumose, or featherlike, with antennomeres bearing long, slender, flexible extensions (rami)
- clavate, with outermost antennomeres gradually enlarged to form a distinct symmetrical club
- capitate, with outermost antennomeres abruptly enlarged to form a round or oval symmetrical club
- *lamellate*, with outermost antennomeres flat, forming a distinct, lopsided club
- geniculate, or elbowed, with a long, slender scape with pedicel and flagellomeres attached at a distinct angle; pedicel and flagellomeres (including club), are collectively referred to as the *funicle*

THORAX AND ITS APPENDAGES

As with all insects, the beetle thorax is divided into three segments, the *prothorax*, *mesothorax*, and *metathorax*, each bearing a pair of legs. The underside of the thorax is sometimes modified with impressions or distinct grooves that accommodate the antennae or legs.

The prothorax is always exposed and forms the distinctive "midsection" of the beetle body, while the remaining wing-bearing mesothorax and metathorax, collectively known as the pterothorax, are hidden beneath the modified mesothoracic wings, or elytra. The prothorax is either firmly or loosely attached to the pterothorax. The dorsal sclerite of the prothorax, or pronotum, is sometimes hoodlike and extends forward to partially (e.g., Corylophidae) or completely (e.g., Lampyridae) obscure the head when viewed from above. In some males, the pronotal surface is modified with horns, punctures, tubercles, or ridges that are useful in species identification. The sides, or lateral margins of the prothorax are partly or completely sharply ridged or carinate (e.g., Carabidae, Gyrinidae, Dytiscidae), or distinctly rounded (e.g., Meloidae, some Cerambycidae). The lateral and posterior margins of the pronotum are sometimes narrowly or broadly flattened (explanate), or may have a narrow seam, or marginal bead, along the edge. The portion of the pronotum below the lateral carina is called the hypomeron, sometimes referred to as the pronotal epipleuron. The central portion of the underside of the prothorax, or prosternum, is sometimes attenuated into a spinelike structure directed toward the head or backward. The prosternum is flanked on either side by the propleuron. Sometimes the propleuron is divided into two sclerites by the pleural suture; the sclerite in front is called the proepisternum, while the sclerite behind is the proepimeron. A distinct line or suture that delimits the outer portion by separating the propleuron from the hypomeron is called the notopleural suture in families in the suborder Adephaga, including Carabidae, Gyrinidae, Haliplidae, and Dytiscidae. The front legs are inserted into prothoracic cavities called procoxal cavities. Although sometimes very difficult to see, the nature of these cavities is important in the identification of families, subfamilies, and tribes of beetles. If the cavities are enclosed behind by the proepimeron, or the junction of the proepimeron and the prosternum, they are said to be "closed behind" (Fig. 7a). If these cavities open directly to the mesothorax, they are said to be "open behind" (Fig. 7b).

The thoracic segments of the pterothorax are broadly united with one another and are covered by the elytra. The mesothorax bears the middle legs below and is evident dorsally in many beetles by the presence of a small



Figure 7. Procoxal cavities. a. closed; b. open.

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triangular or shield-shaped sclerite called the *scutellum*. When visible, the scutellum is always located between the posterior pronotal margin and *elytral suture*, the line straight down the back when the elytra meet one another.

The metathorax bears the hind legs and, if present, the flight wings folded beneath the elytra. The hind coxae are usually wide, or *transverse*. In the adephagan families Carabidae, Gyrinidae, Haliplidae, and Dytiscidae, the hind coxae are immovably fused to the *metasternum* and extend backward past the first abdominal *ventrite*, and thus are said to completely divide the first ventrite. In crawling water beetles (Haliplidae), the hind coxae form broad plates that conceal nearly the entire abdomen, a feature that distinguishes them from all other beetle families. In non-adephagan beetle families, the hind coxae are "free," or not fused to the metasternum and do not extend past or "divide" the first abdominal ventrite. The segments of the pterothorax are usually somewhat shortened in wingless (*apterous*) and reduced-wing (*brachypterous*) species.

The most conspicuous and unique feature of nearly all adult beetles is their possession of modified forewings called elytra (sing. elytron) that partially or completely cover the abdomen. The elytra are opaque, soft, and leathery, like those in the elateroid families Lycidae, Phengodidae, Lampyridae, and Cantharidae, or hard and shell-like. At rest, the elytra usually meet over the middle of the back along a distinct and straight line called the elytral suture. The tips the elvtra, or elvtral apices, usually meet at the elvtral suture, too, although in some species they are slightly divergent. Distinctly diverging elytral apices, such as those of Lichnanthe (Glaphyridae) are referred to as dehiscent. The bases of the elytra more or less meet at the posterior margin of the pronotum. The outer basal shoulderlike angle of each elytron is called the humerus (pl. humeri). Punctures irregularly scattered over the elytral surface are referred to as *confused*. Elytra with punctures arranged in rows either are (punctostriate) or are not (punctoseriate) connected by narrowly impressed longitudinal lines, or striae. The spaces between striae are called intervals or interstriae. The portion of side margins of each elytron that is folded downward is called the epipleural fold. Bordering the epipleural fold is a narrow inner edge, or epipleuron (pl. epipleura) that is of variable width and may or may not extend to the elytral apices. A pseudepipleuron is when the lateral elytral declivity drops sharply down and inward before the actual epipleuron.

The elytra are typically short in the rove (Staphylinidae), clown (Histeridae), and sap beetles (Nitidulidae), as well as in some genera of longhorn beetles (Cerambycidae). The elytral apices are often *truncate* and straight, appearing as if they were cut off, or emarginate and flanked or not by one or two tooth- or spinelike projections. The elytra of male *Phengodes* (Phengodidae) are abruptly narrowed apically and oar-shaped, while those of *Ripiphorus* (Ripiphoridae) resemble flaplike scales. In flight, the elytra of most species are lifted and separated when airborne. However, in the fruit chafer genera *Cremastocheilus*, *Cotinis*, and *Euphoria* (Scarabaeidae), and in metallic wood-boring beetles in the genus *Acmaeodera* (Buprestidae), the elytra are partially or totally fused along the elytral suture. When taking to the air, these fast-flying beetles lift their elytra slightly as the membranous flight wings are unfolded and extended through broad notches along the lateral margins near the bases.

The membranous flight wings are supported by a network of hemolymph-filled veins that help them to expand or fold. Some of these veins are hinged so that the wings can be carefully tucked and folded under the elytra. Flight wings are seldom used to identify genera or species, but their venation patterns do offer important clues to the relationships of families. The flight wings of *brachypterous* species are reduced in size, while those lacking these wings altogether are *apterous*. Adult *larviform* females of some Lampyridae, Phengodidae, and Dermestidae may have elytra greatly reduced in size or absent altogether and superficially resemble larvae (Fig. 8).

Beetle legs are subdivided into six segments (Fig. 9). The *coxa* (pl. *coxae*) is generally short and stout, and firmly anchors the leg into the coxal cavity of the thorax while allowing for the horizontal to-and-fro movement of the legs. The *trochanter* is usually small, freely movable in relation to the coxa, but fixed to the femur. The *femur* (pl. *femora*) is the largest and most powerful leg segment and greatly enlarged in jumping species of Scirtidae and Chrysomelidae. The usually long and slender *tibia* (pl. *tibiae*) is sometimes modified into a rakelike structure on the forelegs of burrowing species. The *tarsus* (pl. *tarsi*) is typically divided into multiple articles called *tarsomeres* that lack their own internal musculature, and is terminated by the claw-bearing segment, or *pretarsus*.

The tarsi are of particular value in beetle identification. Each tarsus consists of up to five tarsomeres. The threedigit tarsal formulas used in this book, such as 5-5-5, 5-5-4, or 4-4-4, indicate the number of tarsomeres on the front, middle, and hind legs, respectively. In some species, the penultimate *tarsomere* is small and difficult to see without careful examination under high magnification. The tarsal formulae of these beetles are typically denoted as "appears 4-4-4, but actually 5-5-5". The front tarsi of some male predaceous diving beetles, such as *Cybister*

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Figure 8. Brachypterous, apterous, and larviform females. a. *Pleocoma* (Pleocomidae); b. *Diphyllostoma* (Diphyllostomatidae); c. *Pleotomus* (Lampyridae); d. *Microphotus* (Lampyridae); e. *Zarhipis* (Phengodidae); f. *Thylodrias* (Dermestidae).

and *Dytiscus* (Dytiscidae), are highly modified with adhesive pads underneath that enable them to grasp the female's smooth and slippery elytra while mating. In male *Phanaeus* (Scarabaeidae), the front tarsi are absent altogether. The feet of some longhorn beetles (Cerambycidae) and leaf beetles (Chrysomelidae) are equipped with broad, brushy pads underneath that are tightly packed with setae, enabling them to walk on smooth vertical surfaces or cling to uncooperative mates. Cicada parasite beetles (Rhipiceridae) and some click beetles



Figure 10. Claws. a. cleft, *Macrodactylus* (Scarabaeidae); b. toothed, *Polyphylla* (Scarabaeidae); c. appendiculate, *Oberea* (Cerambycidae); d. pectinate, *Melanotus* (Elateridae); e. serrate, *Synuchus* (Carabidae); f. simple, *Alaus* (Elateridae).

(Elateridae) have tarsomeres bearing membranous flaps that project outward.

The claws of beetles are frequently modified (Fig. 10). *Cleft* or *incised* claws are finely split at the apex. *Toothed* claws have one or more distinct teeth underneath on the claw blade. *Appendiculate* claws have a broad flange at the base of the blade. *Serrate* claws have finely notched blades resembling the teeth of a saw, while *pectinate* claws have blades with fine, comblike teeth. *Simple* claws, which are typical of many beetles, lack any such modifications.

ABDOMEN

Beetles typically have 10 abdominal segments, but only five or six segments are usually visible. Each of these segments is more or less ringlike and consists of only two sclerites: a dorsal *tergum* (pl. *terga*) or *tergite*, and the ventral *sternum* (pl. *sterna*). Beetle tergites covered by the elytra are usually thin and flexible, but those exposed in beetles with short elytra tend to be thicker and more rigid. The penultimate and ultimate tergites are called the *propygidium* and *pygidium*, respectively. The pleural membranes are usually more or less hidden from view. Breathing pores, or *spiracles*, are located in the pleural membrane and/or in the lateral-most regions of the tergites or *ventrites*.

The visible abdominal sternites are called *ventrites*, and each is numbered beginning from the base of the abdomen regardless of the true morphological segment it represents. For example, ventrite 1 is usually abdominal sternite 2 or 3. The ventrites are of varying lengths in relation to one another and are either distinctly or barely separated by deep to shallow sutures or narrow membranes. Ventrites that are fused together, as evidenced by shallow or obsolete sutures, are *connate*, while "free" ventrites are those that are separated by distinct sutures or membranes. In some families, some or all of the ventrites are connate.

The remaining abdominal segments are internal, the most posterior of which are variously modified for reproductive activities: egg laying in females and copulation in males. Long *ovipositors* are characteristic of beetles that deposit their eggs deep in sand or plant tissues, while short and stout ovipositors are indicative of species that deposit their eggs directly on



Figure 11. Larviform female pink glowworm with three males, *Microphotus angustus* (Lampyridae).

the surface of various substrates. The often elaborate and distinctive male reproductive organs are of considerable value in species identification and are sometimes the only means of distinguishing closely related species.

BEHAVIOR AND NATURAL HISTORY

The mating behaviors, developmental strategies, and life cycles of all beetles in western North America assure their reproductive success by maximizing their efforts to locate mates, eliminating competition for food and space between larvae and adults, and adapts them to cope with dramatic seasonal shifts in temperatures that typify a temperate climate. With their compact and armored bodies, chewing mouthparts, and modified legs, beetles are equipped to occupy and thrive in diverse habitats. Both adults and larvae chew, burrow, mine, and swim their way through sandy coastal beaches, chaparral, coastal and montane forests, arid desert dunes, backyards, urban parks, and agricultural fields. The ability of most beetles to fly increases their chances of finding food and mates, and affords them opportunities to seek out and colonize new habitats.

MATING BEHAVIOR

With relatively short lifespans lasting only weeks or months, most beetles have little time to waste in finding mates. They have evolved various channels of communication that enhance their efforts at finding a mate, including scent, sight (Fig. 11), or sound. These strategies are often remarkably effective, luring in numerous eager mates from considerable distances. Sex-attractant pheromones are used by many species to attract and locate mates over long distances. Males of these species often have longer or more elaborate antennal structures (e.g., Scarabaeidae, Ptilodactylidae, Rhipiceridae, Phengodidae, some Elateridae, Ripiphoridae, Cerambycidae) that provide more surface area for incredibly sensitive sensory pits capable of detecting just a few molecules of the female's pheromone wafting about in the air. These males typically track and locate females by flying in a zigzag pattern until they cross through the female's "odor plume" of pheromone. Once the plume is located, the male follows the increasing concentration of pheromone molecules directly to its source.

The best-known example of visual communication in beetles is that of *bioluminescence*. Bioluminescence is characteristic of some western fireflies, larval and adult

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female glowworms (Fig. 12), as well as some click beetles. The whitish, greenish-yellow, or reddish light emanating from these insects is produced by special abdominal (e.g., Lampyridae, Phengodidae) or pronotal (e.g., Elateridae) organs. The tissues within these light-producing organs are supplied with oxygen via numerous tracheae. The brightness and duration of the light are controlled by the nervous system that regulates the amount of oxygen reaching these organs and reacting with the pigment luciferin, a chemical reaction sped up by the presence of the enzyme luciferase. The quality of the light produced varies depending on species, as well as temperature and humidity. Bioluminescence in fireflies is virtually 100% efficient, with almost all the energy that goes into the system given off as light. In fact, the light produced by just one firefly produces 1/80,000 of the heat produced by



ABOVE: Figure 12. Bioluminescent Zarhipis (Phengodidae) larva.

a candle flame of the same brightness. By comparison, notoriously inefficient incandescent lightbulbs lose up to 90% of their electrical energy as heat.

Some male death-watch beetles (Ptinidae) tap their heads against the walls of their wooden galleries to lure females into their tunnels, but most beetles produce sound by rubbing two ridged or roughened surfaces together, a behavior known as stridulation. Stridulation generally occurs during courtship, confrontations with other beetles, or in response to other stressful situations, such as attack by a predator. Longhorn (Cerambycidae), June (Scarabaeidae), and bark beetles (Curculionidae) stridulate by rubbing their elvtra with their leas or abdomen to create a chirping or squeaking sound when alarmed, possibly to startle predators; some aquatic species stridulate by rubbing their elytra and abdomen together. Stridulatory communication between larvae and adults of the same species occurs, too, possibly as a means to help keep offspring and their parents in close proximity to one another, a theory partly supported by the dependence of some larvae on adults for a steady food supply. For example, hungry Nicrophorus larvae are summoned to feed on carrion specially prepared by their parents. These stridulating beetles rub a pair of abdominal files against the underside of their elytra to produce sounds likened to ringing a dinner bell.

Elaborate courtship behaviors in beetles are rare, although some species may engage in nibbling (Cantharidae), licking (Cerambycidae), or antenna pulling (Meloidae) just prior to copulation. In most species of beetles, the male typically mounts the female from above and behind (Fig. 13). Females usually have enormous reserves of eggs awaiting



Figure 13. Mating jewel beetles, Gyascutus planicosta (Buprestidae).



Figure 14. Mate guarding or postinsemination association, Cicindela hirticollis gravida (Carabidae).

fertilization, but need to mate only once, despite being courted by numerous enthusiastic males responding to their pheromones. Sperm is usually stored internally in a saclike reservoir called the *spermatheca*. Fertilization does not occur until her eggs travel past the spermatheca, just as they are about to be laid. In these females, it is the sperm of the last male that fertilizes the eggs. To assure their paternity, male tiger beetles (Carabidae) continue to tightly grasp their partners with their mandibles (Fig. 14) after copulation is completed until the eggs are laid, a behavior called *postinsemination association*.

Not all species of beetles must mate to reproduce. *Parthenogenesis*—development from an unfertilized egg—occurs among several families of beetles, including leaf beetles (Chrysomelidae) and weevils (Curculionidae). Males of parthenogenetic species are rare or unknown



Figure 15. Canthon indigaceus (Scarabaeidae) on dung ball.

altogether. The females of these species are solely responsible for maintaining the population and do so by producing cloned offspring.

PARENTAL CARE

For most beetles, care of offspring is limited to selection of the egg-laying site by the female. However, some species engage in relatively elaborate behaviors to ensure the survival of their eggs and larvae. For example, some ground beetles (Carabidae) deposit their eggs in carefully constructed cells of mud, twigs, and leaves, while a few water scavenger (Hydrophilidae) and minute moss beetles (Hydraenidae) enclose their eggs singly or in batches within cocoons made of silk secreted by special glands in the female's reproductive system. Depending on the species, leaf beetles (Chrysomelidae) apply a protective coating of their own feces to their eggs that are laced with distasteful chemicals sequestered from the tissues of the host plant. Leaf-mining metallic wood-boring beetles (Buprestidae) and weevils (Curculionidae) provide their offspring with both food and shelter by sandwiching their eggs between the upper and lower surfaces of leaves. Some longhorn beetles provide their larvae with dead wood by girdling, or chewing, a ring around a living tree branch and laying their eggs on the soon-to-be-dead outer tip. Dying branch tips quickly turn brown, a phenomenon called *flagging*, and stand in stark contrast to healthy green foliage. The girdle eventually weakens the branch, causing it to break and fall to the ground where the larvae can feed and develop inside, undisturbed. Female leaf-rolling weevils (Attelabidae) cut the leaf's midrib before laying their eggs in the rolled-up portion of the leaf.

Dung scarabs (Scarabaeidae) and Nicrophorus burying beetles (Silphidae) exhibit varying degrees of parental care well beyond the egg stage. Both males and females may cooperate in digging nests for their eggs and provision them with dung (Fig. 15) or carrion, respectively, for their brood. Dung and carrion are rich in nutrients, and competition for these resources can be fierce. Many dung- and carrionfeeding beetles have evolved tunneling or burying behaviors to quickly hide excrement or dead animals from the view of other scavenger species. Burial not only secures food for their young, it also helps to maintain optimum moisture levels for successful brood development. Nicrophorus beetles exhibit the most advanced form of parental care known in beetles. They meticulously prepare corpses as food for their young by removing feathers and fur, reshape them by removing or manipulating legs, wings, and tail, all while coating the carcass in saliva laced with antimicrobials

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that slow decomposition. Females deposit their eggs in the burial chamber and remain with their young larvae as they feed and develop. The brood's first meal consists of droplets of chewed carrion regurgitated by their mother in a broad depression on the carcass.

Ambrosia and bark beetles (Curculionidae) also provide food and shelter for their young, carving elaborate galleries beneath the bark of trees or in galleries that penetrate the sapwood. Adult females cultivate and store *ambrosia* fungus in their *mycangia*, specialized pits on their bodies. As they colonize and tunnel into new trees, they introduce the "starter" ambrosia fungus into the brood chambers, where it will be used as food for both themselves and their developing larvae.

METAMORPHOSIS AND DEVELOPMENT

Beetles develop by a process called *holometaboly*, or complete metamorphosis, that usually involves four distinct stages: egg, *larva*, *pupa*, and adult (Fig. 16). The egg stage is sometimes absent in telephone-pole beetles (Micromalthidae), while the pupal stage may be greatly modified in female glowworms (Phengodidae) and some female fireflies (Lampyridae). Each developmental stage is adapted to a particular season and set of environmental factors that ultimately enhance the individual beetle's ability to survive unfavorable conditions. Adults and larvae are often not found together in the same place at the same time, thereby functioning in the environment as two distinct species. The spatial and temporal separation of the larvae and adults within the same species effectively eliminates competition for the basic resources of food and space.

Females lay their eggs singly or in batches (Fig. 17) through a membranous and sometimes very long tube, or *ovipositor*, usually on or near suitable larval foods. Aquatic species lay their eggs singly or in small batches on submerged rocks, plants, or chunks of wood and other objects. Ground-dwelling beetles that scavenge plant and animal materials often deposit their eggs in soil, leaf litter, compost heaps, dung, carrion, and other sites rich in decomposing organic materials and animal waste. Plantfeeding species drop their eggs at the base of the larval food plant or glue them to various vegetative structures; some species carefully apply a protective coating of their own feces on the eggs. Wood borers, such as longhorn beetles (Cerambycidae), deposit their eggs in cracks, crevices, and wounds of bark.

Most beetle larvae bear little or no resemblance whatsoever to the adults with regard to their form and food preferences. Their growth is typically rapid, and the



Figure 16. Larvae, pupae, and adult mealworm, Tenebrio molitor (Tenebrionidae).



Figure 17. Female Harmonia axyridis (Coccinellidae) laying eggs.

outgrown exoskeleton is replaced with a new and roomier one secreted by an underlying layer of epidermal cells, a process called *molting*. The stage between each larval molt is called an *instar*. Most species pass through three to five instars, although some may have as few as two (Histeridae) or as many as seven (Dermestidae) or more (Pleocomidae).

Beetle larvae (Fig. 18) are incredibly diverse, although many may be grouped according to their overall body form. The slow and caterpillar-like larvae of lady beetles (Coccinellidae) and some leaf beetles (Chrysomelidae) are called *eruciform*; they typically have well-developed heads, legs, and fleshy abdominal protuberances. Sluggish, C-shaped *scarabaeiform* grubs have distinct heads and well-developed legs suited for burrowing through the soil or rotten wood and are characteristic of scarab beetles and their kin (Lucanidae, Trogidae, Scarabaeidae, etc.). The *elateriform* larvae of click beetles (Elateridae) and many darkling beetles (Tenebrionidae) have long, slender bodies

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Figure 18. Beetle larvae.

a. Calosoma (Carabidae); b. Amblycheila (Carabidae);
c. Tropisternus (Hydrophilidae); d. Sinodendron (Lucanidae);
e. Cotinis (Scarabaeidae); f. Nosodendron (Nosodendridae);
g. genus unknown (Buprestidae); h. Eubrianax (Psephenidae);
i. Brachypsectra (Brachypsectridae); j. Lygistopterus (Lycidae);
k. Microphotus (Lampyridae); l. Pacificanthia (Cantharidae);
m. Alaus (Elateridae); n. Anthrenus (Dermestidae); o. Harmonia
(Coccinellidae); p. Aphorista (Endomychidae); q. Coelus
(Tenebrionidae); r. Dendroides (Pyrochroidae); s. Collops
(Melyridae); t. Cypherotylus (Erotylidae); u. Aethina (Nitidulidae);
v. genus unknown (Cerambycidae); w. Trirhabda (Chrysomelidae).





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with short legs and tough exoskeletons. Thick, legless, maggotlike weevil grubs are called *vermiform*, while the flattened, elongate, and leggy predatory larvae of ground (Carabidae), whirligig (Gyrinidae), predaceous diving (Dytiscidae), water scavenger (Hydrophilidae), and rove beetles (Staphylinidae) are *campodeiform*. The broadly oval, distinctly segmented, turtlelike water penny larvae (Psephenidae) are *cheloniform*, while the sowbug-like larvae of some Silphidae are referred to as *onisciform*. *Fusiform* larvae are broad in the middle and more or less tapered at each end.

Each successive instar is generally like the last in form, just larger in size. The parasitic larvae of cicada parasite beetles (Rhipiceridae), blister beetles (Meloidae), and wedge-shaped beetles (Ripiphoridae) all develop by a special type of holometaboly called hypermetamorphosis, a developmental process characterized by two or more distinct larval forms. The first active and leggy instar, or triungulin, is adapted for seeking out the appropriate host. Once the triungulin has located a host, it molts into a decidedly less active larva with short, thick legs and begins to feed. This form is followed by a fat, legless grub that eventually develops into a more active short-legged grub that spends most of its time preparing a pupal chamber. Although not parasites, the larvae of telephone-pole beetles (Micromalthidae) also develop by hypermetamorphosis and, under the right conditions, can reproduce additional larvae by laving eggs or giving live birth to another larva. The phenomenon of asexual reproduction by larvae is called paedogenesis.

Instead of compound eyes, most beetle larvae possess from one to six simple eyes on each side of the head called *stemmata*, while others lack any visual organs whatsoever and are blind. The mouthparts of most larvae are adapted for crushing, grinding, or tearing foodstuffs. Predatory larvae are liquid feeders and use their mouthparts to pierce and drain prey of their bodily fluids. Some species have sickle-like and grooved mouthparts that channel digestive fluids into insect prey to liquefy their tissues and organs. The antennae of beetle larvae typically consist of only two or four simple segments, but those of Scirtidae (p.114) have long, multisegmented filiform antennae. Giant water scavenger larvae (*Hydrophilus*), known as water tigers, use their sharp, pointed antennae in concert with their mandibles to tear open insect prey.

The beetle larva thorax consists of three very similar segments, the first of which may have a thickened plate across its back. Legs, if present, typically have six or fewer segments. Larvae with legs greatly reduced or absent generally feed inside plant tissues or parasitize other insects.



Figure 19. Larval urogomphi, Dendroides (Pyrochroidae).

Most beetle larvae have 9- or 10-segment abdomens that are soft and pliable, allowing their food-filled bodies to rapidly expand without having to molt. Although legless, the abdomen in some terrestrial species possesses segments equipped with fleshy wartlike protuberances that afford the larva a bit of traction as it moves about. The abdomen of some aquatic larvae in several families (e.g. Gyrinidae, Haliplidae, Hydrophilidae, Eulichadidae) possess simple or branched gills laterally or ventrally. The terminal segment of some larvae may end in a pair of fixed or segmented projections called *urogomphi* (Fig. 19).

Many terrestrial beetle larvae live in leaf litter, rotten wood, and various kinds of fungi where they consume a wide variety of organic tissues. Phytophagous, or plantfeeding, larvae consume living and decomposing flowers, fruits, seeds, cones, leaves, needles, twigs, branches, trunks, and roots. Leaf-mining species tunnel between the upper and lower surfaces of living leaves, creating discolored blotches, blisters, or meandering tunnels trailing in their wake. Wood-boring larvae tunnel between the bark and wood and, depending on species, either pupate there or tunnel into the sapwood. Still others attack only the heartwood and leave the outer, living sapwood intact. Some larval carrion beetles (Silphidae) feed on accumulations of plant material, while dung-feeding larvae (e.g., some Hydrophilidae and Scarabaeidae) eat plant materials that have been partially decomposed within the digestive tracts of vertebrates.

The fleet-footed *campodeiform* larvae found in several beetle families actively hunt for prey in leaf litter or under bark, while decidedly stationary tiger beetle larvae (Carabidae) ambush prey that stray too close to the entrance of their vertical burrows. Some larval ground

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beetles and rove beetles (Staphylinidae) actively seek out and consume the pupae of leaf and whirligig beetles, and flies. Glowworm larvae (Phengodidae) overpower millipedes by coiling themselves around the front of a millipede's body (Fig. 20) before biting it just behind and underneath the head. Through its sharp and channeled sickle-shaped mandibles, the larva injects into its victim gut fluids laced with paralyzing toxins and digestive enzymes. Immobilized almost instantly, the millipede is unable to release its noxious defensive chemicals and guickly dies as its internal organs and tissues are liquefied. The phengodid larva consumes all but the millipede's exoskeleton and defensive glands. The larvae of blister beetles (Meloidae) attack underground grasshopper egg masses or invade subterranean nests of solitary bees to raid their stores of pollen and nectar, as well as consume their brood. Rhipicerid and ripiphorid larvae are ectoparasitoids that attack cicada nymphs and various mudnesting wasps, respectively.

Beetle larvae employ a variety of morphological and chemical strategies to defend themselves. Dermestid larvae (Fig. 21) have clusters of bristly hairlike setae that function as irritating deterrents to predatory mammals, reptiles, and birds. Located on the upper surface of the abdomen, these setae are arrayed like a defensive fan to ward off potential enemies and entangle the mouthparts of ants and other small arthropod predators. These very same structures are common components of household dust and are implicated in triggering allergic reactions and asthma attacks. Tortoise beetle larvae (Chrysomelidae) carry racks of fecal material and old larval exoskeletons over their backs (Fig. 22) under which they can hide, while other leaf beetles construct protective cases from their waste that cover their entire bodies (Fig. 23).



Figure 20. Glowworm larva, *Phengodes* (Phengodidae), attacking a millipede.



Figure 21. Dermestes (Dermestidae) larva.



Figure 22. Tortoise beetle larvae, *Gratiana* (Chrysomelidae), with defensive rack of fecal material and cast larval exoskeletons.



Figure 23. Case-bearing leaf beetle larva (Chrysomelidae, Cryptocephalinae).



Figure 24. Pupa, Harmonia (Coccinellidae).

The last larval instar, sometimes referred to as the prepupa, develops into the pupa. Dramatic physiological and morphological transformations take place during the pupal stage (Fig. 24) that marks the end of the larval life adapted primarily for feeding and the beginning of the adult mode of life dominated by reproduction. It is during the pupal stage that the physical details of the adult are revealed. Most beetle pupae are of the adecticous exarate type and lack functional mandibles (adecticous) and have legs not tightly appressed (exarate) to the body. Some species (Ptiliidae, some Staphylinidae, Clambidae, Coccinellidae, some Chrysomelidae) have adecticous pupae with legs that are tightly appressed (obtect) along the entire length of the body. Many pupae have functional abdominal muscles that allow for some movement. Some of these species have specialized teeth, or sharp edges along the opposing abdominal segments known as gin-traps that snap shut on the appendages of ants, mites, and other small arthropod predators and parasites.

Many beetles overwinter as pupae within chambers located deep in soil, humus, or the tissues of plants where they are less likely to be subjected to freezing temperatures. Some scarab beetle larvae (e.g., Cotinis, Cremastocheilus, Dynastes, Euphoria), among others, construct protective pupal chambers from their own fecal material. Leaf beetles (Chrysomelidae) generally pupate in the soil, sometimes inside a *cocoon* within a specially dug chamber, although the larvae of Ophraella typically anchor their meshlike cocoons up on their host plant. In glowworms (Phengodidae) and some fireflies (Lampyridae) the females undergo a modified pupal stage and emerge from the pupa, or eclose, as an adult that closely resembles the previous larval instar. Adult larviform females lack wings or have greatly reduced elytra relative to the male, and are best distinguished from the larvae by the presence of compound eyes externally and reproductive organs internally.

ADULT EMERGENCE

The requisite combination of time, temperature, and moisture triggers adult emergence, or *eclosion*, from the pupa. Freshly eclosed adults are typically soft and pale, or *teneral* (Fig. 25). Their exoskeleton hardens and darkens as it undergoes chemical changes akin to the tanning of leather. Adult beetles are full-grown and never molt again; however, the abdomens of some soft-bodied leaf and blister beetles are capable of limited expansion so they can stuff themselves with food, or become filled with eggs. Once fully developed, adult beetles may or may not feed, but they are ready to mate and reproduce.

FEEDING

Equipped with powerful mandibles, beetles can cut, grind, or chew their way through all kinds of fungal, plant, and animal tissues, living or dead. Most beetles are herbivores and many obtain their nutrition by consuming living plant tissues. Scarabs (Scarabaeidae), blister beetles (Meloidae), leaf beetles (Chrysomelidae), and weevils (Curculionidae) are particularly fond of leafy foliage and will strip leaves of their tissues or completely defoliate plants. Pestiferous beetles in these families hungrily consume turf, garden vegetables, ornamental shrubs, and shade trees as well as agricultural or horticultural crops, while their subterranean larvae frequently attack the roots.

Pollen- and nectar-producing flowers are particularly attractive to some species (e.g., Scarabaeidae, Cantharidae, Lycidae, Meloidae, Mordellidae, Cerambycidae), but the role of beetles as pollinators (Fig. 26) requires further study. Many wood-boring beetles (e.g., Buprestidae, Cerambycidae, Curculionidae) feed on dead or dying wood. Their tunneling and feeding activities in twigs, limbs, trunks, and roots hasten



Figure 25. A freshly eclosed and teneral lady beetle, *Harmonia* (Coccinellidae).





Figure 26. Flower-visiting beetles that eat pollen. a. *Eupompha* (Meloidae); b. dasytine melyrid beetles (Melyridae).

decay and attract a succession of additional beetles and other insects that prefer increasingly rotten wood. Scavengers prefer their plant foods to be first "cured" by the action of fungi and bacteria. Dung-feeding beetles (some Hydrophilidae, Scarabaeidae) consume plant materials already partially broken down by the digestive tracts of horses, cattle, dogs, and other vertebrates. Some of these species not only consume feces, they also bury it as food for their young, and are among the most beneficial, yet least appreciated insects.

Many beetles are directly or indirectly dependent on fungi. In fact, the larvae of some wood-boring species are unable to complete their development in wood unless the tree has been previously weakened or killed by fungus. To this end, bark beetles (Curculionidae) introduce fungal spores that kill twigs and branches, and such infections may eventually kill the entire tree. Some of these species have special cavities associated with the head or thorax called mycangia that are specifically adapted for storing fungal spores. Ambrosia beetles chew chamberlike tunnels in wood and introduce into them a specific type of fungus that lines the walls, thus providing food for both themselves and their larvae. These and other fungi like them are entirely dependent on beetles for their dispersal and survival. Adults and larvae of featherwing (Ptiliidae), round fungus (Leiodidae) (Fig. 27), minute brown scavenger (Latridiidae), and others are frequently found with mold and other fungi, and slime mold. Some flat bark (Trogossitidae), pleasing fungus (Erotylidae), handsome fungus (Endomychidae), some darkling (Tenebrionidae), and tetratomid beetles (Tetratomidae), and fungus weevils (Anthribidae), among other families, are also associated with sac fungi (Ascomycota) and mushrooms, puffballs, bracket fungi, and their kin (Basidiomycota).

Ground and tiger beetles (Carabidae) are formidable hunters that rely on speed and powerful mandibles (Fig. 28)



Figure 27. Agathidium (Leiodidae) on fungus.



Figure 28. Calosoma (Carabidae) eating a white-lined sphinx moth caterpillar, Hyles (Sphingidae).

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to overpower and tear apart a broad range of insect and other invertebrate prey. Rove (Staphylinidae) and clown beetles (Histeridae) hunt for maggots, mites, and other small arthropods living among leaf litter, dung, carrion, under bark, in decaying plant and fungal tissues, and sap flows: some are specialists living in bird and mammal nests. Predaceous diving (Dytiscidae) and whirligig (Gyrinidae) beetles both attack aquatic invertebrates or terrestrial insects trapped on the water's surface. Many water scavenger beetles (Hydrophilidae) consume both animal and plant tissues. Predatory scarab beetles (Scarabaeidae) are rare, but adult Phileurus have been observed eating various insects, while ant-loving scarabs (Cremastocheilus) prey on ant brood. Checkered beetles (Cleridae) and some soldier beetles (Cantharidae) prey on wood-boring and sapfeeding insects, respectively. Lady beetles (Coccinellidae) consume a variety of foodstuffs, especially pollen and molds, but are also predators of aphids, mealybugs, and other plant pests.

Carrion and burying beetles (Silphidae) scavenge freshly dead carcasses, occasionally preying on fly maggots that compete for the same juicy and nutritious resource. Hide beetles (Trogidae) derive most of their diet from keratin-rich feathers, fur, claws, and hooves. Ham beetles (Cleridae) gnaw on dried tissues and will attack dried meats, while skin beetles (Dermestidae) will also infest study skins and insect specimens. Natural history museums around the world enlist the services of select dermestid beetles to clean animal skeletons used in research collections and exhibits, while related species are strictly monitored and controlled as museum pests.

DEFENSE

Beetles are continually beset by various insectivorous predators and parasites, as well as disease-causing agents known as entomopathogens that typically infect insects. Birds, bats, rodents, other small to medium-sized mammalian predators (Fig. 29), reptiles, amphibians, and fishes are among the vertebrates that regularly utilize them as food, while spiders, ants, robber flies (Fig. 30), and other beetles rank high among invertebrate predators of beetles. To avoid becoming meals for hungry predators, most beetles rely on morphological and behavioral adaptations. Predation by birds and other diurnal predators is likely to have played a dominant role in the evolution of cryptic and aposematic coloration in beetles, while the stridulatory, chemical, and non-aposematic defenses of nocturnal species are especially effective deterrents against mammal, amphibian, and invertebrate predators.



Figure 29. Mammalian carnivore feces packed with beetle remains.



Figure 30. Robber fly, *Diagmites* (Asilidae) preying on a flower chafer, *Euphoria* (Scarabaeidae).

Ground and tiger beetles (Carabidae) back up their bursts of speed to evade predators with sprays of noxious chemical compounds. Tortoise beetles (Chrysomelidae) simply stay put. When attacked, they hunker down by using their oily and bristly feet to cling mightily to the surface of vegetation. Their tortoise-like carapace with broadly flanged edges nearly all around completely covers the beetles' appendages, thwarting the efforts of ants and other predators in their attempts to dislodge it. Adult flea (Chrysomelidae) and some marsh beetles (Scirtidae) have muscular hind jumping legs that propel them out of harm's way in an instant.

Click beetles (Elateridae), false click beetles (Eucnemidae), and throscids (Throscidae) jump by "clicking" themselves away from danger. Elaterids accomplish this feat by contracting ventral muscles that bring a prosternal spine up against a corresponding groove on the mesosternum (Fig. 31). As tension builds, the spine



Figure 31. Clicking mechanism of a click beetle, *Alaus* (Elateridae).

suddenly snaps into the groove with a clearly audible and startling click, propelling the beetle into the air. For some large longhorn beetles (Cerambycidae) and scarabs (Scarabaeidae), size alone—backed up by powerful mandibles, horns, and claws—may be enough to deter all but the most determined predators.

Death feigning, or *thanatosis*, is a behavioral strategy employed by hide beetles (Trogidae), certain darkling beetles (Tenebrionidae), zopherids (Zopheridae), weevils (Curculionidae), and many others. When disturbed, these beetles "play possum" by pulling their legs and antennae up tightly against their bodies; some of these species have special sulci to receive and protect these appendages. Faced with impenetrable bodies that lack any movement, most small predators quickly lose interest and move on.

Other beetle species avoid detection by predators by blending into their backgrounds by employing varying degrees of camouflage. Somber-colored brown or



Figure 32. Caterpillar feces mimic, Neochlamisus (Chrysomelidae).

gray wood-boring beetles and weevils easily blend in with the rough bark and gnarled branches of their food plants. Pale tiger beetles (Carabidae) almost disappear on the sandy shores of beaches, rivers, and streams. Even a few members of the usually brightly colored lady beetles (Coccinellidae) are tan or striped, and thus remain undetected among pine needles. Some seemingly conspicuous bright metallic green beetles (e.g., Scarabaeidae, Buprestidae, Chrysomelidae) also disappear among the needles and leaves of their food plants. Longhorn beetles (Cerambycidae) and fungus weevils (Anthribidae) have markings that make them difficult to find on lichen-covered bark. The small, dark, and chunky warty leaf beetles Chlamisus, Exema, Neochlamisus, and Pseudochlamys (Chrysomelidae) hide in plain sight and are often overlooked by predators and collectors alike because of their strong resemblance to caterpillar feces (Fig. 32).

Although incapable of inflicting harm themselves, some beetles mimic the appearance or behavior of stinging insects, a phenomenon known as *Batesian mimicry*. Flowervisiting *Acmaeodera* (Buprestidae) and lepturine longhorns (Cerambycidae) all sport boldly marked and sometimes fuzzy bodies that make them striking mimics of stinging bees and wasps. Some bumble bee scarabs (Glaphyridae) with a bright metallic green prothorax strongly resemble halictine bees as they fly over ribbons of sand winding through willow thickets growing along river courses.

Several species of checkered beetles (Cleridae) are boldly colored to resemble pugnacious ants or wingless wasps known as velvet ants. Their quick, jerky movements further reinforce the charade. But stinging insects are not the only models for beetles seeking protection. Several species of click (Elateridae) and longhorn beetles (Cerambycidae) strongly resemble distasteful fireflies (Lampyridae), soldier (Cantharidae), and net-winged beetles (Lycidae).

Eye spots or sudden flashes of bright colors are thought to startle or confuse would-be predators. The outsized eye spots of eyed click beetles (Elateridae) (Fig. 33) may momentarily confuse a predator, possibly allowing the beetle an extra moment or two to escape. *Trichiotinus* beetles (Scarabaeidae) have bold eye spots on their pygidium that may suggest the face of a stinging wasp to potential attackers. Many dull-colored metallic wood-boring beetles (Buprestidae) and somberly hued tiger beetles (Carabidae) may startle predators by revealing flashes of bright iridescent blue, green, or red on their abdomens when they lift their elytra to take flight.

Some beetles possess chemical arsenals of noxious substances produced by specific glands in their bodies,

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Figure 33. Eye spots on pronotum of an eyed click beetle, *Alaus* (Elateridae).

or extracted from their food and sequestered in special chambers or within their blood (*hemolymph*) that are later employed as repellents, insecticides, and fungicides. Specialized abdominal defensive glands of ground beetles (Carabidae) known as pygidial glands produce hydrocarbons, aldehydes, phenols, quinones, esters, and acids and release them as noxious streams through the anus. For example, aposematically colored bombardier beetles (*Brachinus*) release small, yet potent, boiling clouds of hydrogen peroxide gas laced with hydroquinones and various enzymes, among other components, with considerable accuracy through their anal turret with an audible pop. When attacked, carrion and burying beetles

(Silphidae) emit oily, smelly anal secretions with a strong ammonia odor. Most rove beetles (Staphylinidae) and darkling beetles (Tenebrionidae) have *eversible* abdominal or anal glands that produce a wide range of defensive substances. Stink beetles (*Eleodes*) assume a defensive posture by lowering their heads and raising the tip of their abdomens high before releasing defensive chemical compounds with a characteristically noxious odor.

Net-winged (Lycidae), soldier (Cantharidae), lady (Coccinellidae), blister (Meloidae), and milkweed beetles (Cerambycidae) are relatively sluggish insects that boldly display their aposematic colors for all to see. Their conspicuously bright and bold patterns warn experienced predators that their bodies contain noxious chemical compounds that render them distasteful. For example, the bright red, black-spotted beetles in the genus Tetraopes (Cerambycidae) are specialist herbivores that feed only on milkweeds, plants with tissues containing paralytic toxins known as cardiac glycosides. Undeterred by the presence of this compound, Tetraopes larvae feed upon the roots and sequester the milkweed's toxin in tissues destined to become elytra in the adult. Adults eat leaves of milkweed, but limit the amount of cardiac glycosides they ingest by first cutting the leaf's midrib with their mandibles and bleeding off its toxic, milky sap before they start feeding.

Both aposematically colored lady and blister beetles engage in a behavior known as *reflex bleeding* and will purposely exude bright orange or yellow hemolymph laced with noxious chemicals from their leg joints (Fig. 34) to repel



Figure 34. Reflex bleeding from femorotibial joints on oil beetle, *Meloe* (Meloidae).



Figure 35. *Pedilus* (Pyrochroidae) on oil beetle, *Meloe* (Meloidae).

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Figure 36. A pseudoscorpion.



Figure 37. Phoretic mites on burying beetle, *Nicrophorus* (Silphidae).

predators. Cantharidin is an incredibly caustic chemical compound found in the tissues of blister (Meloidae) and false blister beetles (Oedemeridae). It functions as a powerful feeding deterrent to predators and, even in low doses, will blister and burn mucous membranes and other sensitive tissues. Male antlike beetles (Anthicidae) gather cantharidin from dead or dying blister beetles for their own protection and to attract mates. Males pass along large amounts of cantharidin to the females through copulation that-in turn-is passed along to the eggs and larvae as a defensive chemical compound. Other anthicids have thoracic glands that produce chemicals that are particularly distasteful to ants, the primary predators of ground-dwelling insects. Neopyrochroa and Pedilus (Pyrochroidae) also sequester cantharidin, possibly from blister beetles (Fig. 35) or other natural, yet unknown cantharidin sources.

SYMBIOTIC RELATIONSHIPS

Some beetles have intimate and specialized, or *symbiotic*, relationships with other organisms. Symbiotic relationships that benefit both the beetle and its partner organism are examples of *mutualism*. *Commensalism* is a form of symbiosis where one symbiotic organism clearly benefits while the other is not adversely affected by the relationship. *Parasites*, on the other hand, live at the expense of their hosts.

All plant-feeding beetles, including wood-boring species, are more or less reliant upon mutualistic *endosymbiotic microorganisms*, such as bacteria, fungi, and yeasts that live within special pockets called *mycetomes* in their digestive tracts and assist in digesting the primary component of all plant-based foods, cellulose. The larvae of these species do not begin their lives with these vital organisms in place and must either obtain them by consuming their eggshells, which were coated by their mothers in residues laden with endosymbionts, or by consuming adult waste (*feces*, *frass*) that is teeming with them.

Larger species, such as Polyphylla decemlineata (Scarabaeidae), Prionus species, and Trichocnemis spiculatus (Cerambycidae) often harbor one or more pseudoscorpions (Fig. 36) under their elytra, which are occasionally found in killing jars used to dispatch these big beetles. Pseudoscorpions are small scorpion-like arachnids without a stinging tail. They hunt under tree bark for small insect larvae and mites among the chewed galleries and frass left in the wake of wood-boring insects. As their prev populations are depleted, pseudoscorpions seek out and attach themselves to a beetle to hitch a ride to another fallen tree where food is more abundant. Pseudoscorpions depend on their beetle hosts for transportation, a type of commensalism known as phoresy. Burying beetles (Silphidae) possess phoretic mites that prey on the eggs of carrion-feeding flies (Fig. 37), thus reducing the competition for their host beetles. Other mite species are not phoretic, but are parasites that feed on the bodily fluids of beetles.

Ant-loving beetles, or *myrmecophiles*, in the families Staphylinidae, Histeridae, Scarabaeidae, and Tenebrionidae, among others, are adapted for living in the nests of ants. Some myrmecophilous beetles may simply be opportunists, living on the fringes of colonies where they scavenge bits of food left behind by the ants (Fig. 38). Other species are much better adapted to living with ants and have evolved various degrees of behavioral, chemical, or tactile mimicry to integrate themselves into the host ants' social system. Host ants tolerate their beetle guests with varying degrees of hospitality, but the benefits derived from the relationship nearly always favor the beetle. Species

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Figure 38. Araeoschizus (Tenebrionidae) carried by a red harvester ant, Pogonomyrmex (Formicidae).

in these and other families similarly adapted to living with termites are referred to as *termitophiles*.

A few beetle larvae are ectoparasitoids of other animals. For example, the larvae of *Brachinus* and *Lebia* (Carabidae) attack the larvae and pupae of aquatic beetles and leaf beetles, respectively. The larvae of cicada parasite beetles (Rhipiceridae) attack cicadas, while those of wedge-shaped beetles (Ripiphoridae) parasitize solitary wasps. Larval passandrids (Passandridae) and bothriderids (Bothrideridae) attack the larvae and pupae of wood-boring longhorn (Cerambycidae) and jewel beetles (Buprestidae). Perhaps the most unusual ectoparasitic beetle known in all North America is *Platypsyllus castoris* (Leiodidae). Both the flattened, louselike ectoparasitic adults and their larvae live on beavers, where they feed on their host's skin and bodily fluids.

AQUATIC BEETLES

Aquatic beetles are variously adapted behaviorally and morphologically for living on the surface of, within, or on the bottom of standing and flowing bodies of water. Winged species are generally good to strong fliers and are, on occasion, attracted to lights at night in large numbers. Based on adult modes of locomotion, water beetles are divided into two basic groups: swimmers and crawlers.

The flattened middle and hind legs of swimmers (Haliplidae, Gyrinidae, Dytiscidae, and some Hydrophilidae) are fringed with setae and used like oars to propel their mostly smooth, rigid, streamlined bodies through standing or slow-moving waters. All but the gyrinids spend most of their adult lives submerged underwater and must regularly bring fresh supplies of air into contact with *spiracles* through which they breathe. Water scavengers (Hydrophilidae) accomplish this by breaking through the surface tension headfirst with their antennae to draw a layer of air over the underside of their abdomen. Crawling water (Haliplidae) and predaceous diving beetles (Dytiscidae) both trap air under their elytra in the *subelytral cavity* by breaching the water surface with the tips of their abdomens. Diving beetles sometimes expose this bubble on the tip of the abdomen where it acts as a physical gill (Fig. 39). For a brief time, oxygen is replenished inside the bubble by passive diffusion.

Whirligig beetles (Gyrinidae) are adapted for life on the surface of standing and slow-moving waters, although they can dive when threatened and remain submerged for short periods of time. They propel themselves with paddlelike middle and hind legs, and steer with the rudderlike tip of the abdomen that bends down almost at a right angle. The compound eyes of gyrinids are completely divided into two functionally different sets of lenses, allowing them to see in both air and water. With special organs in their antennae, whirligig beetles can detect surface vibrations emanating from other gyrinids, predators, and struggling insect prey. Dead and dying insects are grasped with *raptorial*, or grabbing front legs.

Contrastingly, beetles that crawl in the water (Hydraenidae, some Hydrophilidae, Elmidae, Dryopidae, and some Curculionidae) have legs adapted not for swimming, but for clinging, as evidenced by their long pretarsi tipped with well-developed claws. They are partly or wholly clothed in a dense, velvety, and water-repellent *pubescence* called a *hydrofuge* that continuously envelops their bodies in a silvery bubble. This thin layer of air allows a steady supply of dissolved oxygen from the surrounding water to diffuse inward to the spiracles, while permitting the respiratory gas carbon dioxide emitted from the spiracles



Figure 39. A predaceous diving beetle, *Thermonectus* (Dytiscidae) using a bubble of air as a physical gill.



Figure 40. Japanese beetle, Popillia japonica (Scarabaeidae).

to diffuse outward—a system called *plastron breathing*. Plastron breathing is not very efficient and is largely restricted to sedentary grazers in the families Dryopidae and Elmidae living in shallow, well-oxygenated waters. Once submerged, plastron-breathing beetles seldom, if ever, need to surface or leave the water.

BEETLES AS PESTS

As a group, beetles are among the most beneficial of all animals, but it shouldn't be a surprise when species that have evolved to scavenge animal nests, carrion, dead insects, seeds, and decaying plant materials in nature are also adapted to exploit these very same materials improperly stored in our pantries, warehouses, and museum collections. Beetles in several families infest and damage stores of grains and other cereal products, dried meats and fruits, legumes, nuts, and spices. Others are serious museum pests that destroy often-irreplaceable study skins, and insect and herbarium specimens.

Wood borers are essential for breaking down and recycling nutrients bound up in dead wood, while other phytophagous species help to keep plant populations in check via consumption of reproductive and vegetative structures. However, when these beetles direct their activities to ornamental and horticultural plants, agricultural crops, forests managed for timber, or wood products, the results can be catastrophic. The damage they cause can result in significant monetary losses as a direct result of lost production, trees killed, damaged goods, and pest control efforts. For example, ptinids and bostrichids that normally tunnel into dry wood may severely damage wood carvings, furniture, flooring, and paneling. Both native and adventive bark and ambrosia beetles (Curculionidae) regularly attack



Figure 41. Asian longhorn beetle, Anoplophora glabripennis (Cerambycidae).

and kill trees in forests and along city streets, usually focusing their efforts on recently dead, injured, or felled trees, or on trees stressed by drought or overwatering. Others attack the roots and branches of fruit and nut trees in orchards, severely impacting crop yields. The tunneling activity of these and other wood-boring beetles disrupts a tree's ability to transport water and nutrients, and introduces debilitating and lethal fungal infections.

Three of the most notorious beetle pests in North America were accidentally introduced from Asia. The Japanese beetle, Popillia japonica Newman (Fig. 40) (8.9-11.8 mm) has a coppery green head, pronotum, and legs. Its brown elytra are distinctively flanked by five white abdominal tufts. Adults of this very destructive pest feed on the flowers, fruits, and foliage of more than 300 species of ornamental and landscape plants, garden crops, and commercially grown fruits and vegetables. The larvae consume the roots of turfgrass and other plants, often causing severe damage. Since their discovery in a New Jersey nursery in 1916, Japanese beetles have become established throughout much of the eastern United States and southern Ontario. The grubs are easily transported with roots and soil, while flying adults are known to hitchhike on airplanes, trains, and automobiles, thus posing a serious and continuous threat to agriculture in western North America. Japanese beetles are regularly intercepted in western states, and provinces and several small, isolated infestations in the West have been eradicated.

A native of China and Korea, the Asian longhorn beetle, *Anoplophora glabripennis* (Motschulsky) (12.0–39.0 mm) (Fig. 41) is a large, black longhorn beetle (Cerambycidae) with irregular white spots on the elytra and bluish or white legs. It has long antennae that are ringed in pale blue or white and extend past the elytra by five antennomeres

in the male, but by just one or two in the female. The elytra are smooth, shiny, or dull, and only rarely densely spotted or spotless. The tunneling activities of the larvae weaken and kill otherwise healthy trees and threaten millions of street trees and the maple syrup industry. Infestations of this beetle were first reported in New York in 1996, but it was probably introduced about 10 years earlier in untreated wood used to crate heavy equipment. Infestations of this destructive beetle have since been reported from New Jersey, southern Ontario, northeastern Illinois, and Ohio, with additional individuals captured elsewhere, including California. Efforts to eradicate this destructive species involve cutting down, chipping, and burning thousands of trees. This species poses a serious threat to street trees, parks, and forests in western North America. Although this beetle has been intercepted in California, it is not known to be established anywhere in western North America.

The emerald ash borer, Agrilus planipennis Fairmaire (Fig. 42) (8.0–14.0 mm), is a slender, bright metallic green, rarely blue-green or violet jewel beetle (Buprestidae), much larger than any species of Agrilus native to North America. It also has a distinct ridge down the middle of the pygidium that extends beyond the tip. Emerald ash borers were first discovered in Detroit, Michigan and Windsor, Ontario during the summer of 2002, but they likely arrived in wood packing materials from eastern Asia in the early 1990s. Since then, this species has become established throughout much of the Northeast and upper Midwest. It has destroyed millions of ash trees in Michigan, southern Ontario, and Québec and threatens to destroy ash trees across North America. Ash species are important street trees and a vital source of wood for making furniture, tool handles, and baseball bats. Efforts to control the spread of the emerald ash borer



Figure 42. Emerald ash borer, Agrilus planipennis (Buprestidae).

include quarantines that ban the movement of firewood within and from infested areas, and the introduction of biological control agents imported from China.

Sightings of these beetles anywhere in western North America, preferably supported by specimens or good photos, should be reported immediately to provincial, state, or county departments of agriculture.

BEETLES AS BIOLOGICAL CONTROLS

Biological control involves the use of a pest's natural enemies, such as predators, parasitoids, and pathogens as control methods, rather than complete reliance on pesticides that may adversely affect wildlife. The modern practice of utilizing predatory insects to control pests using natural enemies from their land of origin began in 1888. Shipments of several species of Australian lady beetles (Coccinellidae) arrived in California and were purposely released in the state to combat the cottony cushion scale, an Australian insect inadvertently introduced into the state that was wreaking havoc with the fledgling citrus industry. The vedalia beetle, Rodolia cardinalis (Mulsant), was hailed at the time as a miracle of science and, to this day, continues to help keep the cottony cushion scale in check. The success of this program led to the import of many other coccinellid species, but the benefits of these introductions have been mixed, especially with the Asian multicolored lady beetle, Harmonia axyridis (Pallas), that is sometimes viewed more as a nuisance, rather than a beneficial species. The role of these introductions in the observed declines observed in lady beetles indigenous to North America requires further study.

Biological control projects involving beetles are not limited to insect predators, as several species of phytophagous jewel beetles (Buprestidae), leaf beetles (Chrysomelidae), and weevils (Curculionidae) have been imported as biocontrol agents of introduced weeds, especially in rangelands. For example, the St. John's wort beetle, *Chrysolina hyperici* (Forster) (Fig. 43), and its close relative, the Klamath weed beetle, *C. quadrigemina* (Suffrian), were the first insects imported into North America to control *Hypericum perforatum*. This European weed, known in the West as Klamath weed, and elsewhere as goatweed or St. John's wort, is especially detrimental to cattle, but also negatively impacts sheep by displacing palatable forage. In the absence of better forage, livestock forced to graze on Klamath weed become hypersensitive to sunlight. Blisters



Figure 43. Saint John's wort beetle, Chrysolina hyperici (Chrysomelidae).

soon develop on areas exposed to direct sun and the animals lose weight as sores develop around their mouths and scabs on their skin.

Chrysolina females lay their eggs on *Hypericum* leaves, either singly or in small clusters. In about a week, the eggs begin to hatch into plump and humpbacked orange larvae that eventually turn grayish pink as they mature. The young larvae completely defoliate plants before they reach maturity by hungrily consuming leaf buds and developing leaves. As a result, the release and subsequent establishment of these beetles to control Klamath weed is generally viewed as effective, especially in warmer, drier habitats.

The application of biological controls to wildland environments, or conservation biocontrol, is more complex than programs targeting invasive species in agricultural systems and rangelands, as evidenced in the effort to eradicate tamarisk (Tamarix species). Also known as saltcedar, tamarisk was introduced from Asia into North America about 200 years ago. Early in the 20th century, they expanded guickly into natural and contrived riparian systems and became associated with the decline of cottonwood-willow woodlands, mesquite bosque, and other native plant complexes west of the Mississippi River, becoming the third most common tree in riparian systems in western United States. The dominance of tamarisk in these habitats is believed by many to increase soil salinity, reduce local water resources, and provide poor habitat for native wildlife relative to displaced native plant communities. To reduce its negative environmental impacts. hundreds of species of herbivorous insects that appeared to feed only on tamarisk were studied to determine which species would become part of a biological control program to suppress tamarisk infestations. Several beetles were selected, including the splendid tamarisk weevil, Coniatus splendidulus (Fabricius), and northern tamarisk beetle, Diorhabda carinulata Debroschers des Loges (Fig. 44).

The initial success of the northern tamarisk beetle in defoliating tamarisk quickly became controversial. Wildlife agencies became increasingly alarmed that a significant reduction of the tamarisk canopy where federally endangered southwestern willow flycatchers nest would expose the birds to increased temperatures and predation. This concern was exacerbated by the lack of a habitat restoration plan once tamarisk was eliminated. Such conflicts highlight the need for governmental and private agencies charged with conserving wildlife and protecting natural resources to work together. By cooperatively developing a strategic plan early





Figure 44. Beetles used as biological controls to eradicate tamarisk. a. Splendid tamarisk beetle, *Coniatus splendidulus* (Curculionidae); b. Northern tamarisk beetle, *Diorhabda carinulata* (Chrysomelidae).

in conservation biology programs, science-based monitoring protocols can be developed to assess multiple key parameters that include soil and water dynamics, wildlife habitat use, and habitat restoration.

BEETLES AS INDICATORS OF PAST ENVIRONMENTS

While anthropogenic climate change is likely a contributing factor in a series of widespread droughts that have plagued western North America recently, paleoenvironmental records indicate that such periods of infrequent precipitation are nothing new. Evidence of climate change and its impacts are all around us, but historical records that provide such evidence are less than 200 years old. To fill in this gap, scientists can analyze microfossils consisting of plant and animal remains, especially those of beetles and other insects, to reconstruct ancient climate patterns.

A better understanding of terrestrial paleoenvironments will undoubtedly lead to more accurate predictions of future climatic shifts.

Recent advances in radiocarbon dating make it possible to determine the age of larger insect fragments as far back as 50,000 years. Some dated and identifiable beetle fragments are species of Carabidae and Tenebrionidae that are still extant today. As generalist predators and scavengers, these beetles are not tied to a particular plant or habitat, but instead move into more suitable habitats as temperature, food availability, and other conditions change. As a result, their populations respond relatively quickly to environmental fluctuations, often within a matter of decades rather than centuries, when compared with other groups of organisms, such as plants. For well-documented beetles, knowledge of their life cycles, habitat preferences, and distribution makes them ideal climatic indicators, both present and past, affording researchers with incredibly detailed insights into changing environmental conditions dating back tens of thousands of years.



Figure 45. A collection of 44,000-year-old beetle and other arthropod fragments discovered inside the skull of an extinct camel found at Rancho La Brea Tar Pits in California.

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For example, a reliably dated cache of 44,000-yearold fragments of insects and other arthropods (Fig. 45) was discovered inside a skull of an extinct camel at the Rancho La Brea Tar Pits in southern California. Careful analysis of this treasure trove revealed, among other things, that the late Pleistocene climate of the Los Angeles Basin was much warmer and drier than previously hypothesized based on plant fossil analysis alone. Further, within this incredible sample were the remains of the nearly cosmopolitan Necrobia violacea (Linnaeus), a synanthropic species long regarded here in North America as adventitious. The discovery of this species' remains in the sample clearly demonstrates that it was established in North America long before the arrival of humans on the continent. This evidence suggests that this beetle is either a Holarctic species that naturally occurs throughout the Northern Hemisphere, or was native to the Nearctic and was subsequently introduced into the Old World by human agency.

THREATENED AND ENDANGERED BEETLES

Habitat loss and fragmentation resulting from urban, commercial, and agricultural development, as well as pesticide use, invasive species, and climate change all contribute to the extirpation or extinction of beetles. In California alone, at least three species or subspecies of beetles are known to have become extinct in the last 150 years: the oblivious tiger beetle, *Cicindela latesignata obliviosa* Casey, the San Joaquin valley tiger beetle, *Cicindela tranquebarica joaquinensis* Knisley and Haines (Carabidae), and the Mono Lake hygrotus diving beetle, *Hygrotus artus* (Fall) (Dytiscidae).

Western North America is particularly susceptible to species loss because of the sheer number of beetles specifically adapted to living in unique and sensitive habitats, especially coastal and desert sand dunes, as well as restricted riparian habitats. Yet only five species of beetles that occur west of the Continental Divide are currently listed as threatened (T) or endangered (E) by the U.S. Fish and Wildlife Service, all of which occur in California: Ohlone tiger beetle, *Cicindela ohlone* Freitag & Cavanaugh (E); delta green ground beetle, *Elaphrus viridis* Horn (T); Casey's June beetle, *Dinacoma caseyi* Blaisdell (E); Mount Hermon June beetle, *Polyphylla barbata* Cazier (E), and valley elderberry longhorn beetle, *Desmocerus californicus dimorphus* Fisher (T) (Fig. 46). No species of western beetles are afforded federal or provincial protection in Canada. State governments may list additional species as state threatened or endangered, or of special concern.

WHEN AND WHERE TO FIND BEETLES

One of the most appealing aspects of studying beetles is that opportunities to discover and observe unfamiliar species and behaviors abound. You can ramble through backyards, vacant lots, and parks, or explore more distant coastal forests and beaches, chaparral habitats, foothill woodlands, montane forests, and deserts year-round. Visiting familiar areas and habitats throughout the seasons year after year will likely produce a breathtaking diversity of species. Even at higher elevations or in more northern regions, overwintering beetles are found tucked away under snow-covered bark, buried deep in rotten wood or leaf litter, or hiding under boards and other debris to avoid lethal frosts. Many water beetles remain active throughout winter and are sometimes seen swimming under the ice of frozen ponds and lakes; however, some species are adapted to reach peak activity levels in fall and late winter, at least at lower elevations.

Beetles are found year-round in western North America, with the greatest diversity of species most likely to be encountered during the spring and summer months. The beginning of beetle activity varies depending on weather conditions and location, the latter of which is largely influenced by latitude and elevation. Spring conditions arrive later in the north and at higher elevations. As early as January and February, the first sustained periods of warm weather in the coastal plain and low desert of southern California and Arizona will drive many small ground beetles (Carabidae), scarabs (Scarabaeidae), and weevils (Curculionidae), among others, to search for food and mates. As the front of spring progresses northward, brief, yet spectacular bursts of ephemeral wildflowers fueled by rains of the previous winter blanket otherwise parched desert, foothill, and valley landscapes. Among this riot of color are species of beetles with lives as brief as the flowers upon which they feed and mate (Fig. 47). By April and May, coastal forests, chaparral habitats, and inland valleys reach their peak beetle-wise, while June and July mark the first significant levels of sustained beetle activity in coniferous forests at the higher elevations.

Much of the rainfall in the coastal provinces and states of western North America takes place during the fall and







Figure 46. Beetles listed as threatened or endangered in western North America by the U.S. Fish and Wildlife Service. a. Ohlone tiger beetle (E), *Cicindela ohlone* (Carabidae); b. delta green ground beetle (T), *Elaphrus viridis* (Carabidae); c. Casey's June beetle (E), male and female, *Dinacoma caseyi* (Scarabaeidae); d. Mount Hermon June beetle (E), *Polyphylla barbata* (Scarabaeidae); e. valley elderberry longhorn beetle (T), *Desmocerus californicus dimorphus* (Cerambycidae).

winter, although in some years, heavy rains may persist well into spring, especially along the coast. Fall showers begin sweeping across the Pacific Northwest as early as September, and extend further south in October and November. Winter rains during December and January can be quite heavy at times along the coast, eventually turning into snow as storm systems move eastward across the Coast Ranges, Cascades and Sierra Nevada, and Rocky Mountains. These cold, wet bouts of winter precipitation trigger the activity of select beetle species that





are specifically adapted to such conditions. By the middle of June, much of the region is experiencing some level of drought, although summer thundershowers are not unusual in the mountains and deserts. Arizona and adjacent areas typically experience a summer monsoon season that usually begins in July and persists through fall. These late summer thundershowers trigger a new wave of beetle activity across all desert regions of the West.

Time and experience will teach you the best times and places to look for beetles. The following are some

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of the more productive habitats to search for beetles in western North America. Exploring these and other habitats throughout the day and year will likely reveal a surprisingly diverse fauna that will enhance your enjoyment and appreciation of these fascinating animals. Throughout your explorations, always take care not to damage host plants, and return rocks, logs, and bark to their original positions. Such actions not only keep these sites productive for future visits, but also help to preserve the aesthetics of the habitat for the enjoyment of all.

FLOWERS AND VEGETATION

Spring and summer blooms rich in sweet nectar and high-protein pollen are attractive to flower-visiting beetles, especially scarab (Scarabaeidae), jewel (Buprestidae), sap (Nitidulidae), tumbling flower (Mordellidae), blister (Meloidae), and longhorn (Cerambycidae) beetles. These and other species exploit flowers as sources of food, places to mate and reproduce, or habitats in which to hunt for prey. Carefully examine fruits, seedpods, cones, needles, leaves, and roots of grasses, forbs, vines, shrubs, and trees. The young spring foliage of deciduous shrubs and trees is especially attractive to many plant-feeding species. Some herbivorous beetles are specialists and are seldom found on anything other than the adult or larval host plant.

Slime flux is a bacterial disease of trees and shrubs that forces sap attractive to many species of beetles out of limbs and trunks through freeze cracks, insect emergence holes, and other wounds (Fig. 48). Check not only the nooks and crannies of sap-soaked bark for beetles, but also the sap-drenched soil and litter beneath for smaller species and their larvae.

FRESHLY CUT AND BURNED WOOD

The smell of freshly cut or recently burned wood is especially attractive to beetles, particularly those looking for mates and egg-laying sites. Slash piles (stacks of freshly cut branches) in wooded areas are particularly productive, especially in spring and early summer (Fig. 49). You can also attract beetles with bundles of fresh-cut branches placed in forest openings, along woodland edges, or in canopy-covered habitats that are only partially exposed to sunlight. Inspect the bundles at weekly intervals, day and night, and note which beetles are attracted to the branches of which species of tree. Another technique is to lay branches, bark, or a slab of trunk 10–15 cm thick across the top of a fresh-cut stump in spring and check the top







Figure 48. Euphoria leucographa (Scarabaeidae) feeding at a sapping wound on desert broom, Baccharis sarothroides.



Figure 49. Piles of freshly cut pine branches are particularly attractive to many wood-boring beetles during spring and summer.

of the stump regularly for beetles that have taken shelter there. Wood smoke, especially that generated by burning pine trees, also attracts wood-boring and bark beetles.

FUNGI, MUSHROOMS, MOSSES, AND LICHENS

Species in several families are found commonly on fungi, slime molds, mosses, and lichens, Carefully inspect fungi with a hand lens and leave them in good condition so they continue to lure new beetles. Fleshy and relatively ephemeral puffballs and mushrooms are also attractive, while more durable woody shelf fungi provide food and breeding sites for other species. Still other species seek out fungal tissues growing on or under bark, or in the soil. In addition to mycophagous, or fungal-feeding beetles, predatory rove (Staphylinidae) and clown beetles (Histeridae) frequent fungi infested with insects and mites as hunting grounds. Adults and larval pill or moss beetles (Byrrhidae) are obligate moss feeders that graze on vegetative surfaces or burrow in the soils beneath. Tread very lightly in these habitats so that future visits are equally productive. Only when fungal, moss, and lichen examples are in abundance should samples be collected for microscopic examination or the extraction of specimens.

SNAGS, LOGS, AND STUMPS

Standing snags dry from the top down, and most of their beetles are concentrated at or near the base. Moist rather than dry wood harbors more species. Some species prefer primarily shady habitats, while others prefer more open, sun-drenched wood, although this latter niche dries out more quickly. As the wood decomposes, its quality changes in terms of its suitability as beetle food and egg-laying sites, attracting a progression of beetle species over time. Checking these microhabitats every few weeks over a period of years may reveal an amazing diversity of beetle species.

Recently dead trees with tight-fitting bark are more likely to harbor the adults of smaller or flatter species than those with bark that is easier to remove. As the wood dries and its bark loosens, larger and more robust species can take shelter. Peeling back dead bark, or "barking," is best accomplished during the cooler winter and spring months. Use a broadblade knife, screwdriver, or dandelion weeding tool to peel back bark and examine all the freshly exposed areas carefully. Whenever possible, replace the bark by nailing or tying it back in place so the site will continue to be colonized by additional individuals and species. Many small species are best found by placing crumbling and rotten wood onto a light-colored surface for immediate inspection or into a Berlese funnel or some other insect extraction system.

Searching for beetles at night on dead wood with the aid of a headlamp or flashlight on warm spring and summer nights, just as they begin emerging from their hiding to search for mates, is an especially fruitful activity.

STREAM BANKS, LAKESHORES, AND COASTLINES

Plant debris on the surfaces of flumes, streams, and rivers contains flying and crawling beetles trapped by the swirling currents. Some species typically spend their daylight hours hidden under debris washed up on lakeshores and ocean beaches. Flying beetles of all sorts fly—or are windblown—out over lakes and oceans only to drown and be washed back up on shore, sometimes by the thousands. The high waterlines along these shores are often littered with thousands of beetles from various families. Burrowing species that are adapted to living in flat sandy, gravelly, or muddy shorelines are flushed from their burrows by splashing water across the substrate. Ground and tiger beetles (Carabidae) and variegated mud-loving beetles (Heteroceridae) are commonly found on sandy or muddy substrates along the edges of various wetlands.

FRESHWATER POOLS, STREAMS, AND LAKES

While some beetles prefer cold, fast streams, others favor ponds or slow-moving streams. Look for individual *Dineutus* or rafts of *Gyrinus* (Gyrinidae) on the surface of ponds or protected, slow-moving pools scattered along streams. Predaceous diving beetles (Dytiscidae) are often found on gravelly bottoms or beneath submerged objects, while water scavengers (Hydrophilidae), crawling water beetles (Haliplidae), and long-toed water beetles (Dryopidae) are found swimming near emergent plants, crawling among mats of algae, or clinging under logs and rocks. Carefully pick up and examine rocks lifted out of flowing waters for larval water pennies (Psephenidae) and riffle beetles (Elmidae) clinging to their surfaces.

COASTAL AND DESERT DUNES

Various small, sand-loving, or *psammophilic* beetles burrow in flowing sand or hide among plant debris at the bases of dune grasses and other plants. They usually reside down in the moisture layers, or in or under accumulations of *detritus* closer to the surface. Psammophiles typically burrow up and down through the sand as they follow the seasonal moisture and temperature gradients to maintain ideal living conditions, and are active on the surface only for very brief periods of time. These fragile habitats, home to many rare, endangered, poorly known, and undescribed beetle species, are often threatened by off-road vehicles and mining interests.

CARRION

Dead animals provide food and shelter for adult and larval beetles. Look for these beetles on, in, and under the carcass, as well as buried in the soil directly beneath the body. Carrion and burying beetles (Silphidae) feed primarily on fresh, juicy flesh, while most skin beetles (Dermestidae) scavenge dried tissues. Hide beetles (Trogidae) are among the last contingent of insects to visit a carcass and gnaw on the keratin-rich hair, feathers, hooves, and horns. Predatory species (Staphylinidae, Histeridae) seek out and devour the eggs of other carrion-feeding insects and mites. Other beetles are attracted to carrion simply because such microhabitats provide moisture and shelter.

DUNG

The most conspicuous dung-inhabiting beetles in the region belong to the family Scarabaeidae, along with a few species of Hydrophilidae. Native dung beetles are often specialists, preferring the dung of burrowing rodents or deer. Many of the more conspicuous species found in horse and cattle dung originated in Europe and have become widely established in western North America. A few dung scarabs (Digitonthophagus, Oniticellus, Onthophagus, Onitis) were purposefully introduced from sub-Saharan Africa to manage cattle waste. Medium and larger species mostly occur in southern Arizona and are drawn to large wet feces produced by cattle, pigs, horses, and humans. Dog and cat feces attract only a few, mostly introduced species of dung scarabs. Clown (Histeridae) and rove beetles (Staphylinidae) are commonly associated with dung as predators of fly eggs and maggots.

BENEATH STONES AND OTHER OBJECTS

Many beetles occasionally or habitually take shelter under rocks, logs, boards, and other debris on the ground, especially in grassy areas and habitats along the edges of ponds, lakes, streams, rivers, and other wetlands. For the benefit of the people following in your footsteps and the organisms living underneath, always return these objects to their original places and positions. Also look for antlike flower (Anthicidae) and false blister beetles (Oedemeridae) under driftwood that has washed up along coastal beaches and river mouths near coastlines, especially along lower reaches that are regularly influenced by the tides.

LEAF LITTER, COMPOST, AND OTHER ACCUMULATIONS OF PLANT MATERIALS

Layers of leaves and needles that gather beneath trees, accumulate along streams and rivers as flood debris, or wash up on beaches and lakeshores after storms frequently harbor all kinds of beetles. Some beetles use these habitats primarily as shelter, while many rove beetles (Staphylinidae), weevils (Curculionidae), and other species spend their entire lives here. During the winter, beetles living in these habitats are collected by placing debris in plastic bags and bringing the samples inside to check for individuals that have become active. Backyard compost heaps, decaying piles of mulch, and other natural or artificial accumulations of decomposing grass, leaves, branches, and other vegetative matter are particularly productive. Some coastal rove beetles and weevils live under decomposing piles of seaweed washed up along the beach.

LIGHTS

Incandescent, fluorescent, and neon lights on porches and storefronts, especially in undeveloped areas, are very attractive to many kinds of beetles. The bright bluish glow of a mercury vapor streetlight is much more attractive to beetles and other insects than the dull yellowish light emitted by their sodium vapor counterparts. Although many beetles will settle on the ground or wall directly beneath or behind the light, others, especially larger species, may prefer to remain on plants and other surfaces just beyond the light's glow.

INDOORS

Look for living and dead beetles on windowsills and in light fixtures inside houses, garages, sheds, and warehouses. Household and structural pests, as well as other beetles trapped indoors, are usually attracted to sunlit windows and other light sources. High numbers of skin beetles (Dermestidae) or pantry pest species are indicative of infested stored foods, skins, plant materials, wood products, and insect collections.

OBSERVING AND PHOTOGRAPHING BEETLES

Making a beetle collection (see p.58) is the best way to learn about beetles. Only by having specimens in hand will you have the opportunity to critically examine the physical features necessary to facilitate accurate species identification and develop an understanding of their classification. However, some readers may prefer instead to simply observe or photograph beetles alive in the wild.

BEETLES THROUGH BINOCULARS

Close-focusing binoculars allow you to observe beetles on flowers or shorelines less than 2 meters away with amazing color and clarity. The larger the diameter of the evepiece, or objective, the more light that is gathered to form the image. The best binoculars for handheld use are 8 x 42 or 10 x 42. An objective magnification of 8 produces an image as if the viewer were 8 times closer to the subject. A 10-power binocular will make the image larger, but the smaller field of view can make tracking of moving beetles a bit more of a challenge. Lower power binoculars with smaller oculars (e.g., 7×36) are also useful. They are smaller and less expensive, but your subjects will not be as magnified or brilliant. When buying a pair of close-focusing binoculars, compare several brands at the same time to determine which model and magnification works best for you and fits your budget. A close-focusing monocular is also useful, less expensive, and easily stowed in your field kit.

A pair of compact binoculars with the front lenses closer together than the eyepiece lenses (reverse Porro prism design) can be modified for close-up beetle watching. Screw a two-element Nikon 5T or 6T close-up lens into a soft lens hood, place the hood with lens in front of the binoculars, and affix them using heavy rubber bands to achieve a close-focusing capability.

BEETLE MACRO PHOTOGRAPHY

Macro, or close-up photography was once the domain of highly proficient photographers using expensive and complex equipment. Today, good quality macro photographs are relatively easy to make, review, and share. Even the most casual photographer can capture good images with relatively inexpensive point-and-shoot digital cameras or smartphones with macro-like capabilities. The very best images, including most of those that grace these pages, were taken with digital single-lens reflex (DSLR) cameras with dedicated macro lenses with focal lengths of 50 mm, 90 mm, or 100 mm that allow focusing on beetles just a few millimeters from the lens. As of this writing, digital single lens mirrorless (DSLM) cameras are becoming more popular with macro photographers.

The distance between the lens and the beetle is called the working distance. When fully extended, macro lenses allow you to fill the frame of your photograph with an up to life-size (1:1) image of a beetle. Some beetles are a bit skittish at these close working distances, while others seem not to notice the camera at all. Macro lenses with longer focal lengths (150 mm, 200 mm) have greater working distances and still offer 1:1 capability, but they are bulky, difficult to hold steady, and very expensive. To obtain magnifications greater than life size, 1:2 or more, doublers, teleconverters, and extension tubes of 25 mm or greater are placed between the lens and the camera body. Highquality close-up lenses of varying magnifications screwed on the front of the macro lens can be useful, but will reduce already close working distances and sometimes degrade image quality.

In macro photography, focus is best achieved not by using the camera's autofocus feature, but instead selecting the desired magnification in advance based on the beetle's size and the kind of image you want to make. Once the lens is extended, aim the camera at your subject and look through the viewfinder to compose the shot. Then slowly rock back and forth until the subject is in focus and take the picture. Most beetle images look best when the subject, especially the eyes, and background are both in sharp focus. The depth of focus in a photo, usually referred to as the depth of field, is the distance between the nearest and farthest objects in the photo that are in focus. Think of text on a page photographed at an angle-the sentences in the image that are in focus are indicative of the depth of field. Depth of field is determined by the opening at the back of the lens, or aperture. The aperture is expressed as an f-stop; the bigger the f-stop number, the smaller the aperture. Decreasing the aperture, or stopping down to f/16or f/22, increases the depth of field; however, decreasing the f-stop also requires using flash to compensate for the reduced amount of natural light reaching the sensor.

Because of the long barrel of the 100 mm macro lens, the built-in flash on your camera's body will cast a shadow across your beetle and ruin the image; therefore, additional and adjustable external flashes attached to the end of the lens are your best bet. Two adjustable flashes are better than one and always better than the flat lighting provided by a ring flash. Placing these flashes at a 30-degree angle to the long axis of the lens barrel will create the effect of natural morning or afternoon sunlight; however, you may want to adjust one or both flashes to properly expose your subject and its background. Macro photographers often use one flash on the subject while a second flash provides a weaker "fill light" on the nearby background. Distant backgrounds that are underexposed appear dark or black and the overall impression of the photograph is often not pleasing, even if the subject is in perfect focus and properly exposed. The easiest way to compensate for this is by making sure that the background is close enough to the subject to be properly exposed by the flash. Always try to photograph a beetle resting on a leaf or flower rather than one perched on an isolated branch tip. Whenever possible, make sure the background is not so cluttered or busy that it distracts from your subject. Use the highest shutter speed (1/125 sec., 1/250 sec., etc.) possible that synchronizes your camera with the flash system to freeze the action of your subject and mitigate camera movement to make a razor-sharp image.

Take lots of pictures. Experiment with different combinations of apertures, shutter speeds, and flash settings under a variety of conditions, and carefully record these in a small notebook. Compare your notes with the resultant images to establish the settings and conditions that work best for your camera. Carefully review all your images either in camera or on your computer, then select and keep only the very best for each species. There is no point in tving up valuable space on your hard drive with inferior images. Store your images using one of many software applications, and be sure to label each image with locality data and any other pertinent information as if it were a specimen in a collection. This way, your images can be easily retrieved and become part of a permanent record of your travels and observations. Your best images will be those that are well exposed, in focus, and tell a story. The most compelling images of beetles capture them feeding, mating, laying eggs, or otherwise going about their business undisturbed in their own habitat.

There is no one way to photograph a beetle. Every photographer has their own favorite setup and method of working based on a combination of aesthetics, experience, taxonomic interests, available camera equipment, and degree of patience to experiment with said equipment. Most of my images reproduced in this guide were photographed with a Canon EOS Digital Rebel XTi set at ISO 100 with a 100 mm macro lens, up to 50 mm of extension tubes, and a Macro Twin Lite MT-24EX with Meike MK-MT24 diffusers. Each strobe was placed about 90 degrees apart, aimed at about 30 degrees from the axis of the macro lens. I generally used *f*/16–18 and a shutter speed of 1/125 to

1/200 of a second. Instead of using a tripod to steady the camera, I strap on knee and elbow pads to absorb the shock to my joints produced by hunkering down on the ground, or bracing myself against trees and boulders.

It is important to remember that even the best beetle photographs are often insufficient for accurate identification, especially those species that require careful examination of difficult to see characters and internal structures, such as male genitalia. Thus, is it always desirable to collect beetles after you have photographed them so they are available for further study.

BEETLE CONSERVATION

Commercial and residential development, conversion to agricultural lands, agricultural runoff, grazing, logging, mining, inundation by water impoundments, wetland drainage, indiscriminate use by off-road vehicles, and overuse and abuse of pesticides and herbicides in urban and agricultural areas are just a few of the many human activities that adversely affect, alter, or destroy beetle habitats. The evergrowing list of exotic insect introductions, including those purposely introduced as biological control agents, can inflict unintended and possibly catastrophic consequences on indigenous beetle populations by choking out native food plants or outcompeting native beetles for food, shelter, and egg-laying sites. Climate change, too, will certainly affect many beetle populations, for better and worse.

Beetles restricted to ever-shrinking habitats are particularly susceptible to habitat destruction and competition from invasive species. Populations of *saproxylic*, or rotten-wood-feeding beetles (e.g., Tetratomidae, Melandryidae, Stenotrachelidae, Scraptiidae) in old-growth forests are significantly related to forest structure. The impacts of current forest management practices that fragment these mature growth forests and reduce coarse woody debris could severely impact the availability of food for both the larvae and adults. The coastal and desert dune habitats that support unique beetle species are also under constant threat by mining interests and off-road vehicle use.

Although beetles are among the most conspicuous and charismatic of all insects, our overall lack of knowledge of their biology, ecology, and distribution hampers efforts to identify and protect species in need of conservation. Relatively few species in western North America are recognized as threatened or endangered and afforded legal protection. To find out more about rare, threatened, and endangered beetles in western United States, visit the U.S. Fish & Wildlife Service at fws.gov/Endangered/ and the NatureServe Explorer website at explorer.natureserve.org/.

ETHICS OF BEETLE COLLECTING

Unlike most birds, butterflies, macro moths, dragonflies, and damselflies that are easily identified on sight, many beetles must be in hand for close examination or dissection to facilitate accurate species identifications. Their capture and preservation not only assure identification, but also represent the first important step toward their species' conservation. The data associated with these specimens contribute to our understanding of their habitat preferences, activity period, and distribution. Beetle collecting, collections, and collectors all provide critical information that land managers and other decision makers need to develop and implement the best land-use practices to protect beetle populations.

Whether you are a professional biologist investigating a particular avenue of research, or a student or amateur naturalist who wants to learn more about insects and the natural world, you need not worry that your collecting activities will adversely affect most beetle populations. Such activities pale in comparison to the proficiency demonstrated by hungry insectivorous animals, or to the deleterious effects of pesticide use, mowing, vehicular traffic, artificial lights, and bug zappers. Habitat conversion and destruction, combined with competition from invasive species—not collecting or collectors—pose the greatest threats to beetle populations and habitats throughout western North America.

Beetles with small populations living in sensitive, specialized, or patchy and ephemeral habitats, such as species inhabiting sand dunes and vernal pools, or those dependent on populations of rare plants, should be collected only in small numbers. Elsewhere, the reproductive capacity of most beetles is much greater and differs dramatically from that of vertebrates. Birds, fish, reptiles, amphibians, and mammals all produce relatively few young and must invest enormous amounts of time and effort in nest building and caring for their young to ensure the survival of enough individuals to maintain stable populations. Removal of even a small number of these animals-parents or offspring-can have a major impact on local populations; however, a single female beetle may produce hundreds of young that require little if any parental care at all. Of these, only a few need to survive and reproduce to sustain a thriving population.

Adopt a collecting ethic that embraces the need to conserve beetle populations and their habitats, and

recognizes the rights of landowners. Collecting large numbers of the same species at the same time and place adds little to our knowledge of beetles and does not enhance the diversity that is the mark of a good reference collection. Such a collection, supported by accurate specimen label data and field notes, can only be built over time. The collection of beetles listed as endangered or threatened is strictly regulated, and it is the responsibility of the collector to know which species are afforded protection and to adhere to those regulations. When moving beetles, living or dead, be sure to comply with county, state, and federal agricultural and wildlife regulations. Transporting any living beetles or other insects across county, state, or international borders requires written permission from state or federal agricultural authorities, or both.

Always obtain permission to collect on private lands. Collecting on public lands, such as county, state, and national parks, state and national forests, monuments, and recreational areas, as well as indigenous lands, generally requires written permission, but these requirements may vary depending on locality and the purpose for collecting specimens. Managers of public lands are usually happy to issue permits to individuals conducting beetle surveys or other ecological studies, especially if they are affiliated with museums, universities, and other research institutions. Your efforts will provide data needed to effectively manage and preserve habitats for all wildlife. Always conduct your fieldwork within the conditions set forth in your permit and be respectful of other visitors. Once your project is completed, promptly share your data with the permitting agency and other researchers, and deposit voucher specimens in a permanent museum or university entomology collection.

COLLECTING AND PRESERVING BEETLES

The scientific data generated by professionals and dedicated amateurs collecting beetles are important not only to document the fauna of a given jurisdiction or region, but also to track species diversity and faunal composition over time. The collections of amateur coleopterists working in concert with museum scientists are particularly useful for filling gaps in permanent collections of museums and universities and often provide the basis for both scientific and popular publications. On a more basic level, collecting beetles is a great way to get outside, sharpen your skills of observation, and learn firsthand the biology and ecology of the most diverse group of animals in western North America. Beetle collecting is also an excellent way of getting youngsters outdoors and introducing them to the diversity of nature. Many scientists and educators, including the author of this book, cite the activity of collecting beetles and other insects as the spark that launched their lifelong careers of research and public service.

The initial cost of collecting beetles is minimal, since the basic "tools" required are a sharp pair of eyes, patience, persistence, a few containers, and a bit of luck. Nets, beating sheets, and other collecting equipment listed below are also useful. As your knowledge of the seasonal and habitat proclivities of beetles increases, so will your desire to explore new habitats and try out different collecting equipment and techniques. With time and experience, your collecting activities will become more targeted, and these efforts will contribute to the overall diversity of your collection.

As your expertise develops and research collection grows, you will likely want to know more about curatorial and management topics, including safely preparing shipments of specimens for loans or exchange with other coleopterists. For detailed information on entomological techniques and equipment, consult Collecting and Preserving Insects and Mites. Techniques and Tools (Schauff 1986) or Collecting, Preparing, and Preserving Insects, Mites, and Spiders (Martin 1977). The Entomological Collections Network (ECN) is a nonprofit organization that promotes entomological science through the preservation. management, use and development of entomological collections and taxonomy. This organization hosts annual meetings and a lively and informative online forum that disseminates best practices information to collection managers and other interested persons worldwide.

BASIC TOOLS FOR HANDLING AND EXAMINING BEETLES

Forceps made of spring aluminum are known as "featherweights." They are extremely useful for picking up small beetles without damaging them, while camel-hair brushes are used to probe for and dislodge beetles from their resting and hiding places.

Aspirators of various designs are useful tools for sucking small beetles from beating sheets, nets, and other substrates into a glass or plastic vial. Protective gauze over the intake tube prevents the accidental inhalation of beetles and other bits, while an inline fuel filter will extract smaller particles, but neither of these protections will completely prevent the inhalation of molds, spores, insect feces, or the noxious defensive odors produced by many beetles. Blowing aspirators, or those using a suction bulb, do not involve sucking air through a mouthpiece and alleviate these potential hazards, but they are not widely used.

No one who spends any time in the field should be without a good quality hand lens. Available from biological supply companies, hand lenses are small and compact devices for revealing beetle anatomy and other details that might otherwise escape notice by the naked eye alone. Magnifications of 8x or 10x are ideal, with some units employing several lenses in concert to increase magnification. The trick is to hold the hand lens close to your eye and then move in on your subject until it comes into sharp focus.

KILLING JARS AND KILLING AGENTS

Beetles retained as specimens for a collection must be dispatched quickly and humanely. Freezing is an easy and nontoxic method, but the specimens must be kept cool and calm in a small ice chest until they can be placed in a freezer overnight. Using a killing jar with a bit of loosely crumpled paper that is freshly charged with several drops of ethyl acetate or some other killing agent is often a more practical solution. Ethyl acetate is available from biological and scientific supply houses. Although it is relatively safe to use, avoid getting it on your skin, breathing the fumes, or using it near an open flame. The wadded paper toweling not only holds the killing agent, but also absorbs excess fluids produced by your catch and protects your delicate specimens from jostling. Continually opening and closing the killing jar will result in the loss of its potency, so you will have to recharge the killing jar from time to time. A small, 2-ounce squeeze bottle filled with ethyl acetate makes this task easy. Note that ethyl acetate dissolves anything made of styrene, including clear hard plastic bottles and polystyrene foam. Any jar will serve as a killing jar if it has a broad mouth and tight-fitting screw-top lid to retain volatile killing agents. Long cylindrical jars, such as those used for olives, pickled onions, or spices, that are no more than 15 cm tall slip easily into a pocket or collecting bag.

Dark, colorfast beetles with few setae are sometimes killed and temporarily stored by placing them directly in fluid preservative such as 70–95% ethyl alcohol (ethanol) or 70% rubbing alcohol (isopropyl). For long-term storage of larger specimens, pour off the old alcohol and replace it with fresh after a week or two. Although there is no one method for killing beetles for morphological examination, beetles intended for use in tissue studies or molecular analysis must be placed directly in 95% ethanol. Ethanol is generally unavailable to private individuals, except for

prohibitively expensive neutral grain spirits, or pure grain alcohol available for purchase in liquor stores. Isopropyl in concentrations of 70% and 91% is readily available in drug and grocery stores, but over time, 91% isopropyl dries out specimens and makes them quite brittle.

NETS

Nets are essential for capturing beetles on the wing, resting on vegetation, or living in aquatic habitats. Flying beetles are best captured with aerial nets with a rim diameter of 30-40 cm and a handle 1 meter long. The net opening is usually reinforced with canvas or some other heavy material to prevent it from tearing. The net bag is made of cotton bobbinet or some other soft and translucent material that will hold its shape and is long enough to easily fold over the rim to trap beetles inside. The tip of the bag is typically rounded, not pointed, so that beetles and other insects are easily removed after capture. These lightweight and durable nets are easily maneuvered when swung through the air. Aerial nets are also used to capture tiger beetles by clapping them over the beetle and then holding the tip of the net bag so that the beetle will climb up into the net. Heavy-duty aerial nets are available commercially and have a net bag that is half canvas and half mesh; these are also used for light-duty sweeping through herbaceous vegetation.

Sweep nets are used to dislodge beetles from the tops of grasses, shrubs, and tree branches. They have shorter, thicker handles, sturdy net rings, and net bags constructed completely of canvas to endure repeated brushing through dense vegetation. Beetles are more likely captured in a sweep net if the rim is kept vertical to the ground. After completing a series of sweeps, swing the net back and forth several times and fold it over the rim to trap the insects inside toward the tip of the net bag. Slowly open the net to release stinging bees and wasps before removing beetles inside by hand, with forceps, or with an aspirator and transferring them to a killing jar.

Aquarium nets are useful for capturing aquatic beetles swimming along the edges of ponds and slow-moving streams. Long-handled dip nets are helpful for scooping beetles swimming in open water further out. D-frame nets have rims that are flat on one side and are dragged along the bottom of standing and moving waters to dislodge specimens resting on rocks and plants. Each of these nets placed vertically on the substrate in moving waters will capture beetles dislodged by lifting stones or disturbing vegetation upstream.

BEATING SHEET

Beating the branches and foliage of trees and shrubs, day or night, is an incredibly productive method for collecting beetles. Beating sheets are typically square sheets of light-colored canvas or ripstop nylon stretched out with two hardwood dowels or plastic tubes as crosspieces, with their ends slipped into reinforced pockets sewn into each corner of the sheet. To collect beetles, place the sheet beneath the foliage and then strike a large branch directly above with another dowel or net handle (Fig. 50). Beetles and other insects and arthropods jarred loose from their perches fall onto the sheet where they are collected using forceps or an aspirator. Beating during the day is most productive in the cooler morning hours in spring and summer. During the heat of the day, beetles often take flight the moment they hit the sheet. Nighttime beating is the best way to find many nocturnal species, including those that are not attracted to lights or baits.

A similar, more targeted method for sampling small flower visitors and other beetles involves using a white plastic pan (Fig. 51) in place of a beating sheet. Such pans have the added advantage of facilitating the extraction of specimens from handfuls of leaf litter, rotten wood, fungi, moss, and other organic materials.

SIEVING

Beetles are extracted from ground litter, fungi, lichens, mosses, soil, and decaying wood samples using various containers fitted with a screened bottom. The size of the mesh is determined by the size of beetles sought. Place the substrate in the container, shake it gently over a white or light-colored pan, sheet, or shower curtain, and collect the beetles with forceps, aspirator, or camel-hair brush. Kitchen strainers work well for sifting beach sand and other fine, dry



Figure 50. Using a beating sheet is an incredibly productive method of collecting beetles.

COLLECTING AND PRESERVING BEETLES INTRODUCTION TO BEETLES

Figure 51. A white pan is used like a beating sheet or for sorting through handfuls of leaf litter, rotten wood, and other organic materials.



soils. Beetles and larger pieces of debris retained in the screen are dumped onto a light-colored surface for further sorting, or placed in a Berlese or Winkler funnel.

BERLESE AND WINKLER FUNNELS

The *Berlese-Tullgren funnel* (Fig. 52), or simply *Berlese funnel*, uses the combination of light, heat, and desiccation created by a low-wattage incandescent light bulb to extract beetles from debris samples. Place a piece of coarse screen above the opening of the funnel to prevent debris from falling into the jar. Then fill the funnel with beach wrack, fungi, leaf litter, rotten wood, and other plant debris and place the light bulb above to drive beetles and other arthropod inhabitants downward into a glass jar filled with 70% ethanol or isopropyl as a preservative. The time required to extract all the beetles may be several days, depending on the size and moisture content of the sample.

The Winkler/Moczarski eclector, or Winkler funnel, is a more portable system. Rather than depending mostly on desiccation of the sample, this method also relies on the movement of beetles and other arthropods within the sample. Litter and rotten wood are collected at the bases of living trees and stumps, alongside logs, or in depressions. These samples are then placed into a Winkler sifter and shaken vigorously through a coarse screen to remove leaves and branches (Fig. 53). Plastic buckets or bins fitted with 6 or 12 mm mesh hardware cloth bottoms will also



Figure 52. Collapsible Berlese funnel for extracting small beetles and other arthropods from leaf litter.



Figure 53. A Winkler eclector separates beetles and other small arthropods from larger bits of leaf litter. facilitate the separation of beetles from these and other coarse plant materials. Beetles and other litter arthropods accumulate within the fine siftate that passes through the screen. The siftate is poured into one or more mesh bags suspended inside the Winkler bag, which is tied off at the top. The large surface area of each mesh bag increases the chances of beetles and other arthropods moving through the sample to crawl through the mesh and fall into a plastic drink cup below that is half-filled with ethanol or isopropyl. Winkler bags are suspended in a well-ventilated place for up to several days so that all the sample's arthropod inhabitants have fallen into the preservative.

FLOATING

Another useful method for separating beetles from plant materials—particularly clumps of grass, but also fungi,

bark, and dung—is to drop the materials into a bucket of water. Beetles and other insects will float to the surface, where they can be scooped up with a small kitchen strainer or collected by hand.

FLUMING

Collecting beetles and other insects from flumes is called fluming. Flumes traversing foothills, particularly along the western slopes of the Sierra Nevada in California, were constructed to divert water from streams and rivers to generate hydroelectricity, irrigate crops, and provide municipalities with drinking water. Functioning as both pitfall trap and conveyor belt, flumes are literally awash in plant debris during the spring and summer that is laden with insects, especially beetles. Sometimes flowing for miles through steep terrain and varied habitats, flumes carry an



incredible diversity of trapped insects. Watching the rapidly flowing water to net individual specimens as they float by is not nearly as productive as systematically skimming the water to secure a diversity of beetles. One such method involves employing pool nets to capture debris from the water surface, then hauling the nets out and depositing their contents onto a table covered with a white bed sheet for sorting (Fig. 54).

COLLECTING AT LIGHTS

The most productive method of collecting beetles at night involves attracting them with a light suspended in front of or over a white sheet or polyester shower curtain. Almost any light will attract night-flying beetles, but black or ultraviolet light (Fig. 55) is the most effective. Commercially available black lights operate on house current or 12-volt batteries. Mercury vapor lights using 175-watt bulbs are also very attractive to beetles and other night-flying insects, but require house current or a generator to operate. Note that these bulbs become extremely hot and will break if they come into contact with rain or other sources of moisture. Suspend a freshly laundered sheet between two trees or poles over a ground sheet. Place the light about a foot away and parallel to the upright sheet at about eye level to achieve maximum illumination. Be sure to regularly patrol the ground and nearby shrubs just beyond the illuminated area to find beetles crawling on the ground or wandering about plants, trees, stumps, and logs. Using a headlamp instead of a flashlight will keep both your hands free for

collecting specimens. Warm spring and summer nights (65 °F or higher), especially with little or no moon, are the most productive. Most beetles arrive at lights within two hours after sunset, but some, especially larger species, fly later in the evening. Light traps (Fig. 56) use a black light suspended over a funnel placed over a 3- or 5-gallon bucket. Acrylic or metal vanes help to direct beetles and other insects down the funnel and into the bucket. Supplying the bucket with paper egg cartons or wadded-up paper towels will reduce the wear and tear on beetles and other insects caught in the trap. Always use a collecting jar dedicated to beetles, as mixing them with other insects, especially moths, often results in beetles covered in scales, or other insect specimens damaged by beetle claws.

TRAPPING BEETLES

Methods for trapping beetles, with or without the use of baits, lures, lights, and other attractants, are just as diverse as the beetles themselves. The performance of these traps depends on the selected trap site, time of year, and local conditions. Pitfall traps are designed to capture beetles crawling on the ground. Using a trowel or small shovel, dig a hole just large enough to accommodate a 16-ounce plastic deli or drink cup. Place the cup in the hole so the rim is flush with the surface of the ground. Then place an identical cup within the first cup. Nesting the cups in this fashion allows easy inspection of the trap without having to re-dig the hole each time. Cover the trap with a flat stone or



LEFT: Figure 55. An ultraviolet light powered by a 12-volt battery suspended in front of an upright sheet to attract beetles and other insects.

RIGHT: Figure 56. A 12-volt blacklight bucket trap.



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slab of wood raised on small stones, leaving a space large enough for beetles but small enough to keep out larger animals. Place unbaited pitfall traps along natural barriers, such as rock ledges and logs. Otherwise, use wood, metal, or plastic drift fences to increase the effective surface area for each trap (Fig. 57). Pitfalls baited with small amounts of fresh dung, carrion, rotting fruit, or chopped mushrooms will attract and capture beetles over a large surface area without the aid of physical obstacles. Solid and liquid baits are wrapped in cheesecloth or placed in small plastic sauce cups, respectively, and suspended over the trap opening with sticks, wires, or string (Fig. 58). Liquid baits consisting of equal parts molasses and water, or malt with a pinch of yeast, attract species naturally drawn to sap flows. For traps that are checked daily, place crumpled paper towels or leaves at the bottom to provide beetles with a bit of cover. Pitfalls left out for a week or more are supplied a 50–50 mix of propylene glycol and water to kill and preserve beetles. Unlike ethylene glycol (antifreeze), propylene glycol is not toxic to wildlife. Fruit traps made from plastic drink bottles, cups, or corncob bird feeders (Fig. 59) and hung at various heights in trees and shrubs are very attractive to beetles. Be sure to check these traps regularly and provide a metal or plastic rain guard to prevent specimens from being washed out of the trap. Pan traps, especially bright yellow ones filled with about 50 mm of water (Fig. 60), are



Figure 57. Pitfall trap array.



Figure 58. Pitfall trap with soapy water sunk beneath a stick baited with feces.





LEFT: Figure 59. Fruit traps. a. trap made from a plastic soft drink bottle; b. ripe banana placed in a corncob squirrel feeder.



Figure 60. Yellow pan trap filled with soapy water to attract flower-visiting beetles and other insects.





especially attractive to some jewel beetles (Buprestidae), tumbling flower beetles (Mordellidae), and other flowervisiting insects. A drop or two of dish soap added to the water will break the surface tension, making it harder for the beetles to escape.

Flight intercept traps (Fig. 61) generally consist of one or more upright clear plastic panels suspended over a series of pans containing soapy water or propylene glycol. Beetles colliding with the screen fall into the fluid, where they are killed and temporarily preserved. A plastic roof placed over the top of the trap will prevent rainwater from diluting the fluid. A Malaise trap (Fig. 62) is essentially a tent with a wall or partition on the inside. Flying beetles strike the interior walls and fly up into a collecting jar filled with 70% ethanol or isopropyl alcohol. A shallow trough or series of roasting pans filled with fluid are placed under the partition to capture specimens that fall to the ground rather than fly up into the collecting jar. Both traps produce large numbers of diurnal and nocturnal species that are not readily collected via other methods.

Lindgren funnel traps (Fig. 63) consist of a series of four or more black funnels suspended over one another and hung from a branch, rope between two trees, or some other hanger. At the bottom of the funnels is a collecting container that is either dry or partially filled with propylene glycol or some other preservative. The stack of funnels resembles a tree trunk and is attractive to wood-boring beetles and other species that crawl or land on tree trunks. Lindgren funnel traps are sometimes baited with alpha-pinene (a component of turpentine) and ethanol, chemical compounds that mimic those released by injured and dying conifers and hardwoods. Specimens captured in dry collection containers are easily damaged and are best removed every few days, while those with preservative may be inspected weekly or every two weeks.



ABOVE LEFT: Figure 61. A V-shaped flight intercept trap.

ABOVE RIGHT: Figure 62. Malaise trap.

LEFT: Figure 63. Lindgren funnel trap.

TEMPORARY STORAGE OF SPECIMENS

Beetle specimens should be prepared immediately after they are collected and killed, but this is not always possible. Specimens left in killing jars charged with adequate amounts of ethyl acetate will remain relaxed for several days or weeks and can be handled without damage. They can also be transferred to a tightly sealed container and stored in the freezer. For longer periods of storage, carefully place specimens between layers of paper towels moistened with a few drops of ethyl acetate or preserved by adding chlorocresol crystals and store in soft plastic storage boxes with airtight lids. Specimens stored in this manner will keep indefinitely, but delicate colors will fade and setae become matted. Large numbers of beetles collected from Berlese or Winkler funnels, pitfalls, and blacklight traps can be placed in 70% ethanol or isopropyl alcohol. After about a week, replace the fluid with fresh alcohol. Specimens intended for molecular studies must be killed and preserved in 100% ethanol. All specimens preserved in alcohol should be kept cool, especially those intended for subsequent DNA work. Always include basic collecting information (locality, date, collector) inside each container, using pencil or permanent ink on good quality acid-free paper. Samples without this information are of little value and should be discarded.

RECORDS AND FIELD NOTES

Always record the date, place, and collector's name for your specimens. Be sure to include the country, province or state, and county, as well as the name of the nearest city or town, mileage and direction from the nearest road junction, latitude and longitude, and any other locality data that will help fix your collecting locality on a map. These data will become the basis for the locality labels for your specimens and serve as directions to others who may want to retrace your steps to find a specific locality to search for a species.

Dead beetles in collections reveal little of their lives, so it is important to spend some time observing their behaviors whenever possible and record them in your field notes. Your observations should always include time of day, temperature and humidity, plant or animal associations, and reproductive and feeding behaviors; such details are all worthy of note and could easily be new to science. Whenever possible, record these observations in the field, as they are happening. Never trust your memory for long because it is all too easy to confuse bits of information in time and place. With practice, you will settle on a routine for recording your observations.

Maintaining a detailed and accurate field notebook is an important component of a carefully curated beetle collection. The value of the notes is enhanced if they are clearly associated with specific specimens, especially those identified to species. Select a well-bound notebook with acid-free paper that is small enough to pack in your field kit, but large enough not to be easily lost or misplaced, and will withstand the rigors of field use. Pencils and finetip marking pens with permanent black ink, such as those manufactured by Prismacolor and Pigma Micron, are available from art supply stores and are the most reliable for taking notes in all sorts of weather.

MAKING A BEETLE COLLECTION

There is still much to learn about the beetles of western North America, Carefully prepared collections, notes, and photographs add enormously to our understanding of their distribution, seasonal activity, and food and habitat preferences and provide a historical record that will offer insights into the possible impacts of climate change. If properly cared for, beetle collections will last hundreds of years to inspire and inform future generations of coleopterists and naturalists. Coleopterists-professionals and amateurs alike-are but temporary caretakers of collections that ultimately belong to the greater scientific community. Should you lose interest, lack adequate storage space, or simply want to preserve the legacy of your hard work long after you are gone, consider donating your collection and its associated records to an appropriate research institution dedicated to housing permanent insect collections and making them available to researchers and students. Below are some tips and tools for building and maintaining a scientifically valuable and aesthetically pleasing beetle collection.

PINNING AND POINTING SPECIMENS

Dead, dried beetles are very brittle, and touching them will result in broken and lost appendages that will make their identification difficult, if not outright impossible. For specimens to be manipulated without damage, they must be mounted on pins that are safely used as handles. Always use black-enameled or stainless-steel insect pins because sewing pins are too short and thick and will corrode. Insect pins are available through entomological supply houses in packets of 100 in several sizes (diameters). Sizes 0–3 are suitable for most of the species found in western North America. Sizes 00 and 000 bend easily and are not recommended for mounting beetles.

Pin beetle specimens when their appendages are still pliable enough to manipulate without damage. Working only with beetles collected at the same place and time, temporarily place your specimens on a folded tissue or paper towel for several minutes to absorb excess moisture. After selecting the appropriate-size pin, grasp your specimen firmly between the thumb and forefinger or brace it on the table with its topside up. With your other hand, push the pin through the base of the right elytron with the pin exiting underneath between the middle and hind legs. Before driving the pin all the way through, check the relative alignment of the specimen



Figure 64. Proper longitudinal and transverse orientation of a beetle specimen on pin.

carefully to make sure the shaft of the pin is perpendicular to the long and transverse axes of the body (Fig. 64).

Once the pin is all the way through, use the highest or shortest step of your pinning block to adjust the height of the beetle on the pin so a space of about 25 mm is left between the top of the specimen and the head of the pin. A pinning block (Fig. 65) is a small block of hardwood with three or four fine holes drilled successively deeper in 12 mm increments, beginning with 12 mm. Using this simple tool will enable you to consistently space the head of the pin above the specimen and the intervals between the specimen and its labels underneath.

Specimens that are 5 mm or less or very narrow and likely to be damaged by direct pinning are best preserved on points (Fig. 66). Points are isosceles triangles of acid-free card stock that are about 7 mm long and 2 mm wide at the base. The occasional point can be cut with sharp scissors, but a point punch, available from entomological supply houses, is desirable for making large numbers of uniform points. Push an insect pin (no. 2 or 3) through the broad end of the point and adjust its height on the shaft using the highest step on your pinning block. Using fine-



Figure 65. Pinning block.





Figure 66. Proper longitudinal and transverse orientation of a beetle specimen affixed to a point.

tipped forceps, slightly bend down the tip of the point before attaching it to the specimen. For the sake of convenience, prepare several dozen points in advance to have them ready. Affixing a beetle to a point is best done under wellilluminated magnification provided by an optical visor or binocular dissecting microscope. Place the specimen to be pointed on its back (*dorsum*) or underside (*ventrum*) on a

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smooth, light-colored surface so the head is to the right and you have unfettered access to the beetle's right-hand side. Then dip the tip of the point into adhesive that is soluble in water (e.g., Elmer's blue gel) or alcohol (shellac, polyvinyl acetate) and affix it to the area of the thorax between the middle and hind legs. Be sure that there is enough glue to securely attach the specimen to the point, but not so much that it spreads and obscures important features needed for identification. Alcohol-soluble adhesives normally thicken with use and can be thinned by adding a bit more alcohol. If too thin, leave the container open for a brief period to allow excess alcohol to volatilize. Once the beetle is glued to the point, minor adjustments can be made so that its body axes are perpendicular to the shaft of the pin.

SPREADING SPECIMENS

Accurate species identification in beetles often requires careful examination of a specimen's appendages, mouthparts, body segments, and genitalia. Familiarity with these features will help guide and improve your efforts to properly prepare and spread specimens. A spreading board (Fig. 67) is the best way to position and set a beetle's antennae and legs in place. Purchase a small sheet of polystyrene foam 2.5 cm thick (30 x 46 x 2.5 cm) from a craft store and wrap it in newsprint to prevent claws and mouthparts of dried specimens from catching on the board's rough surface and breaking off. Start by pinning a temporary locality label in the upper left corner of the spreading board. To the right of the label, push the first pinned beetle into the spreading board so the underside of the body rests directly on the board's surface. Carefully position the legs and antennae with brace pins so that these structures are symmetrical and observable from all angles. Tuck in legs and antennae, since specimens with



Figure 67. Spreading board with beetle specimens.

outstretched appendages take up valuable space and are likely to be broken. Be sure to keep spread specimens from each locality separate so they can be accurately labeled when they are dry. It may take a week or so for specimens to dry, depending on the size of the specimen and relative humidity. You may want to keep your spreading boards in a protected yet airy space, such as in a covered box, in a cupboard, or on shelves with doors so that your specimens don't get dusty. Once the specimen is dried, carefully remove the brace pins to avoid damaging the now brittle appendages.

LABELING

To be of any scientific value, each specimen must have a permanent, carefully composed, and neatly produced locality label. Using word processing software, type locality labels in columns in a bold sans serif font (Arial, Geneva, Helvetica) at a size of 4- or 5- point size. Each finished label should be no more than 2 cm across and five or six lines long, although some adjustments may be required depending on the length and the nature of the label data. Labels are printed on acid-free 176 g/m² card stock with a laser printer set at 1200 dpi or 600 dpi professional. Cut the printed labels into strips and then individually with sharp scissors so that all four sides are neatly trimmed right up to the text.

Locality labels should include the following information on the first line: country (abbreviated as USA or CAN), state or province (e.g., CA for California, BC for British Columbia), and county. The remaining four or five lines of the label include the general locality, specific locality (if applicable), elevation (in feet [ft], or meters [m]), latitude and longitude (preferably in decimal degrees), date (with month spelled out, or as a Roman numeral [eg., vii for July] and full year), collector name(s), and collecting method. A sample locality label is shown below:

USA: AZ, Santa Cruz Co. Santa Rita Mts., Madera Cyn. Santa Rita Lodge, 4900 ft. elev. 31.7257° N, -110.8804° W 25 July 2021, A.V. & P.G. Evans at black light

An additional label may be added to more fully flesh out the method of collection, host plant, and other ecological data, as well as a cross-reference number that connects the specimen to photographs and field notes. Once the beetle is identified to species, a determination label containing the

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species name, name of determiner, and year of determination (as shown below) can be added as the very last label:

Dynastes grantii (Horn, 1870) det. A.V. Evans, 2021

Align the pinned specimen and its label so the beetle's head is directed toward the label's left margin. Center the specimen over the label and push the pin partway through. Select the appropriate step on the pinning block to adjust the height of the label on the pin. When labeling pointed specimens, center both the beetle and the point over the label with the point directed toward the label's left margin and the beetle's head off to the right of the point.

RELAXING SPECIMENS

To prepare dried specimens, or to reposition appendages or dissect those already mounted, specimens must first be "relaxed." Beetles that are not delicately patterned or colored, or those lacking any kind of setose or waxy vestiture that could become matted, discolored, or dissolved are placed directly in hot water. Simply bring filtered or distilled water to a boil and then add a drop of dish soap as a wetting agent. After several minutes, specimens submerged in this solution should become pliable enough to manipulate safely; larger and bulkier specimens may take longer.

For delicate specimens with pubescence that should not come into direct contact with water, it is best to use a relaxing chamber. Place a layer of clean sand, cardboard, blotter paper, or some other relatively sterile and porous substrate in a soft (polyethylene) plastic shoe box or



Figure 68. Beetle collections are stored in pest-proof cardboard specimen boxes or glass-topped drawers supplied with unit trays.

food storage container. Saturate the substrate with warm water and pour off the excess. Place dry specimens in a plastic jar lid so they will not come in direct contact with wet surfaces. Add a couple of mothballs to the chamber to discourage mold. Smaller beetles with more delicate bodies will become sufficiently relaxed overnight, but larger, heavier-bodied specimens may take several days to soften. Inspect the chamber every few days for mold that will damage or destroy specimens. Insect pins that corrode in a relaxing chamber should be replaced.

PRESERVING LARVAE AND PUPAE

Larvae and pupae, especially those with ecological data and positively associated with adult voucher specimens, are extremely valuable and should be permanently preserved. Place them in boiling water for several minutes to fix their tissues and kill the microorganisms that will hasten internal tissue decay. Then place them directly in 70% ethanol or isopropyl alcohol. After a day or so, place these specimens (one species per collection) in polyethylene vials with screw caps supplied with a fresh supply of alcohol for permanent storage. Each vial must have its own label inside to be of any scientific value. Long shelf life for wet labels can be problematic because of the effects of preservatives on various papers, ink, and laser-printed text and is still undergoing study. For now, the simplest solution is to use acid-free 100% rag paper with pencil or to print laser labels at 1200 dpi or 600 dpi professional. Before cutting the sheet into individual labels, coat it with clear acrylic spray sealer to increase its durability. Readers interested in building and maintaining extensive collections of beetle larvae and pupae would do well to keep up with published literature and online forum discussions on the latest materials and techniques.

COLLECTION STORAGE

Sturdy, airtight specimen boxes with tight-fitting lids are a must for the permanent storage of beetle specimens. Dermestids, both larvae and adults, and booklice (Psocodea) can slip through the narrowest of spaces and, in a relatively short period of time, reduce pinned beetle collections to dust. Fluctuating temperatures, humidity, and sunlight will also destroy collections over time, so it is important to store them in dark and temperature-controlled spaces.

Storing specimens in tightly sealed glass-topped drawers that are kept in sealed cabinets is the best hedge against light and pest damage, but these systems are expensive. Wooden specimen boxes with tight-fitting lids, known as Schmitt or Schmitt-type boxes, also provide adequate protection for specimens, but are also pricey. Entomology departments at museums or universities occasionally offer surplus drawers and boxes at reasonable prices. A relatively inexpensive system consists of commercially available cardboard specimen boxes with separate lids and foam bottoms (Fig. 68) that are slipped into 2-gallon resealable plastic bags to keep out pests.

None of these systems is completely effective, especially if beetles left out on spreading boards or open trays become infested with the eggs or larvae of pests and are then introduced into otherwise pest-proof containers. Constant vigilance for fine powder accumulating beneath specimens is essential for identifying those infested with booklice or dermestid larvae. Remove these specimens immediately, take their labels off the pin, and immerse the specimen in alcohol for at least one day. If several specimens within the same box are affected, place the entire box in a very cold freezer for at least a week. This process may need to be repeated, as freezing will usually kill all the dermestid larvae present but may leave unhatched eggs unaffected.

CURATING YOUR COLLECTION

Align your specimens in neat columns and rows using either the label or specimen itself as a guide to create nice, straight rows. Orient each specimen so that the head of the pinned beetle or the tip of the point is directed toward the top of the box. Avoid entangling legs and antennae by not overcrowding specimens. Organize your collection first by family and subfamily, then by tribe, genus, and species (see p.564). A good reference collection not only contains well-prepared specimens accompanied by accurate label data, but is also organized to facilitate the easy retrieval of those specimens. As your collection grows in size and diversity, you might consider adopting a glass-topped drawer system housed in cabinets. These drawers are supplied with interchangeable cardboard trays of various sizes lined with polyethylene foam bottoms called unit trays. Unit tray systems simplify curation and are easily expanded to accommodate the addition of new taxa and specimens. Glass-topped drawers with pinned beetles intended primarily for display must be kept dry and away from extreme temperatures to avoid the growth of mold, and out of direct sunlight to prevent fading. Display cases fitted with UV-filtered Plexiglas will slow, but not prevent, the fading of specimens exposed to sunlight.

BEETLES ON THE WEB

Information on beetles abounds on the Internet. Some of the most useful websites are those maintained by societies and institutions, but there are also helpful sites that are managed by knowledgeable amateurs through social media. The Coleopterists Society website contains not only information about society membership, but also listings of news, events, resources, and other items of interest to those fascinated by beetles.

There are several websites, including BugGuide, iNaturalist, and What's That Bug? where good images of beetles and other insects accompanied by geographic location and other pertinent information may be submitted for identification by knowledgeable members of the community. If you have a beetle that you want to identify, you can also browse images on these websites to search for possible matches. Facebook users can also upload images to several pages that are dedicated to insect identification, including "Pacific Northwest Bugs" and "SW U.S. Arthropods" that focus on insects, including beetles, of western North America.

One of the best ways to identify beetles is to compare them with reliably identified specimens. As it is not always possible to visit a collection in person, several museums have posted high-quality images of identified beetles in their collections online. For example, the Museum of Comparative Zoology at Harvard University has created the MCZBase: The Database of the Zoological Collections. Through online searches, users can locate and examine identified specimens, including holotypes, allotypes, and paratypes, the actual specimens upon which scientists based their original scientific descriptions of those species. Types have a special function in zoological nomenclature in that they serve as the physical standard for species that are formally described in the scientific literature. The Symbiota Collections of Arthropods Network (SCAN) has a collection of images submitted by more than 100 North American arthropod collections for all arthropod taxa, including beetles identified by experts. The New World Cerambycidae is an incredibly useful online resource for identifying longhorn beetles and contains images of types and other specimens that are authoritatively identified.

Access to recently published research articles that monograph beetles, offer identification keys, hypothesize their phylogenetic relationships, and other scientific research are often accessible only through paid subscriptions or to persons with institutional library affiliations. However, some authors immediately post their work at ResearchGate. Older, yet still important publications are often freely