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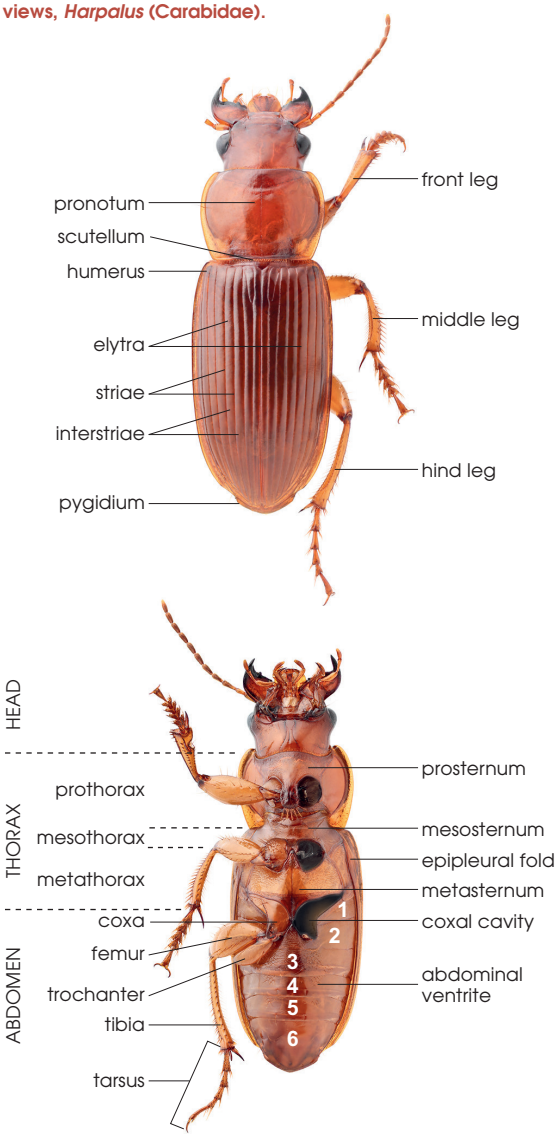
INTRODUCTION TO BEETLES

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.

Figure 1. Dorsal and ventral views, *Harpalus* (Carabidae).



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, parallel-sided 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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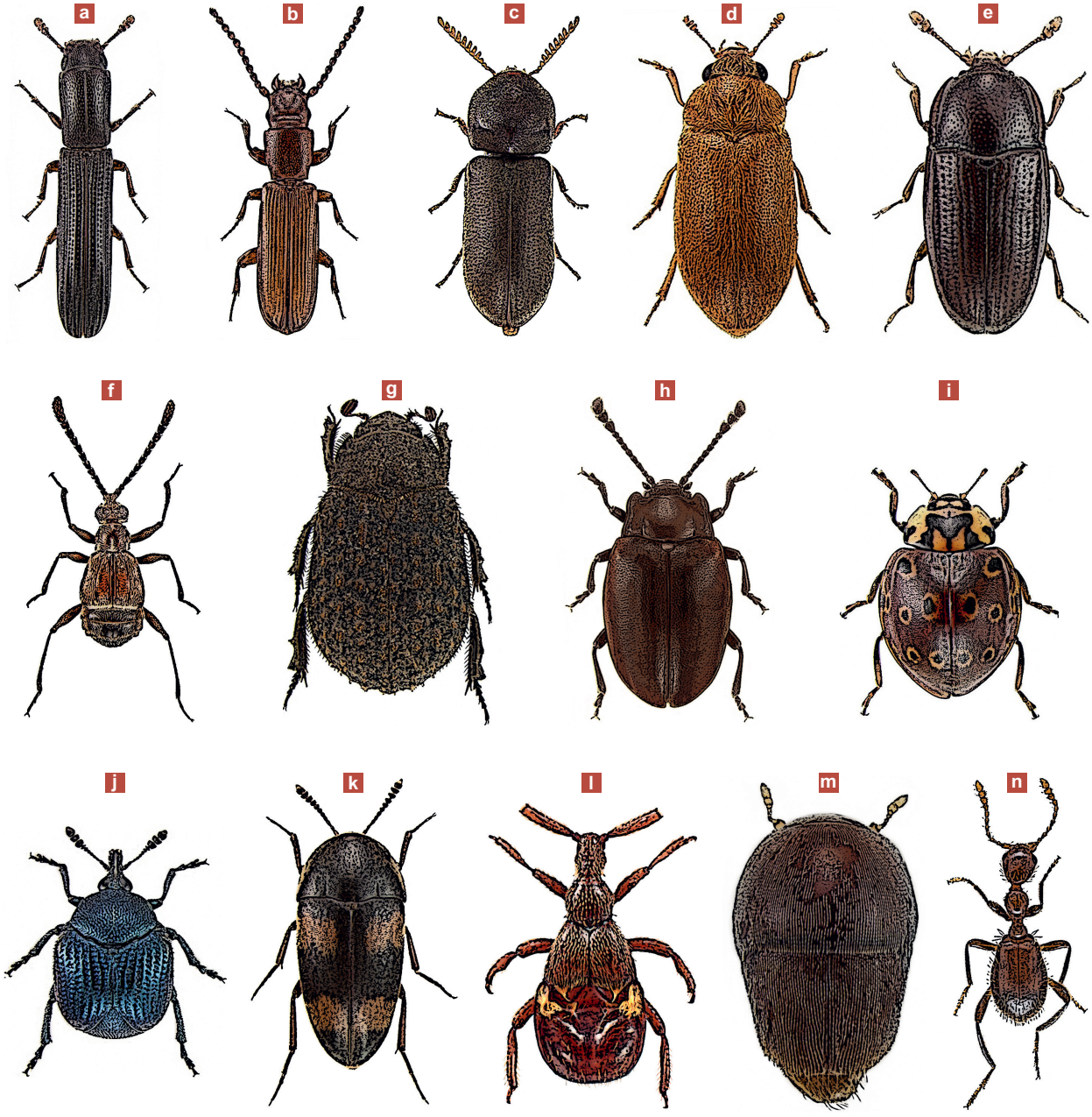

Figure 2. Body shapes.
a. elongate, Zopheridae; b. elongate, Passandridae; c. elliptical, Ptinidae; d. elongate-oval, Byturidae; e. elongate-oval, Cerylonidae; f. elongate-oval, Staphylinidae; g. oval, Trogidae; h. oval, Endomychidae; i. broadly oval, Coccinellidae; j. broadly oval, Brentidae; k. obovate, 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

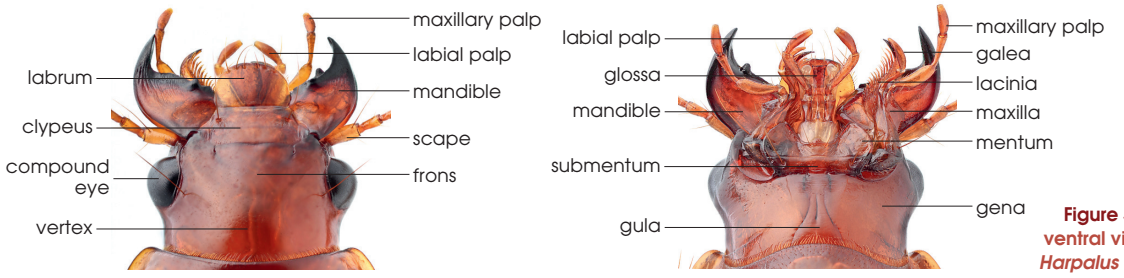

Figure 3. Dorsal and ventral views of head, *Harpalus* (Carabidae).

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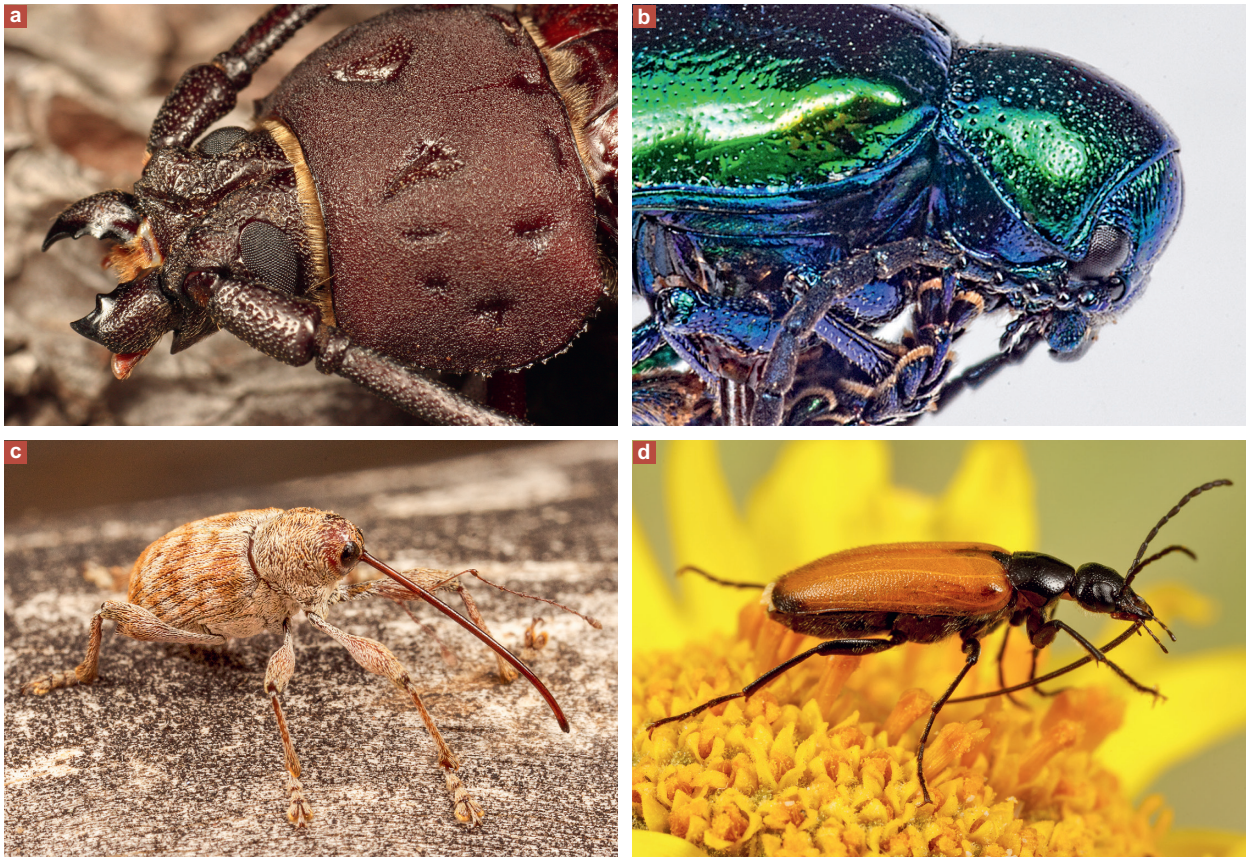
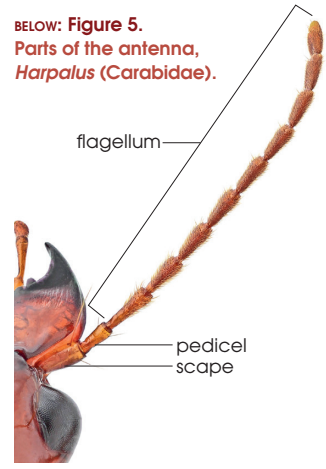


Figure 4. Mouthpart orientation.
a. prognathous head, *Trichocnemis* (Cerambycidae); b. hypognathous mouthparts are directed downward, perpendicular to the long axis of the body, *Chrysochus* (Chrysomelidae); c. rostrate mouthparts are directed downward and are typical of most plant feeding beetles, *Curculio* (Curculionidae); d. maxillae form elongate sucking tube extending posteriorly under body, *Nemognatha* (Meloidae).

BELOW: **Figure 5.** Parts of the antenna, *Harpalus* (Carabidae).



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

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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

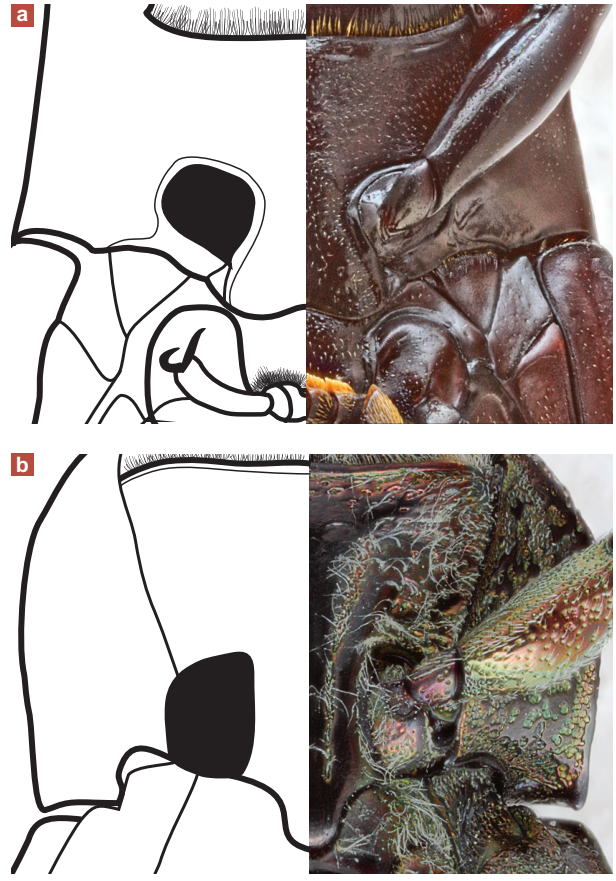

Figure 7. Procoxal cavities. a. closed; b. open.

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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 elytra, or *elytral apices*, usually meet at the elytral 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 three-digit 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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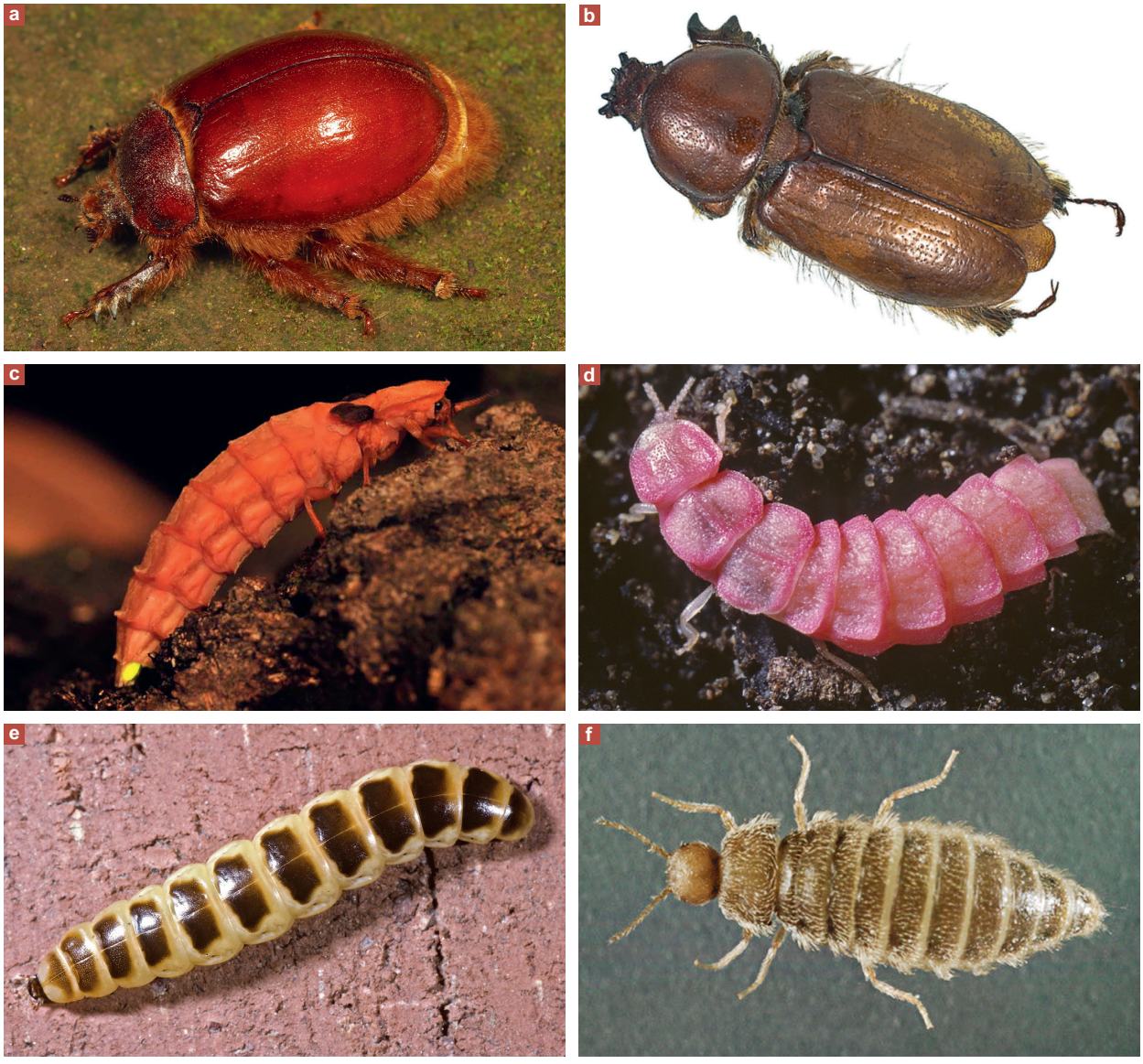

Figure 8. Brachypterous, apterous, and larviform females. a. *Pleocoma* (Pleocomidae); b. *Diphyllostoma* (Diphyllostomatidae); c. *Pleotomus* (Lampyridae); d. *Microphotus* (Lampyridae); e. *Zarhipis* (Phengodidae); f. *Thylodrias* (Dermestidae).

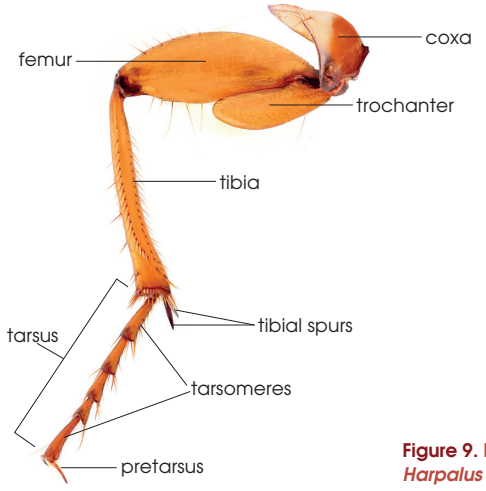

Figure 9. Hind leg, *Harpalus* (Carabidae).

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

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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

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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 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.

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

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

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

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 elytra with their legs 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).

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

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

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 carrion-feeding 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.

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

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. Plant-feeding 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 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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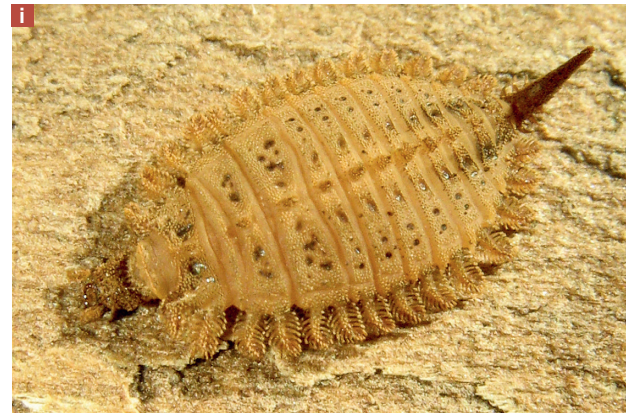

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Figure 18. Beetle larvae.
a. *Calosoma* (Carabidae); b. *Amblycheila* (Carabidae); c. *Tropisternus* (Hydrophilidae); d. *Sinodendron* (Lucanidae); e. *Cotinis* (Scarabaeidae); f. *Nosodendron* (Nosodendridae); g. genus unknown (Buprestidae); h. *Eubrianax* (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 laying 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 plant-feeding, 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 quickly 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 mud-nesting 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).

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