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MYXOPHAGA

Myxophaga was the last of the four beetle suborders proposed and is comprised of about 120 species classified in four small families, including Lepiceridae (Neotropical), Torrindincolidae (Afrotropical, Neotropical), Sphaeriusidae (all continents except Antarctica), and Hydroscaphidae (Afrotropical, Nearctic, Neotropical, Oriental, Palearctic). Despite its relatively small size, the suborder has an outsized role in elucidating the evolutionary history of Coleoptera.

Myxophagans are characterized by their small size, algae-feeding habits, and preference for mostly hygropetric habitats. The largest species measure 1/10 in (2.7 mm) in length, but most species are much smaller. Hygropetric species typically inhabit the thin layers of water that cover rocks, algae, and aquatic plants found along streams and rivers, especially in warm, humid climates. Adults and larvae occupy interstitial spaces in wet sand and gravel along rivers, algal-covered seeps and stream banks, or spray zones associated with waterfalls. Adults are also occasionally found in association with flood debris or among tropical leaf litter some distance from water.

BEETLE FAMILY: SPHAERUSIDAE

The 22 species of Sphaerusidae are among the smallest and least studied of Myxophaga. These hygropetric species are distinguished mostly on the basis of their size and surface sculpturing, but recent molecular studies suggest that cryptic species with similar external features are likely. Specimens are seldom collected and little is known of their natural history or distribution. Based on comparisons of modern-day *Sphaerius* with two extinct genera (*Bezesporum* and *Burmasporum*) known from inclusions in 99-million-year-old Burmese amber, Sphaerusidae has maintained its morphology and riparian habits for at least 100 million years. Thus, beetles in the genus *Sphaerius* could be considered highly specialized living fossils.

Larval examples of all myxophagan families are known, save for Lepiceridae. Myxophagan larvae are small, flattened, and possess spiracular gills. These features are all likely associated with their preference for hygropetric habitats. The dense arrangement of muscles and other structures, along with the unusual shape and size of the head, likely evolved due to their very small size. Their strong degree of miniaturization thwarted initial attempts to examine their internal organs by dissection and serial sections. Fortunately, the use of computer-generated, three-dimensional reconstructions eventually enabled researchers to develop detailed descriptions of their internal features.

← *Hydroscapha natans* (Hydroscaphidae) is a skiff beetle that inhabits algal mats along cold streams and hot springs in western North America and adjacent Mexico.

ADEPHAGA

Adephaga are an ancient group of beetles with a fossil record dating back to the early Triassic or Late Permian. The suborder includes approximately 45,000 species in the families Haliplidae, Gyrinidae, Noteridae, Meruidae, Aspidytidae, Amphizoidae, Hygrobiidae, Dytiscidae, Trachypachidae, Cicindelidae, and Carabidae.

Adephagan adults and larvae are mostly predators, although some groups are decidedly not hunters at all. Larval haliplids nibble on algae, while rhysodine carabids consume slime molds and some harpaline carabids eat seeds.

Most adephagan families occur in all major zoogeographic realms except Antarctica. However, several families are considered to have relictual distributions (meaning they were previously more widespread). For example, amphizoids, represented by only five species in the genus *Amphizoa*, are known only from western North America, central and eastern China, and North Korea. *Hygrobius*, the sole genus of Hygrobiidae, comprises six species that are patchily distributed in the western and eastern Palearctic, and across Australia. The two known species of Aspidytidae, *Aspidytes niobe*

MERU PHYLLISAE

The sole member of Meruidae, *Meru phyllisae*, is the smallest species of aquatic Adephaga. Commonly known as comb-clawed cascade beetles, they were first discovered in 1985 in Venezuela, but were not described scientifically until 2005. Few beetles have been found since and little is known of their biology. Less than a millimeter in length, these tiny, pale tan beetles inhabit the edges of a whitewater cascade that forms a slow-flowing film over exposed granite bedrock. This rock formation is part of the Guiana Shield, a region known for its biodiversity, and is home to many species found nowhere else.

↑ *Amphizoa insolens* (Amphizoidae) ranges from Alaska to southern California, east to Alberta and Wyoming; the genus also occurs in Asia.

and *Sinaspidytes wrasei,* occur in South Africa and China, respectively. The sole species of Meruidae, *Meru phyllisae*, occurs in southern Venezuela. Trachypachidae is represented by only two genera. Three of the four species of *Trachypus* live in western North America, while the fourth species occurs in the Palearctic. Both species of *Systolosoma* occur in central and southern Chile.

Supported by both adult and larval features, the monophyly of Adephaga is undisputed. Based on habitat, adephagan beetles may be separated into two groups, the terrestrial Geadephaga (Trachypachidae, Cicindelidae, Carabidae) and the remaining aquatic Hydradephaga, but recent phylogenetic studies don't support the monophyly of either group.

POLYPHAGA

With more than 335,000 species, Polyphaga is the largest suborder of beetles. It was the first suborder recognized within Coleoptera and is currently represented by 191 families. Nearly two-thirds of all known beetles occur in just eight polyphagan families, including Staphylinidae (around 55,000 species), Curculionidae (around 51,000), Chrysomelidae (around 37,000), Cerambycidae (around 35,000), Scarabaeidae (around 32,000), Tenebrionidae (around 20,000), Buprestidae (around 15,000), and Elateridae (around 10,000). Many of the species classified in these families are well known because of their large size, horn-like armaments, spectacular colors, curious behaviors, or pest status.

WIDE RANGING

Polyphagan beetles occupy all zoogeographic realms except Antarctica and occur in both terrestrial and aquatic habitats. As the name of the suborder suggests, polyphagan beetles feed on all kinds of organic tissues, including those of plants, fungi, and animals, both living and dead. Most herbivorous species consume the roots, trunks, branches,

CLASSIFICATION—AN ONGOING EXPLORATION

Advanced molecular analyses of multiple genes not only help to refine our hypotheses of evolutionary relationships, but also enable us to estimate the actual age of a taxon by estimating its point of divergence with it nearest relative. These activities, coupled with the implementation of ever more sophisticated techniques for examining and elucidating fine morphological structures of both modern and fossil species, will continue to challenge our current assumptions about the classification of Coleoptera at and within the subordinal level well into the foreseeable future.

stems, leaves, flowers, fruits, and seeds of plants. Many of these species are generalists that consume a broad range of plant species, while others are more selective and specialize on plants in just one family or a single genus. Some species prefer their plant materials already decayed by fungi and other microorganisms or to have passed through the digestive systems of other animals. Several polyphagan families are largely composed of species with adults and larvae that eat only fungal tissues, including fruiting bodies and spores.

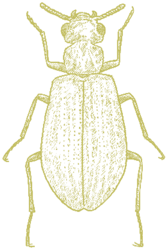
PREDATORS

Predation has evolved several times in Polyphaga. Adults and larvae of some checkered and click beetles hunt for wood-boring beetles and other insects. Predatory soldier beetles attack aphids and other sap-sucking insects, while the terrestrial larvae of fireflies prey on other beetle larvae, slugs, and earthworms. Adult ant-loving scarabs will invade the nests of select species of ants to eat their larvae, too. The larvae of several beetle families are parasitoids of the larvae of other beetles, as well as those of bees and wasps.

FAR FROM SETTLED

The classification of families within Polyphaga, as well as its relationship with other suborders, is still undergoing revision. For example, species classified in the family Jurodidae appear to have affinities with both primitive and advanced beetles. Known from multiple fossils and a single example of a living species (*Sikhotealinia zhiltzovae*) found dead in a forest cabin window in the Russian Far East, jurodids are distinguished from all other beetles by the presence of three ocelli (simple eyes) on the head. Tentatively placed in Archostemata based in part on the similarities of its thoracic structures, Jurodidae was recently moved to Polyphaga because of the similarity of their wing venation to other polyphagan species. As with its former placement in Archostemata, the affinities of jurodids within Polyphaga are uncertain.

↓ The single known specimen of *Sikhotealinia zhiltzovae* (Jurodidae) was found in the Sikhote-Alin Mountains in the Russian Far East.



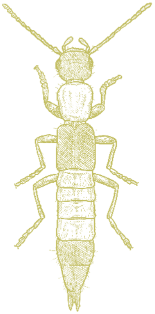
EXOSKELETON

Tough, yet light in weight, the exoskeleton covers a beetle's body and protects its vital internal organs while also providing an internal scaffolding for the attachment of powerful muscles. It consists of cuticle secreted by the underlying epidermis that is one cell thick. The epidermis also contains specialized cells that form sense organs or glands that secrete various compounds on the exoskeletal surface, including a thin layer of water-repellant wax.

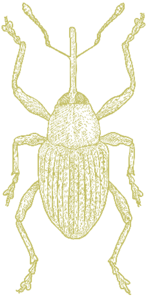
After molting, the soft, pale cuticle soon hardens and darkens as a result of a chemical process called sclerotization. The segments that make up the head, thorax, and abdomen are either distinct or obscure and are composed of plate-like sclerites that are sometimes delineated by cuticular membranes or narrow, groove-like sutures.

The outer surface is smooth and shiny, or variously sculpted with fine cracks, raised pebble-like tubercles, and pit-like *punctures*, the latter of which sometimes contain a single hair- or scale-like *seta*.

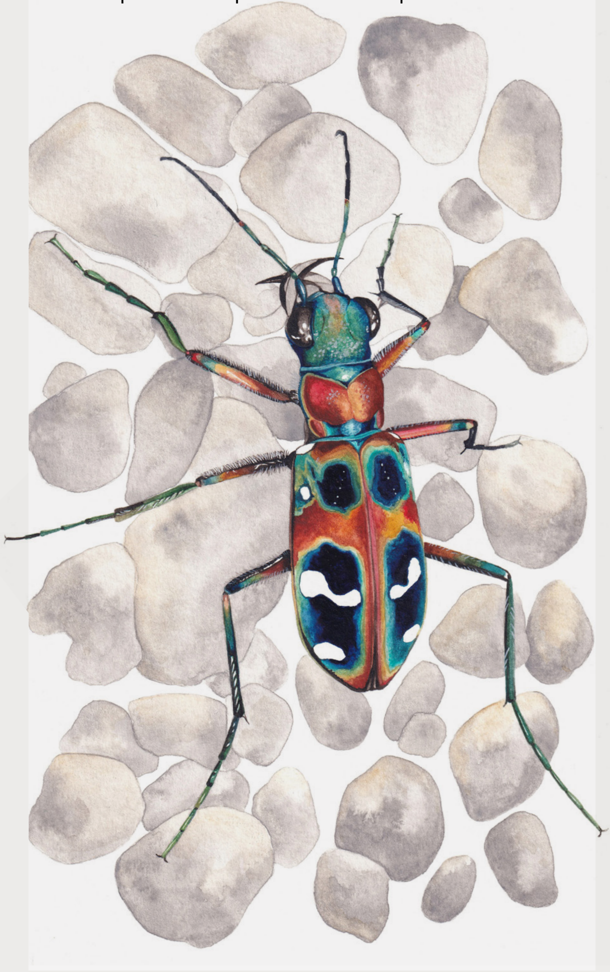
↓ European *Paederus riparius* and other rove beetles (Staphylinidae) have short elytra that typically expose several abdominal segments.



↓ Like many curculionids, the European willow gall weevil, *Archarius salicivorus* (Curculionidae), has a long and slender rostrum.



→ The color patterns of tiger beetles (Cicindelidae) assist with thermoregulation and also provide camouflage. Although conspicuous on the ground, the metallic red, blue, and green color patterns of *Sophiodela japonica* from Japan may help them to evade predatory birds and robber flies while they are in flight.



COLORS AND PATTERNS

Beetle colors are critical for mate recognition, camouflage, thermal regulation, and defense. Colors and patterns help *diurnal* species to recognize one another as potential mates. Beetles cryptically clad in somber brown and black *scales* are difficult to see against tree bark. Black desert darkling beetles quickly absorb the sun's energy in order to move about on relatively warm winter days, while their white counterparts reflect sunlight to beat the desert heat. Beetles boldly marked in contrasting patterns of black with reds or yellows warn potential predators of their chemical defenses, or mimic noxious insects so defended.

↓ The brilliantly colored golden tortoise beetle, *Charidotella sexpunctata* (Chrysomelidae), is widely distributed in the eastern United States.

INTRASPECIFIC VARIATION

The multicolored Asian lady beetle, *Harmonia axyridis*, exhibits extraordinary intraspecific variation, as evidenced by its more than 200 different elytral color patterns. These color patterns are regulated by a single pannier gene that simultaneously promotes black pigmentation while suppressing red pigmentation. Inhibition of the pannier gene during the pupal stage results in the loss of black color patterns and normal red pattern formation. The differences in color pattern are associated with the DNA sequence of the first intron of the pannier gene, a discovery that sheds light on how intragenic chromosomal inversions can drive morphological evolution in organisms.

TINTS

Colors are either pigment-based or created by physical properties of the cuticle. Pigment-based compounds absorb or reflect various wavelengths of light. Melanin synthesized by beetles produces shades of black and brown that are more or less permanent, while colors created by food-based carotenoids (yellow, orange, red) and other pigments soon fade after death. The golden tortoise beetle, *Charidotella sexpunctata*, temporarily changes its colors from shiny red or golden orange to brilliant gold by moving pigment inside the cuticle. Its transient metallic colors are produced by light reflecting off pockets of liquid pigment within the cuticle.

SHIMMERING

Iridescent and metallic properties are produced by the exoskeleton's physical properties that scatter light. Iridescence is often created by ordered surface structures such as scales or layered nanostructures within the cuticle that reflect intense colors and shift depending on the angle of view. Beetles sporting these dazzling colors are often difficult to see in their natural environments.

HEAD

Borne on flexible, membranous necks and partially or almost completely sunken within the prothorax, beetle heads are equipped with two vital structures that help them make sense of their surroundings: compound eyes and antennae.

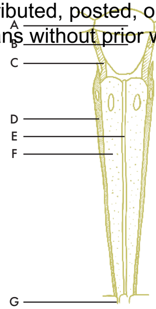
EYES

The sometimes kidney-shaped compound eyes are covered with multiple facetlike lenses. Each hexagonal lens sits atop a tube-shaped ommatidium that contains a cone, followed by a cluster of photoreceptor cells, or rhabdom, surrounded by pigment cells that detect light. Light funneled through the lens and cone onto the rhabdom stimulates the surrounding pigment cells and is ultimately transmitted to the brain as an electrical impulse. Each lens "sees" a portion of an entire scene. The greater number of lenses that receive light in each eye, the greater the beetle's visual acuity. Abundant light combined with light-adapted ommatidia provide diurnal beetles with good visual resolution. Nocturnal species have dark-adapted eyes that allow them to see in only low levels of available light, but this configuration sacrifices overall visual acuity. Beetles that inhabit dark caves and other subterranean habitats often have few ommatidia or lack them altogether and are completely blind.

Whirligig beetles live on the surfaces of ponds and stream pools and have compound eyes that are completely divided by a strip of cuticle called the canthus. The upper portions of their eyes are adapted

MALES WITH HORNS

The heads of some males, scarab beetles in particular, are adorned with spectacular horns that function as pinchers, spikes, crowbars, or scoops. These imposing structures are used to defend food sources and nesting sites attractive to females from rival males.



← The basic visual structure of beetles and other insects is called the ommatidium and this consists of the following: (A) cornea, (B) crystalline cone, (C–D) pigment cells, (E) rhabdom, (F) photoreceptor cells, (G) optic nerve.

for seeing in the air, while the lower portions are adapted for seeing in water. In addition to compound eyes, some adults possess a simple eye, or ocellus, on the front of the head between the compound eyes.

ANTENNAE

The antennae are a beetle's primary organs of smell and touch. Diverse in form, they are located between the compound eyes and mandibles and usually consist of three basic parts: scape, pedicel, and flagellum. Each antenna usually has 11 articles called antennomeres. Some species possess 10 or fewer antennomeres, while a few species may have 12 antennomeres or more. Males often have longer or more elaborately modified antennae than the females, a form of sexual dimorphism. Greater antennal development in males is not only associated with increased sensory capabilities for locating females via their scent, or sex pheromone, but is also sometimes associated with guarding females while laying their eggs.

MOUTHPARTS

The chewing mouthparts of beetles usually consist of a labrum, a pair of mandibles and maxillae, and a labium. Mandibles are variously modified to cut plant and animal tissues, grind spores and pollen, or strain nutrients from various fluids. The mandibles of some species, especially in males, are greatly enlarged. Mandibles such as these are not organs of ingestion, but are used as weapons in pitched battles with rival males, and thus play a vital role in reproduction. Associated with the maxillae and labium are pairs of flexible, fingerlike palps that help beetles locate and handle food. The chewing mouthparts of weevils are often borne on a long, snout-like rostrum. Female weevils use this structure to chew a hole deep inside plant tissues, into which they can lay their eggs out of harm's way.

THORAX

The three-segmented thorax houses powerful legs and wing muscles. The first thoracic segment, or prothorax, bears the front legs and may be armed dorsally with horns and tubercles, or scooped out like a bulldozer blade. The modified forewings, or elytra, and middle legs attach to the mesothorax, while the folded membranous hindwings and hind legs are joined to the metathorax. The meso- and metathoracic segments are obscured by the elytra.

WINGS

The leathery or shell-like elytra are modified mesothoracic wings that partially or completely cover the abdomen at rest and function as stabilizers in flight. Their surfaces are variously sculpted with punctures, ridges, or grooves. Beneath them are the metathoracic hind wings. When functional, the hind wings are nearly always longer than the elytra. Hinge-like veins enable beetles to fold their hind wings beneath the elytra when not in use.

FEATHERWING BEETLES

Featherwing beetles (Ptilidae) are the smallest known beetles and are the subjects of studies on miniaturization. Their fringed and slender or paddlelike wings resemble those of similarly small wasps called fairyflies. Unlike fairyflies, ptiliids can fold and unfold their wings. They fold their wings by using special microsculptured patches on their abdominal tergites. Ptilids unfold their wings with the aid of an elastic protein called resilin, spreading curved cross-sections like retractable metal measuring tape, or by increasing blood pressure within major wing veins. Studying the patterns and mechanisms of the folding and unfolding of ptilid wings may provide clues for engineers designing miniature flying robots.

↑ Male Asian Atlas beetles, *Chalcosoma atlas* (Scarabaeidae), have cephalic and prothoracic horns, unlike the females.

LEGS

Each leg is anchored to a socket-like cavity beneath the thorax by its coxa, the first of six leg segments. The coxa articulates with a small trochanter that is usually fixed to the large and muscular femur. Following is a relatively long and slender tibia that is often modified on the front legs with rakelike extensions for digging. The tarsus, comprising up to five tarsomeres, may have adhesive or brushy pads underneath to help gain purchase on slippery surfaces, including those of food plants and the elytra of mates. Each leg terminates in the pretarsus, a segment that usually bears a pair of claws, although some dung beetles lack tarsi altogether on their front legs. In sexually dimorphic species, the legs of males and females sometimes differ in structure and/or length.

ABDOMEN

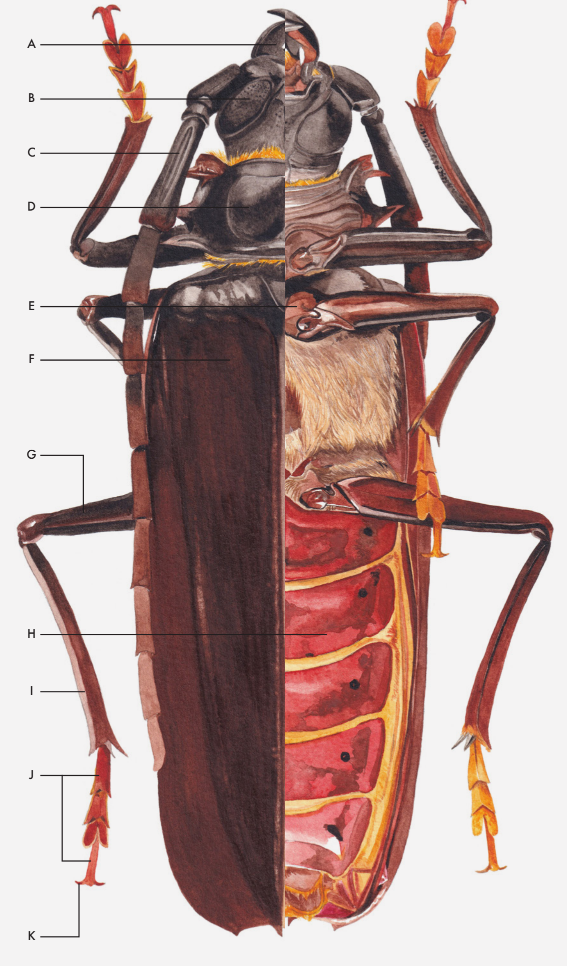
The typical beetle abdomen consists of ten segments, the last two of which are variously modified as reproductive organs and are not visible externally. A long, egg-laying tube, or *ovipositor*, is typical in females that deposit their eggs deep in soil or plant tissues. Short and stout ovipositors are usually found in species that glue their eggs to various surfaces. Male reproductive organs are often distinctive sclerotized structures that are of considerable value in species identification.

The remaining eight ring-like abdominal segments consist of a *dorsal* and *ventral* sclerite. The dorsal sclerites are called tergites. Tergites tend to be thin and flexible but are thicker and more rigid in beetles with short elytra. The posterior-most tergite is the *pygidium*. The ventral sclerites are called sternites. When visible externally, sternites are called ventrites. The breathing pores, or *spiracles*, are located along the sides of the abdomen in or near the membrane separating the tergites and ventrites.

↓ The flat, round, and brownish larvae of *Psephenus herricki* (Psephenidae) and other water pennies resemble small, segmented coins.

↓ The horn of the male European rhinoceros beetle, *Oryctes nasicornis* (Scarabaeidae), is first visible in the pupal stage.

→ A dorsal and ventral view of the North American *Derobrachus forreri* (Cerambycidae). (A) mandible, (B) compound eye, (C) antenna, (D) pronotum, (E) middle coxa, (F) elytron, (G) hind femur, (H) ventrite, (I) hind tibia, (J) hind tarsus, (K) hind claw.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EGGS, LARVAE, AND PUPAE

Beetle eggs are usually smooth and soft, but some are distinctly sculptured and hard-shelled. The egg's shell, or chorion, is permeable to oxygen, although the eggs of some species have specialized breathing holes known as aeropyles. All eggs have micropyles, minute openings in the chorion located mostly at the end that allow sperm inside the egg for fertilization. The number of micropyles varies among and within species.

SEXLESS EATING MACHINES

Larvae have distinctive heads with chewing mouthparts for crushing, grinding, or tearing foodstuffs. Some predaceous larvae have sickle-like mouthparts to pierce and inject their prey with enzymes that liquefy the victim's tissues and organs, then use these same mouthparts like straws to suck up the fluids. Instead of compound eyes, beetle larvae usually possess one or more pairs of simple eyes called stemmata on each side of the head, although some larvae lack eyes and are blind. The antennae of most beetle larvae consist of three simple segments. Water tigers (*Hydrophilus*) use their sharp, pointed antennae in concert with their mandibles to cut up insect prey.

BEETLE PUPAE

Beetle pupae are typically of the adecticous exarate type. They lack functional mandibles (adecticous) and have legs that are not tightly appressed (exarate) to the body. Pupae often have functional abdominal muscles that allow for some movement. In some species, opposing abdominal segments have specialized teeth, or sharp edges, known as gin-traps, which defensively clamp down on the appendages of small arthropod predators such as ants and mites.

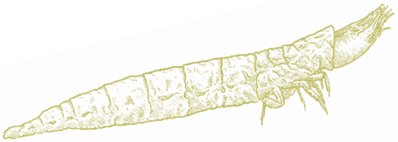
The larval thorax consists of three very similar segments, the first of which may have a thickened dorsal plate. Legs, if present, have six or fewer segments, but are often greatly reduced or absent in species that feed inside plant tissues or parasitize other insects.

Most larvae have nine- or ten-segmented abdomens. Soft and pliable abdomens allow rapid expansion as the larva feeds and reduces the number of times they have to shed their exoskeleton in order to increase their capacity. Some legless terrestrial larvae possess fleshy, wartlike protuberances on their abdomens that help provide traction as they move about in soil or wood. Aquatic larvae may have simple or branched abdominal gills laterally or ventrally. The abdomens of many beetle larvae terminate in a pair of short, fixed, or segmented extensions called urogomphi.

LARVAL FORMS

Larval beetles are grouped together based on their body form. The eruciform larvae of lady beetles and some leaf beetles are slow and caterpillar-like in appearance. The plump, C-shaped scarabaeiform grubs of scarab beetles and their relatives have distinct heads and well-developed legs suited for burrowing in soil and rotten wood. In spite of having well-developed legs, the larvae of flower chafers (Scarabaeidae) generally crawl on the backs. Larval click beetles, as well as those of many darkling beetles, are elateriform and have long, slender bodies with short legs and tough exoskeletons. Stout, legless weevil grubs are considered vermiform because of their maggot-like appearance. In contrast, campodeiform larvae of ground, whirligig, predaceous diving, water scavenger, and rove beetles are long, flat, and leggy. The cheloniform water penny larvae are broadly oval, distinctly segmented, and turtlelike, while the pillbug-like larvae of some carrion beetles are referred to as onisciform. Fusiform beetle larvae are broad across the middle and tapered at each end.

→ Aquatic *Hydrophilus* (Hydrophilidae) larvae are voracious predators of insects and other invertebrates, as well as tadpoles and small fish.



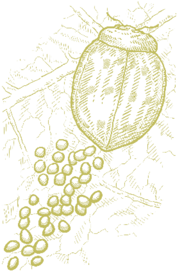
HOLOMETABOLY

Beetles, butterflies and moths, ants, bees, wasps, flies, fleas, and their relatives all develop by holometaboly. Commonly known as complete metamorphosis, holometabolous development is characterized by four distinct developmental stages: egg, larva, pupa, and adult. Each of these stages is adapted to a particular suite of environmental factors that enhances the overall chances of a beetle surviving and thriving, especially in temperate climates. Most adults and their larvae lead largely separate lives, thus limiting interspecific competition for food and space.

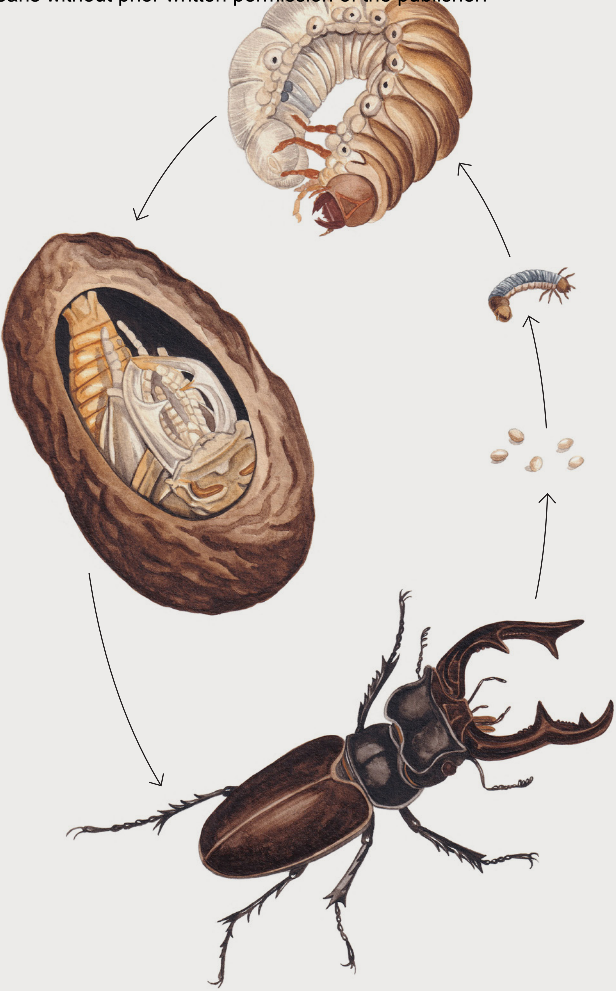
Although considered one of the key evolutionary innovations that led to the incredible diversity of beetles and other insects, there is currently little consensus as to how or why holometaboly evolved. While the idea that holometaboly allows a single species to occupy multiple niches and utilize different resources is certainly appealing, it reveals little about the selective mechanisms that led to its evolution, including the unique development of the relatively inactive and purely transformational pupa.

↓ The pupae of most beetles are adecticous (lacking functional mandibles) and exarate, meaning that the appendages are free.

↓ Most beetles reproduce sexually and must mate before they can produce and lay viable eggs.



→ European stag beetles, *Lucanus cervus* (Lucanidae), lay eggs in decaying wood. The larvae pass through three instars before pupating within a case made of soil and coated insided with gut secretions. Adults live nearly a year or longer in captivity.



GROWTH

Upon hatching, most beetle larvae begin feeding almost immediately and grow rapidly. As with all insects, growth and development is driven by complex hormonal interactions regulated by an endocrine system composed of neurosecretory cells within the central nervous system and specialized endocrine glands. High levels of juvenile hormone released into the hemolymph by the corpora allata inhibit the development of adult structures, while increased amounts of ecdysteroids produced by the prothoracic glands induce molting and stimulate growth.

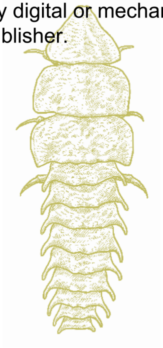
MOLTING

Working in concert, fluctuating levels of juvenile hormones and ecdysteroids trigger the reorganization of tissues and the shedding of the exoskeleton, a process known as molting. The outgrown exoskeleton is replaced with a new and roomier version secreted by an underlying layer of epidermal cells. The stage between each larval molt is referred to as an instar. Most species pass through a definite

HYPERMETAMORPHOSIS

Typically, each successive instar resembles a larger form of its predecessor. However, parasitic species undergo a special type of holometaboly called *hypermetamorphosis*. For example, the larvae of cicada parasite beetles, blister beetles, and wedge-shaped beetles are all characterized by having two or more distinct larval forms. The active and leggy first instar, or *triungulin*, is adapted for seeking out the appropriate host. Once a host has been located, the triungulin molts into a more sedentary larval form with short, thick legs. It goes on to metamorphose into a fat, legless grub that eventually develops into a more active short-legged grub that spends most of its time preparing a pupal chamber.

number of instars, usually ranging from three to five. Hister beetle larvae have as few as two instars, while those of some skin beetles may have as many as seven. In western North America, rain beetles (*Pleocoma*) may undergo more than a dozen instars.



↑ Larviform females of *Dulticola* (Lycidae) are commonly known as trilobite beetles because of their resemblance to the long extinct marine arthropods.

PUPATION

Concurrent with a reduction of juvenile hormone at the onset of pupation, increased levels of ecdysteroids stimulate the beginning of structural differentiation. Larval tissues and organs once dedicated to eating and growing are restructured for locating mates and reproduction. Lacking functional mouthparts and appendages, beetle pupae are non-feeding and mostly sessile. However, some species do have the ability to flex their abdomens just a bit, sometimes as a limited means of defense. Consensus on the evolutionary origins of the pupal stage has yet to be achieved. Some researchers suggest that the pupa is derived from a final larval stage, while others believe it is a modified preadult.

Glowworms and some fireflies undergo a modified pupal stage. In these species, adult females closely resemble the last larval instar and are referred to as *larviform*. Larviform females typically have reduced elytra, if they have them at all. These wingless adults are best distinguished from larvae externally by the presence of compound eyes and internally by their reproductive organs.

ECLOSION

The requisite combination of time, temperature, and precipitation triggers adult emergence from the pupa (known as eclosion). At first soft and pale, the exoskeletons of these *teneral* adults soon begin to harden and darken as they undergo sclerotization, a chemical process akin to the tanning of leather. Fully developed adult beetles will never molt again and are soon ready to mate and reproduce.

DIGESTION

The digestive tracts of beetles are variously adapted for ingesting and processing an astonishing variety of foods. Species that consume nutrient-rich animal tissues don't need the long and convoluted gut required by herbivorous beetles to extract sufficient nutrition solely from plant materials. Like those of most insects, the digestive tract of beetles is divided into three functional regions: foregut, midgut, and hindgut.

FOREGUT: INTAKE

The foregut is the site of ingestion, mechanical breakdown, and temporary storage of food. Food cut and ground or strained by the mandibles is drawn into the esophagus by powerful cibarial and pharyngeal muscles, sometimes with the aid of saliva. The esophagus usually extends to an expanded storage chamber, the crop. Behind the crop is the proventriculus, a valve that controls food moving into the midgut and, in predatory ground beetles and plant-feeding weevils, serves as a food-grinding organ.

MIDGUT: ABSORPTION

The midgut produces and secretes digestive enzymes, absorbs nutrients, and transports remaining food and waste to the hindgut. Inside the abdominal cavity are worm-like Malpighian tubules that are involved in excretion and osmoregulation. These blind-ended excretory organs originate near the junction of the midgut and hindgut and extract water and waste from the hemolymph. Some beetles rely on symbiotic microorganisms living in the midgut to assist them with digestion.

HINDGUT: WASTE MANAGEMENT

The remaining contents of the midgut pass through the pyloric valve before entering the hindgut. Here water, salts, and other minerals are absorbed prior to elimination of feces through the rectum and out the anus.

THE ROLE OF SYMBIOTIC BACTERIA

In beetles and other holometabolous insects, symbiotic bacteria are either fully integrated with their morphology or physiology (obligate symbionts) or not (facultative symbionts) and are not utilized just as digestive aids. Wood-feeding longhorn beetle and bark beetle larvae depend on nitrogen-fixing symbiotic bacteria to make up for the low nutritional quality of their carbohydrate-rich diets. Other species depend on their bacterial symbionts to help manage and suppress potentially dangerous toxins associated with their foods. Coffee berry borers (*Hypothenemus hamepi*) rely on facultative gut bacteria to break down harmful caffeine, while those of cowpea beetles (*Callosobruchus maculatus*) help them to detoxify pesticides.

↓ This predatory European golden ground beetle, *Carabus auratus* (Carabidae), is in the process of attacking an earthworm.

SENSES

Beetles sense the world around them with the aid of highly sensitive receptors borne on various surface structures, especially on their heads. The complex nervous system of beetles integrates external stimuli with internal physiological information to generate a diverse array of behaviors.

BASIC NEUROLOGY

The nervous system of beetles consists of the visceral nervous system, peripheral nervous system, and central nervous system (CNS). The visceral nervous system innervates the gut, endocrine and reproductive organs, and the tracheal system. The peripheral nervous system connects the muscles with the CNS and visceral nervous system, as well as the cuticular sensory structures that receive visual, chemical, tactile, and thermal stimuli from the beetle's immediate environment.

The CNS is the primary division of the nervous system and consists of a series of bundled nerves, or ganglia, connected by ventral paired nerve chords called connectives. Inside the head are the brain and suboesophageal ganglion. The brain innervates the primary sense organs (eyes, antennae) and receives signals from elsewhere in the body, while the suboesophageal ganglion supplies nerves to the mouthparts.

MOSTLY DEAF

The ability to hear is rare among Coleoptera, but some tiger beetles and dynastine scarabs have earlike structures capable of hearing ultrasounds, including frequencies used by echolocating bats. Tiger beetles (Cicindelidae) have a pair of domed tympanic membranes atop their first abdominal segment, while rice beetle (Scarabaeidae) "ears" are located on the neck membrane just behind their heads.

EYES

Most beetles have a pair of well-developed compound eyes to help them navigate their environments and avoid danger. Dung-rolling scarab beetles use the sun, moon, and the Milky Way as visual cues to help keep them on a straight path. The bulbous eyes of diurnal tiger beetles affords them binocular vision that helps them gauge the distance of prey. The arrangement of simple eyes, or stemmata, not only affords both far and near vision to larval sunburst diving beetles (*Thermonectus marmoratus*), but it may also give them depth perception.

↑ The fan-like surfaces of male *Polyphylla* antennae possess many structures for sensing odor released by females.

ANTENNAE

Primarily organs of smell and touch, the antennae of beetles are paired appendages possessing special receptors for finding food and detecting pheromones. Males often have longer or more elaborate antennal structures resembling fans or feathers, modifications that increase the surface area available for sensory structures. The antennae of some ground beetles and rove beetles sometimes have special comb-like structures used for grooming their legs and feet. During courtship, male oil beetles use their antennae to grasp those of their partner. Whirligig beetles use their antennae to detect ripples generated by insect prey trapped on the water surface, but claims of their ability to navigate by echolocation remain unsubstantiated.

MOUTHPARTS

The fingerlike palps associated with a beetle's maxillae and labium serve primarily as touch and taste receptors. The tips of these paired structures are usually membranous in both adults and larvae and bear short sensilla thought to be associated with taste. In some beetles, these structures are greatly modified, suggesting that they might have additional sensory functions. Snail-eating *Cychrus* ground beetles on the hunt bring their elongated palps tipped with enlarged, spoon-shaped flanges in contact with the soil, presumably to detect their prey's slime trails.

LOCOMOTION

The mobility and strength of beetles is driven by antagonistic pairs of internal muscles fused with and working against rigid exoskeletal segments. Adults have stiff cuticular exoskeletons, while their soft-bodied larvae rely on a hydrostatic skeleton made turgid by thousands of criss-crossed body wall muscles pressing against a fixed volume of hemolymph within the body cavity.

HERCULEAN FEATS

Beetles can perform extraordinary feats of strength for their size. For example, the male horned dung beetle *Onthophagus taurus*, which measures only ²/₅ in (10 mm) in length, can pull up to 1,141 times its own body weight. This is equivalent to an average-sized male lifting six double-decker buses packed with commuters. Male dung beetles use their power to push rival males out of underground tunnels occupied by a female.

AQUATIC BEETLES

Locomotion in aquatic beetles is dominated by the forces of drag, buoyancy, viscosity, and surface tension. While most species move in aquatic environments by swimming through the water or crawling on submerged plants and other substrates, some rely on the cohesive forces of water molecules at the water–air interface to get about. Whirligig beetles are the best known for their utilization of the water's surface. Recently, small hydrophiloid beetles have been observed crawling and resting on the underside of the water's surface. An understanding of the mechanisms enabling this activity could assist in the development of bio-inspired aquatic adhesives and robotics.

AGILITY

The legs and wings are powered by muscles that are concentrated within the thorax. By relaxing and contracting muscle pairs associated with variously modified legs, beetles can walk, run, climb, burrow, or swim as they search for food and mates. While these methods of getting about work well for covering short distances, the power of flight enhances their abilities to disperse over larger areas.

AIRBORNE

Before taking flight, beetles lift their elytra to free the membranous flight wings folded underneath. The flight wings quickly expand as the blood pressure within their network of veins increases. Once airborne the elytra act as stabilizers, while the flight wings function as airfoils that simultaneously provide beetles with maneuverability and the prerequisite aerodynamic qualities to keep them aloft.

← A glorious jewel scarab, *Chrysina gloriosa* (Scarabaeidae), from the American Southwest and adjacent Mexico, takes to the air.

GAS EXCHANGE

The exchange of the respiratory gases oxygen and carbon dioxide is facilitated by an internal system of branching, air-filled tubes called trachea. Extending throughout the body, the tracheal system directly supplies internal organs and tissues with oxygen and removes carbon dioxide. Oxygen enters the tracheal system through valved spiracles that are openings located along the sides of the body. Carbon dioxide generated by cellular metabolic processes exits the body via the trachea and spiracles.

In aquatic beetles, gas exchange is accomplished by keeping the spiracles in contact with the air. Hydrophilids (water scavenger beetles) and dytiscids (predaecous diving beetles) regularly surface to replenish bubbles trapped beneath their bodies or elytra, respectively. Sedentary grazers like riffle beetles (Elmidae) and long-toed water beetles (Dryopidae) that inhabit shallow, well-oxygenated waters rely on *plastron respiration*. Clothed in dense, velvety, and water-repellant pubescence called a *hydrofuge*, their bodies are permanently enveloped by a thin layer of air called the plastron. Dissolved oxygen from the surrounding water steadily diffuses into the plastron as carbon dioxide diffuses out.

← A bubble temporarily exposed at the elytral apices of a predaceous diving beetle (Dytiscidae) draws in dissolved oxygen from the water.

↙ The abdominal spiracles of the larvae of the coconut rhinoceros beetle, *Oryctes rhinoceros* (Scarabaeidae), are clearly visible along the sides of their abdomens.

→ Using micro-computed tomography, the tracheal system of the adult mealworm, *Tenebrio molitor* (Tenebrionidae), can be visualized and grouped into functional areas or modules. The cephalon-prothoracic module is represented in orange, while the thoracic and abdominal modules are shown in red and olive green, respectively.

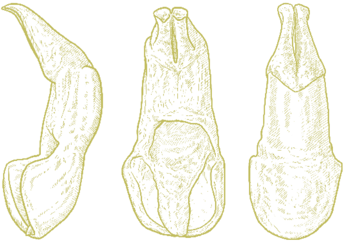
REPRODUCTIVE SYSTEM

Most beetles must reproduce sexually. The basic structure and function of the reproductive systems of beetles resemble those of vertebrates. The male's testes produce sperm inside packets called spermatophores, while the female's ovaries produce eggs. During copulation, males deposit their spermatophores directly inside the female by inserting their penis-like reproductive organs into her genital tract. These ornately shaped organs are thought to correspond specifically with the vagina of females of the same species. This unique fit, combined with species-specific pheromones and behaviors, works like a lock and key and is thought to prevent beetles from mating with the wrong species.

In addition to sperm, the spermatophore also contains other vital compounds and nutrients. Females temporarily store sperm in a special gland called the *spermatheca*. Sperm released from the spermatheca fertilize the mature eggs as they pass down from the ovaries and out the body through the egg-laying tube, or ovipositor.

↓ The structure of the male's reproductive organs, especially the parameres, are often considered diagnostic and are useful for distinguishing closely related beetle species. Shown here are three different views of the parameres of *Pentodon idiota* (Scarabaeidae).

→ Male and female Hercules beetles, *Dynastes hercules* (Scarabaeidae), preparing to mate. One of the most recognizable beetles in the world, this species is found from Mexico southward to northern South America, and also on several Caribbean islands.



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