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ANT NESTS AND COLONIES

Modern social ants arose from wasp-like ancestors about 100 million years ago during the Cretaceous period, when dinosaurs walked the earth. They rose to ecological dominance, and still play a major role as predators and scavengers in most land ecosystems. An ant colony is a superorganism controlled by a reproductive queen which produces thousands of infertile workers that forage and hunt for the colony, defend it, and rear more workers. There is a view that an ant colony is a single composite organism, because the queen is the only individual capable of reproducing, and the workers produced and controlled by the queen are like an extension of her body. Based on the combined weight of their workers or the volume of food they consume, ant colonies are some of the largest predators on earth. Troops of workers hunt other invertebrates and sometimes even vertebrates: African driver ants can overcome big animals such as dogs and goats that are caged or tethered, and their marching columns are used by African people to clear their homes or crop fields of pests. These driver ants, and their South American equivalents, the army ants, have no fixed nest, but carry the queen and larvae with them in ever-marching columns. Most other ants have a vigorously defended nest, to which they

OPPOSITE | *Paussus* (Carabidae: Paussinae)
This highly modified ground beetle, almost unrecognizable compared to its surface-living relatives, has many chemical and physical adaptations in order to survive in ant nests.

ABOVE | *Limulodes* (Ptiliidae)
Featherwinged beetles, these from the USA, act as cleaners in ant nests, eating fungi and spores.

bring their prey. Not all are predators: the South American leaf-cutter ants form huge colonies with subterranean fungus gardens, where they bring slices of leaves to rot and grow the fungi that they consume. They can defoliate whole trees.

Ant colonies represent a great opportunity: safe, climate controlled, full of stored food and ant larvae, but any beetle taking advantage of them needs to get past the ants. Beetles of several families have developed a suite of adaptations—chemical and physical—to persuade ants to ignore them, mistake them for food, or even welcome them as nest mates, as well as other adaptations such as shortening of limbs and antennae, and fusing of abdomen segments, to protect them from damage during rough handling by the ants. Animals that have adapted to live with ants are called myrmecophiles (ant lovers) and can be recognized by characteristics including clumps of setae called trichomes that provide food or chemicals to the ants, fused segments, short antennae, sometimes loss of pigmentation or eyes, and, in some extreme cases, structures that allow the ants to pick them up and carry them without damage. We can even see such characters in fossils, and can assume they must be myrmecophiles without knowing their actual biology.

Hundreds of species of beetles of many families have become myrmecophiles, the most common of these being Histeridae, Carabidae: Paussinae, some Scarabaeoidea, and particularly Staphylinidae of the subfamilies Aleocharinae and Pselaphinae. The Pselaphinae tribe Clavigerini are almost all compulsory ant associates. Some myrmecophiles are scavengers or cleaners, while others consume the ants' resources, and a few eat the ants themselves as well as their larvae.

TERMITE NESTS AND COLONIES

Tall edifices, seemingly built of stone, are characteristic features of the dry grasslands of the African savanna, the Brazilian Cerrado, and the Australian outback. These are the colonies of termites, each one built and maintained over decades or centuries, and home to thousands or even millions of termite workers. The structures cover extensive subterranean networks of chambers and tunnels. The mounds are built from soil cemented with the saliva and dung of the termites, and are surprisingly strong and weatherproof, although they need regular maintenance by the workers.

Termites are social insects, living in colonies controlled by a reproductive pair, called the "queen" and the "king." The white, sausage-like queens grow huge and are some of the longest lived of insects, typically exceeding ten years and reported at up to fifty. When the queen dies, the supply of a hormone she produces inhibiting reproductive development in the colony stops, and another queen arises and produces the same hormone to inhibit the rest of the colony. Not all termite genera inhabit giant fortified nests; many live in the soil or in arboreal nests made from a lightweight substance called "carton."

Termite colonies have been called the world's oldest societies, with the earliest fossil termites known from the beginning of the Cretaceous period. Evidence suggests that the group is even older; one piece of evidence for the early appearance of termites is a Late Jurassic fossil mammal *Fruitafossor windscheffeli*, described in 2005 in North America, which has been interpreted as a specialist termite predator from its tubular teeth and digging limbs, resembling modern termite eaters.

Termites were for a long time placed in their own order of insects, Isoptera, but recent research combining DNA, fossil, and morphological evidence has shown that they are eusocial relatives of cockroaches (Blattodea). Despite similarities in nest and social structure, they are not closely related to ants. However, like ants they are divided into castes, with the majority of the colony being nonreproductive workers, which maintain the structure of the colony and collect food, or soldiers, which defend it, using large jaws or chemical defenses. The similarity has led to termites being called "white ants" in many parts of the world.

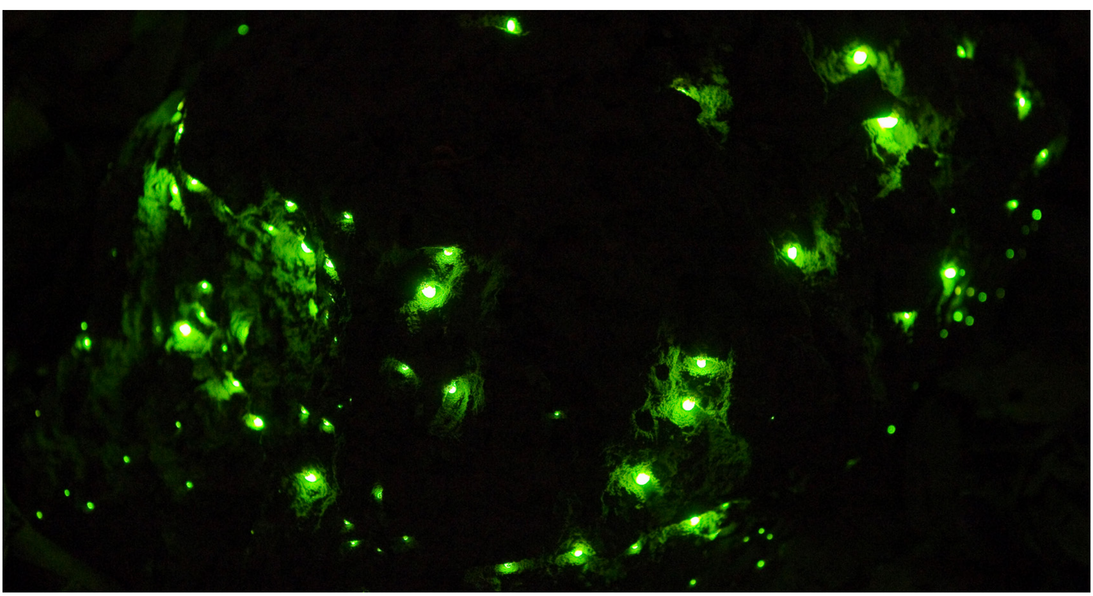
Also like ants, the colonies of termites provide abundant opportunities for nest invaders (called inquilines) to occupy their living space, taking advantage of the constant temperature and humidity, protection from predators, or the reliable supply of food (whether the food of the termites or the termites themselves). Many beetles

LEFT | *Termitotrox cupido* (Scarabaeidae) This blind, flightless scarab beetle was discovered in 2012 in termite nests in Cambodia and named after a Roman god of love.

RIGHT | *Penichrolucanus copricephalus* (Lucanidae) This very small and uncommon hornless stag beetle from Southeast Asia is associated with termite nests.

have adapted to circumvent the termites' defenses. Some have only a superficial relationship, being scavengers in and around the nest, while others have complex physical and chemical systems to deceive their hosts, and are fully integrated into the colony. An extreme example are the larvae of the Australian *Megaxenus* (Aderidae), which imitate the queen termite so that the workers bring them food and clean them. Click beetle larvae of the genus *Pyrearinus* (Elateridae) live in burrows on termite mounds in Brazilian grasslands, using bioluminescence to attract prey to their powerful jaws.

BELOW | *Pyrearinus termitilluminans* (Elateridae) Bioluminescent click beetle larvae light up a termite mound in Brazil's Pantanal. They are predators that use light to attract flying insects, including termites.



CAVES

A whole field of biology called biospeleology is dedicated to the exploration, discovery, and study of organisms that inhabit caves. Caves provide a very stable environment: in their deepest parts almost totally isolated from surface influences; but the cold, damp, and perpetual darkness, and limited supply of nutrients, make them hostile for most life. There is a spectrum of cave insects, from surface fauna that has temporarily moved into the shallower and more accessible parts of caves, to so-called true troglophiles, species that have adapted over long periods of time to cave conditions. The latter, among beetles, are either predators (such as the families Staphylinidae and Carabidae) or scavengers (Leiodidae), since the ecosystems lack living plants (which need sunlight for photosynthesis). Instead of plants, cave ecosystems are based on detritus and organic matter either carried in by water or deposited by larger inhabitants, such as the dung and carcasses of bats or cave-dwelling birds. True troglophiles have a distinctive set of adaptations: because of the darkness, they often lack eyes and pigmentation. To compensate for the lack of light and the uselessness of eyesight, many have developed long, slender limbs and antennae to enable them to feel for food.

Experts studying cave fauna often say that those large caves that humans can enter and explore are, from an insect's point of view, just the most accessible of many holes in a complex network of interconnected crevices, gaps, and fissures in the porous rocks. The troglophile

LEFT | *Leptodirus hochenwartii* (Leiodidae) A true troglophile, this eyeless beetle from the Dinarides in the Balkans shows very long limbs and antennae.

OPPOSITE | *Duvalius gebhardti* (Carabidae) An eyeless ground beetle from caves in Hungary. Many troglophiles lose eyes and most of their pigmentation.

cave fauna, then, are just a part of a sometimes inaccessible interstitial fauna that exists over a much wider subterranean area. If this is the case, then the fauna of a particular cave may not be as isolated as it initially seems, since it may be connected with neighboring caves by cracks and tiny corridors that allow insect populations to pass from cave to cave without having to go outside.

In northern parts of the northern hemisphere, such as Britain, caves are common in chalk and limestone districts and are well studied, but no associated troglophile cave fauna are known. This is thought to be because they were scoured and sterilized by the cold and ice of recent glaciers, and the cave insects have not had any opportunity to recolonize. It is interesting to speculate what might have inhabited these caves before the glaciations of the last Ice Age. Farther south in Europe, for example in Hungary, the Balkans, Italy, or Spain, and at equivalent latitudes in Asia and North America, a rich troglophile fauna of detritivores and small predators adapted to the environment are found, and many unusual new species are being discovered.

The low level of available nutrients means that true cave fauna usually has low populations which are widely spread within the cave and surrounding soil. Biospeleologists use traps set over many months—baited with strong-smelling foods and drinks such as cheese, beer, and wine—in order to lure individuals of this fauna, but even after a year or more a trap may yield only a small number of specimens.

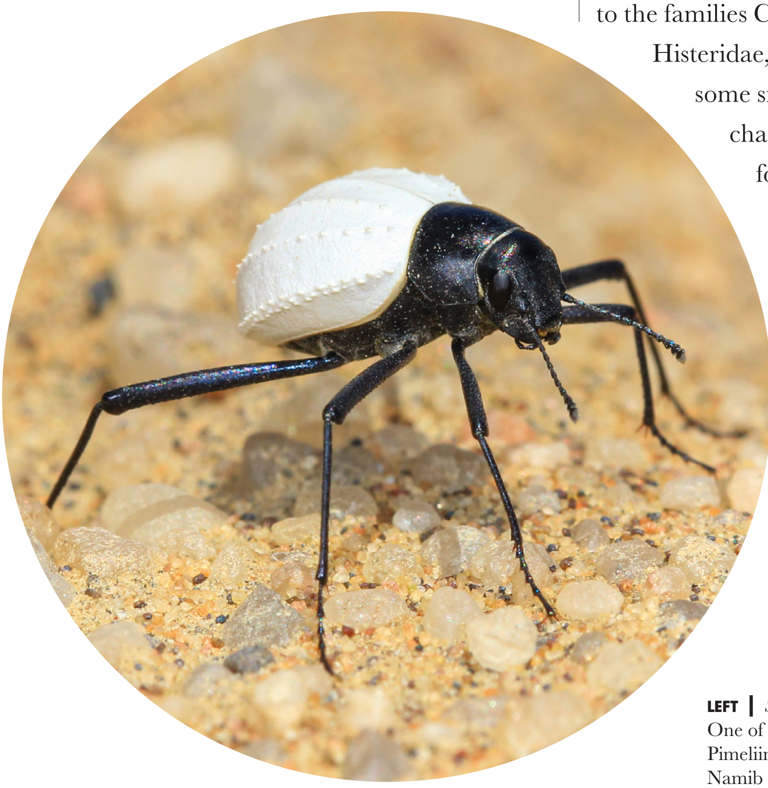
SAND

Loose sand is another specialized habitat that many organisms have failed to colonize, but which supports a varied range of beetle species. Two major environments consist largely of sand: beaches, which may merge into sand dunes, and deserts. While these two habitats have certain features in common, there are many differences, and they are used by different groups of beetles.

Sand, whether on deserts or beaches, contains little or no organic matter, so plants do not grow well on it. As a result, there is little shade, and inhabitants are exposed to the sun and to predators during the day, unless they can hide beneath debris or bury themselves. Sand also does not retain moisture well, so such habitats are usually very dry. Therefore, beetles that inhabit any sandy environments, especially desert beetles, need to be drought tolerant. There is also the question of where food comes from, considering the lack of vegetation.

Beetles that inhabit beaches often obtain their nutrition indirectly from the sea, feeding on marine life that has been washed up on the beach. Whether piles of seaweed or the carcasses of marine animals, ranging from jellyfish to whales, most decaying organic matter is attractive to some beetle scavengers, and often to predatory beetles that eat the larvae of other insects, particularly flies, which can be hugely abundant. The sea may also deposit land vegetation, fruits, drowned land animals, and driftwood, all of which are exploited as a food source by some beach-living beetles. Some beetle species specialize in driftwood, and have been transported around the world in floating timber.

The majority of beach-living beetles belong to the families Carabidae, Staphylinidae, Histeridae, and Tenebrionidae, though some smaller families are also characteristic of beach habitats, for example the Phycosecidae in Australia. The inhabitants of driftwood include wood-boring Curculionidae and Oedemeridae. Many carabids and staphylinids on sandy beaches also feed directly on marine organisms such as sandhoppers (Crustacea: Amphipoda). Almost all



LEFT | *Stenocara eburnea* (Tenebrionidae) One of the white, desert-adapted Pimeliinae, this beetle is from Africa's Namib desert.

LEFT | *Phycosecis litoralis* One of four species of Phycosecidae (Cleroidea), which, at only 1–2 mm long, live between grains of sand on beaches in Australia.

BELOW | *Cicindela hybrida* (Carabidae) Larvae of this fast-running hunter are ambush predators, awaiting small prey in a burrow in the sand, which they close with their head.

beach-living beetles obtain their moisture from their food.

In deserts, there are much fewer options as there is no sea to supply organic matter. Almost all desert beetles in true deserts belong to the family Tenebrionidae, most frequently the subfamily Pimeliinae. They are flightless, with fused elytra, and are covered with a waxy substance to prevent evaporation. In Africa, species of the genera *Stenocara* and *Onymacris* bury themselves in sand to avoid the heat of the sun, and have long legs to raise their bodies off the hot sand surface. They scavenge the desert for fragments of plant and insect matter that have blown in, or in the case of insects, flown in and died. Of course, such material is completely dry, so many species of Tenebrionidae in the world's driest deserts need to obtain liquid from the atmosphere, which they do by the unique behavior of "fog basking," harvesting minute droplets of water from the atmosphere at specific times of day.

FLOWING FRESH WATER

Like most non-marine habitats, flowing fresh water such as streams and rivers is home to many beetles, but fewer than are found in ponds, ditches, and slower-moving water. There are several ecological obstacles that keep some beetle genera and species out of flowing streams. Firstly, most larvae and adult water beetles need to return to the surface fairly often to replenish their supply of air, and in flowing water this exposes them to the risk of being carried away by the current. Secondly, the quantity of organic matter, and so the potential food supply, is usually less in faster-flowing water. Thirdly, fast-flowing water has higher levels of oxygen and is able to support larger populations of fish, many of which will eat the adult and larval beetles. Despite these hurdles, a number of families and genera of beetles have adapted to survive in these environments.

The family Amphizoidae are so closely associated with fast-flowing streams that they are called trout stream beetles. They are large water beetles, 10–15 mm long, represented in the modern fauna only by the genus *Amphizoa*, with five species: three in North America and two in east Asia. They inhabit clean, well-oxygenated, rapid-running mountain streams, where adults and larvae are predators of immature stages of insects such as caddisflies and stoneflies. The long-lived larvae of water penny beetles (Psephenidae) cling to the undersides of rocks in flowing streams, grazing on algae, and are found in small numbers throughout the world. They are so called because their circular larvae resemble small coins. The small, soft-bodied adults are not aquatic, and live short lives on streamside vegetation.

Another beetle group that received its common name from its association with flowing water is the Elmidae, called riffle beetles. Adults and larvae live under stones in fast-flowing streams, grazing on algae and other encrusting organisms. A few elmid genera, such as the usually rare *Stenelmis*, develop as larvae in submerged dead wood at the bottom of streams and rivers. Several genera of Elmidae have developed a "plastron," which enables them to extract oxygen direct from water, removing the need to go to the surface to recharge their air bubble. Elmidae are much more diverse in fast-moving water than they are in ponds or pools, which are preferred by other water beetle families such as Hydrophilidae, Dytiscidae, and Gyrinidae. However, all of those families also have a few species and genera that specialize in moving water.

LEFT | A typical European riffle beetle *Limnius volckmari* (Elmidae), grazing algae on a submerged rock.

LEFT | *Amphizoa sinica* (Amphizoidae) Discovered in China in 1991, this is one of only five species of trout stream beetles.

BELOW | *Sclerocyphon secretus* A water penny (larva of Psephenidae) under a rock in a waterfall stream in Tasmania.

The banks of flowing waters, where there is mud periodically washed by the stream, support large populations of many beetle families. Dryopidae, Heteroceridae, Hydrophilidae, Limnichidae, Hydraenidae, Staphylinidae, and Carabidae can be abundant in temperate stream banks, and can be collected by standing in the stream and splashing water onto the mud, which brings them out of their burrows. In the tropics, larger carabids such as the genera *Scarites* and *Galerita* and tiger beetles (Cicindelinae) can be found in such situations.

SALT WATER

The open sea is one of the last great habitats that has never been conquered by beetles, although beaches, sand dunes, and even the strandline support a rich and varied beetle fauna. Many beetles live in fresh water, but these are descended from land-living ancestors, and the larvae of almost all freshwater beetles have to leave the water to pupate on land, even those which then return to the water as adults. Pupation on land is probably too difficult and unreliable in marine environments, where the distance to the nearest dry land may be enormous and unpredictable.

However, since insects in general are almost absent from the sea, even those insects that do not have a pupal stage, the pupation site cannot be the only reason for the lack of truly marine beetles. There must be other factors that keep them out. It is likely that, having evolved and diversified on land, insects lack physiological adaptations for life in salt water; also most of the available ecological niches are already occupied by crustaceans, which were there first. One of the only truly offshore oceanic insects, not beetles but true bugs, the ocean strider genus *Halobates* (Hemiptera), skate on the water's surface, so they are really inhabitants of the air rather than the ocean, which is beneath their feet.

ABOVE | *Cicindis horni* (Carabidae) A rare semiaquatic beetle of the Salinas Grandes salt pans of Argentina, which enters the salt water to hunt for fairy shrimps.

Although none have colonized the open sea, numerous families of beetles have adapted to and specialized for life on the shoreline, for example huge numbers of Anthicidae, Staphylinidae, Ptiliidae, and Histeridae can be found in piles of rotting seaweed cast up above the high-tide mark, where they feed on fly larvae or decaying organic matter. These beetles can survive temporary immersion, and if dropped into seawater usually climb onto floating debris or skate on the surface tension and immediately take flight.

Other groups, particularly Carabidae, are nocturnal hunters; they shelter under beached flotsam during the day, and patrol along the strandline at night for sand hoppers and other crustaceans or marine worms that have ventured up onto the beach. These include *Eurynebria complanata*, a large and striking, pale yellow and black inhabitant of Atlantic and Mediterranean

coastlines of Europe and North Africa. *Eurynebria* has disappeared from much of its former range in recent years, and the reasons for its decline are not fully understood, as in some cases the beaches it inhabited seem unchanged to the human eye. A few other carabid ground beetles take their association with water even further, submerging themselves temporarily to pursue their aquatic prey in its own environment.

Some water beetles of several families have adapted to live in brackish or even salt water, but these generally only inhabit tide pools in the splash zone on rocky shores, which are rarely inundated by the waves, and take shelter in cracks in the rocks during exceptionally high tides. Other beetles, such as some small Carabidae, Staphylinidae, Melyridae, and Salpingidae, live permanently on rocky shores between the tide lines, emerging at low tide to feed on algae or stranded marine organisms, and returning during high tides to fissures in the rocks where some air is trapped.

TOP | *Ochthebius marinus* (Hydraenidae) Warm, sun-exposed tide pools that are only occasionally refreshed by the sea provide ideal habitats for the European marine moss beetle.

ABOVE | *Ochthebius marinus* (Hydraenidae) A small water beetle adapted to pools of brackish or salt water near the sea, where it grazes on algae.

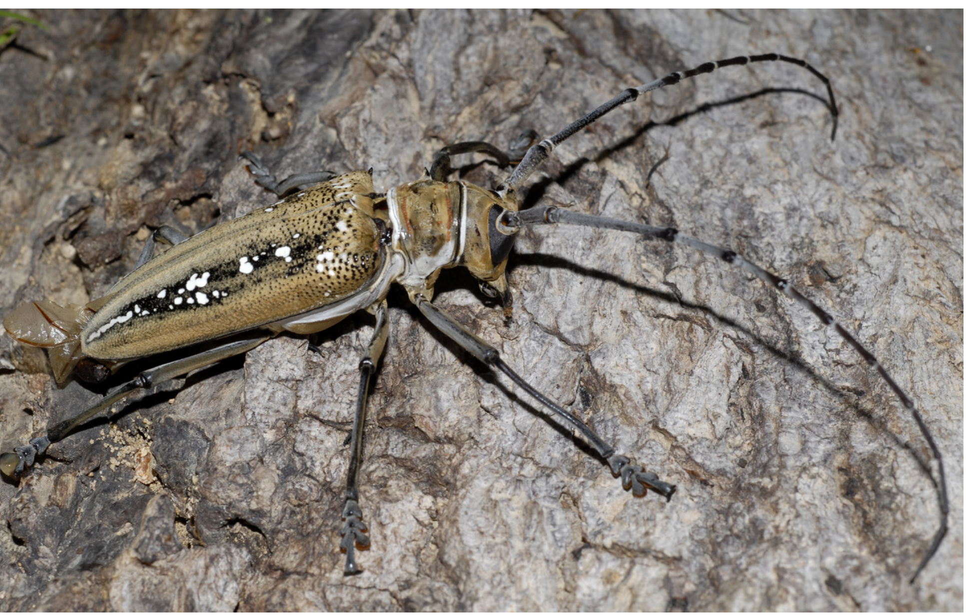
OPPOSITE BELOW | *Aegialites* (Salpingidae) The larva of a genus of small, flightless beetles. The adults and larvae live in cracks in intertidal rocks on both sides of the North Pacific.

BEETLES AND HUMANS

HISTORY OF COLEOPTEROLOGY

The history of the study of Coleoptera dates at least to the Classical period of ancient Greece and Rome. Aristotle (384–322 BCE) and his teacher Plato both mentioned beetles, and many of the generic names used by Carolus Linnaeus, such as *Buprestis* and *Cicindela*, are from *Naturalis Historia* by Pliny the Elder (23–79 CE), the largest surviving book from the Roman Empire. After the fall of Rome, Europe suffered an extended period of comparatively little curiosity-driven academic study, and during these Dark Ages, interest in beetles was restricted to their uses or threats to human health or food security, or to allegorical or superstitious significance. During the Medieval period, monastic texts repeated classical authors, often with stylized images, and ascribed spurious medical properties or even religious significance to beetles.

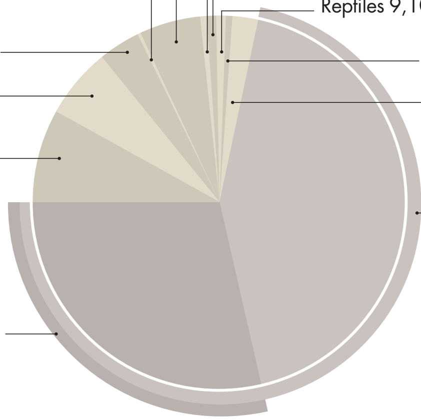
A growth of learning and curiosity about nature marked the Renaissance and the Enlightenment, and by the late 1600s it became more usual for educated, affluent people to have cabinets of curiosities, the progenitors of museum collections. In 1735 Linnaeus published *Systema Naturae*, which provided a framework and system



ABOVE | *Chiasognathus grantii* (Lucanidae) Darwin's Stag Beetle. Charles Darwin, during HMS *Beagle*'s stop in Chile, was among the first to observe the behavior of this beetle.

LEFT | *Batocera wallacei* (Cerambycidae: Lamiinae) From New Guinea, this is one of the largest of its genus, named after Alfred Russel Wallace.

DIVERSITY OF ANIMAL LIFE



LEFT | Diagram showing the relative diversity of different animal groups (total 1,377,716 species). Beetles represent more than a quarter of known animals, outnumbering all non-insects combined.

to classify living organisms, and he accumulated, and in 1758 named, several hundred beetle species. This led to a flowering of interest, as the new naming system was applied ever wider, and sailors and explorers brought back natural objects from far away. Captain James Cook (1728–79) included a naturalist, Joseph Banks (1743–1820), on his famous *Endeavour* voyage, ultimately to New South Wales, Australia. Most of Banks's collections survive, as one of the oldest modern-style scientific collections in the Natural History Museum in London, UK.

Specimens collected by Pierre Dejean (1780–1845), an important entomologist and officer in Napoleon's army, still exist. He supposedly got off his horse during the Peninsular War Battle of Alcañiz to collect a Cebrioninae (Elateridae), which he pinned into his helmet. After his defeat, he was pleased to observe the beetle was still in good condition, and it is now in a museum in Torino, Italy.

By the nineteenth century, the study of beetles had become widespread and popular both as a formal discipline and as a scientific pastime, where affluent private collectors assembled important collections. Countries made collections too, building natural history museums to house the accumulated specimens, generate knowledge, and educate and inspire the population. This environment produced Charles Darwin and Alfred Russel Wallace, two young men who shared a burning interest in collecting beetles and went on to change the world. Darwin said in his autobiography, about his teenage beetle-collecting days, "It seems therefore that a taste for collecting beetles is some indication of future success in life!" He and Wallace are good examples of such success, starting out as beetle collectors and raised to greater heights than anyone could imagine from a platform of dead beetles.

The study of Coleoptera goes on, and museum beetle collections provide vast archives of the beetle knowledge accumulated across the world and down the centuries, ready to answer more questions, some of which society has not yet even thought to ask.

PESTS OF CROPS

One of the reasons for the great success of beetles is the close association of many families with plants, so that almost every plant genus has several species of beetles feeding on it, many of which are host-specific. Furthermore, different beetles will utilize different parts of the plant, which means that a given host plant may support a range of beetles. This intense herbivory is, of course, damaging. Many plants have attempted to avoid it by becoming annual, growing from a seed to a mature plant that produces its own seeds in a single season, then dying off, with its offspring growing some distance away next season. Beetles have responded to this by becoming more mobile and developing senses that allow them to "smell" their target host plants and home in on them over long distances.

During the Neolithic Revolution, some 12,000 years ago, when people started to live in settled societies, they domesticated the first few plants as food crops, and many of these were annual cereals or legumes with large seeds. Arable farming can be an invitation to pests, because farmers grow large numbers of plants of a single species close together in monocultures, in the same place every year. It seems likely that crop pests have been with us as long as agriculture has, and this is supported by evidence of peas bored by Chrysomelidae: Bruchinae (probably the species *Bruchus pisorum*) from archeological sites in Jordan and Turkey some 8,000 to 9,000 years old.

As the selection of crops we grow has increased, so has the selection of potential pests, especially when crops are transported to new areas. A famous example is the Colorado Potato Beetle *Leptinotarsa decemlineata* (Chrysomelidae), a leaf beetle native to the Rocky Mountains of North America, where its original host plant was a native weed, buffalo bur. During the nineteenth century, with widespread planting of potatoes imported from the Andes, the beetle switched host to this new, abundant resource, and within 20 years it was found on potatoes from coast to coast of continental USA. In the 1920s it reached Europe and spread east, until it occupied a belt around the whole northern hemisphere,

LEFT | *Leptinotarsa decemlineata* (Chrysomelidae) The strikingly marked Colorado Potato Beetle is a scourge of potato agriculture across the northern hemisphere.

LEFT | *Anthonomus grandis* (Curculionidae) The Cotton Boll Weevil on a cotton boll that will become only a husk filled with weevil droppings.

BELOW | *Agriotes* (Elateridae) Adults and larvae in Canada on potatoes damaged by the holes of the wireworm larvae.

covering an area of over 6 million sq miles (16 million sq km). It prefers continental steppe climates with cold winters and hot summers, avoiding the warm, damp climate of Britain and Ireland. There was an unsuccessful plan by Germany during the Second World War to introduce Colorado Potato Beetle to England, to destabilize enemy food production. Similarly, when it arrived in East Germany during the 1950s, propagandists tried to blame the new pest, groundlessly, on American interference, calling it "Amikafer" (Yankee beetle).

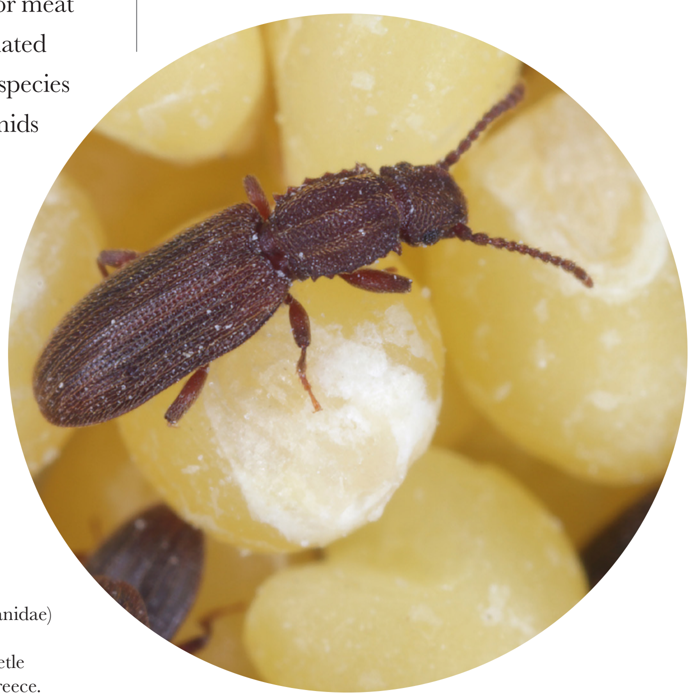
The Cotton Boll Weevil *Anthonomus grandis* (Curculionidae) is a serious cotton pest in southern USA, recently doing up to $300 million worth of damage per year. Strangely, there is a monument to this pest in the town of Enterprise, Alabama, because its depredations forced the area to diversify into other crops, bringing prosperity.

PESTS OF STORED AGRICULTURAL PRODUCTS

With the agricultural revolution, or even earlier with hunter-gatherers, people stored food from times of plenty for future times of need. Like almost every activity, this practice provided opportunities for beetles to exploit. When people travel from place to place, especially large groups over great distances, they usually bring a supply of preserved food for the trip. If food is carried for periods of time in open conditions, or by ship, it might get damp or spoiled, and on reaching the destination will be discarded, distributing any insects it contains into a new environment. As humans have spread all over the world, the insect travelers associated with their food supplies have been carried with them, and at each destination, more species were picked up accidentally and added to the assemblage of "human stored product beetles."

In this way, numerous beetle species that feed on preserved or dried grain, fruit, fish, or meat have been spread throughout the populated world. Remains of the exact same pest species have been found preserved in the pyramids of ancient Egypt and in Native American archeological sites, showing how long they have been with us and how far we have traveled together. The original ranges of these beetles are lost in time, but we can infer their original habitats, since humans are not the first animals to store products, and the habitats provided by human food storage—effectively dark, dry places full of a single kind of food—are not unique in the natural world. Some birds such as jays hoard seeds in hollow trees; rodents such as squirrels, mice, rats, and hamsters store grain in their burrows, and it is thought that some of the most serious pests of grain storage were originally associated with the underground larders of small mammals.

To be associated with stored products, beetles need three main characteristics: to be resistant to dry conditions as adults and larvae, since stored products are, where possible, kept dry; have the ability to disperse over large distances, as supplies of food are scattered in the environment; and for the same reason, like any animal needing an infrequent resource, be able to detect reliably the resource that they will infest. Families of beetles that meet these criteria, and members of which have become cosmopolitan stored product pests, include Tenebrionidae, Laemophloeidae,



RIGHT | *Oryzaephilus surinamensis* (Silvanidae) The earliest known record of the cosmopolitan Saw-Toothed Grain Beetle is from a Neolithic site in northern Greece.

Silvanidae, Latridiidae, Cryptophagidae, Nitidulidae, Bostrichidae, Ptinidae, Chrysomelidae subfamily Bruchinae, and Curculionidae.

The combined costs of these pests, not just financial but in terms of lost livelihoods and even lives, is enormous, especially in tropical countries, where a hot, humid climate promotes insect and fungus growth, and the infrastructure may make safe storage more difficult. The Western Australian Department of Agriculture and Food estimates that a quarter to a third of the world's entire grain crop is lost in storage. The United States Department of Agriculture claims that 10 percent of all food produced in the USA is lost to pests or pest contamination, and that this may rise to over 50 percent in some countries. Although other insects and fungi play a role, beetles are major culprits in the destruction of stored products, costing millions of dollars in damage every year.

ABOVE | *Tribolium castaneum* (Tenebrionidae) The Red Flour Beetle is a major pest of starchy foodstuffs, and has been spread throughout the world.

BELOW | *Callosobruchus maculatus* (Chrysomelidae) A bean beetle infesting mung beans. All they leave behind is a husk packed with droppings that even chickens won't eat.

FORESTRY PESTS

A natural forest is a rich mosaic of habitats, where trees of many species and varying ages, from seedlings to ancient veterans, live with a diverse assemblage of other plants, fungi, mammals, and birds, and hundreds or thousands of species of invertebrates, forming a complex and balanced ecosystem. A plantation forest grown for forestry might look similar to the untrained eye, but usually consists of rows of trees of the same species and age, planted close together so they shade the forest floor, which discourages the growth of other vegetation. It is effectively a monoculture like any other crop, not very different from a barley field. The trees may not even be native species to the country where they are grown. It can be a virtual desert from a biodiversity point of view.

However, as is the case with any monoculture of closely spaced individuals of the same species, a managed forest can be subject to infection, which can spread quickly from tree to tree, especially as the trees in forestry situations may be stressed or overcrowded. Some beetle species, especially of the families Curculionidae and Cerambycidae, can establish large populations in tree monocultures very quickly. These can be harmful to the survival of the trees themselves, or can affect the quality of the timber, making it less valuable when harvested.

BELOW | *Anoplophora chinensis* (Cerambycidae) An Asian species accidentally introduced into parts of Europe. The related Asian Longhorn (*A. glabripennis*) is a pest in North America.

LEFT | *Agrilus planipennis* (Buprestidae) Emerald Ash Borer, an introduced pest from China, emerges from an infested ash tree in the USA.

BELOW | *Ambosiodmus lecontei* (Curculionidae) From North America, this female has laid eggs and is cultivating white fungus for the larvae to eat.

Beetle infestation is more serious if the beetle is a vector of a tree pathogen, and such tree diseases can have serious consequences that can also affect trees grown away from monocultures. The most famous example is the Dutch elm disease fungus *Ophiostoma novo-ulmi*, which is spread by elm bark beetles of the genus *Scolytus* (Curculionidae). The female bark beetle carries fungal spores in special organs called mycangia, and inoculates them into the tree in which she lays her eggs, so that the larvae developing in their tunnels can feed on the fungal fruiting bodies. In the case of Dutch elm disease, the fungus being transmitted by the beetles became extremely pathogenic to the trees, and killed millions of elms in Europe, Asia, and North America.

Insect pests can be much more damaging outside their native range, where the local trees of the genus that they attack have not evolved alongside them, and where specific parasites and predators that usually keep the pest numbers under control are absent. Examples include forestry pests and pests of amenity planting such as street and garden trees, like *Agrilus planipennis*, the Emerald Ash Borer (Buprestidae), and *Anoplophora glabripennis*, the Asian Longhorn (Cerambycidae), both much more problematic in North America than they are in their native China.

Under adverse climatic conditions, even a native species can become a very serious forestry pest. The Mountain Pine Beetle *Dendroctonus ponderosae* (Curculionidae), for example, has been responsible for the death of millions of acres of pine forest in North America, peaking in 2009, after a series of dry summers placed trees under environmental stress. This, coupled with mild winters, failed to reduce the beetle populations to manageable levels.

DOMESTIC PESTS

With at least 400,000 species, utilizing most of the terrestrial habitats of the world, it is not surprising that a few beetles have adapted to take advantage of the opportunities offered by human-altered environments, especially considering the ever-increasing proportion of the earth's surface modified by humans. There are several beetle species that live in our homes and gardens, eating the food we store for ourselves or the plants we cultivate, or even the structure of our houses. These beetles are called "synanthropic" species (from the Greek "with people"), but when they come into conflict with us they are usually just called pests. Here, we use "domestic pests" to distinguish those of houses and gardens from those of agriculture and forestry, which are discussed elsewhere (see pages 54–59).

Every garden and almost every human dwelling is shared with at least a few beetle species, and archeology and paleontology show that this was always the case. Wherever people go, we carry crops and domestic animals, along with soil and animal food and bedding, and all these things carry beetles. Beetles are nature's recyclers, and species that have adapted over millions of years to a certain substrate often don't differentiate between a dead branch on a tree and one that has been carved into a piece of furniture, or animal remains left by predators and skins or meat prepared for human use.

As with synanthropic vertebrates such as rats, mice, and pigeons, it is often the same relatively few species of beetles that we have carried around the world over the centuries with migration and trade. In many cases, these species were with us for so long that their original geographical distribution is unknown. The beetles extracted from the mummies of the pharaohs of ancient Egypt are often the same species found in Viking archeological sites, in medieval burials, and as pests of dried meat products today.

The major limiting factor for beetles in a human dwelling is that it is very dry, since it never rains indoors. Many domestic beetle pests belong to the superfamily Bostrichoidea, which seem best able to cope with the dryness. These include the family Dermestidae, carpet beetles and larder beetles, which feed on dry animal protein such as woolen blankets and rugs, dry pet food, and dry meat and fish. Several genera such as *Anthrenus* and *Reesa* are called museum beetles, and will also attack taxidermy and insect collections, where they can be very destructive. Related beetles

OPPOSITE | *Euophryum confine* (Curculionidae) A wood-boring weevil introduced to Britain from New Zealand, and now very common in damp wood in bathrooms and kitchens.

ABOVE | *Lilioceris lilii* (Chrysomelidae) The Scarlet Lily Beetle is a defoliating pest of cultivated lilies in Europe, and has now been introduced into the USA.

BELOW | *Popillia japonica* (Scarabaeidae) Introduced from Asia to North America in the early twentieth century, this garden pest has spread rapidly, including to Europe.

of the family Ptinidae attack dry plant matter: Woodworm *Anobium* and Death Watch Beetle *Xestobium rufovillosum* can attack beams and timbers, the latter earning their name from the ticking sound they make at night to attract a mate. The cellar beetles (genus *Blaps*) are large, black beetles that can sometimes still be found in very old buildings or stables, and in many European cultures are connected with death; they are also strongly nocturnal, and in both cases the superstitions probably arose because rural people before electricity, sleeping at dusk and rising at dawn, will only have encountered night-active insects in times of sickness.

POLLINATION

Angiosperms, flowering plants, are the dominant plant group in land ecosystems today, in both volume and species diversity. Most of the crops we eat are angiosperms, and as well as feeding us and shaping the habitats of the planet, plants produce the oxygen we breathe. Humans, like beetles and most other animals, rely on plants to exist.

As land plants are stationary, they cannot search for mates like animals do, so to reproduce, they discharge their male gametes, pollen, into the environment, aiming for some to reach the female flowers of another plant of the same species. Many plants rely on wind pollination, producing huge quantities of pollen so that a few grains of the millions will reach the right female flowers, but a more targeted strategy, in many of the higher plants, is to use insects for pollination.

Insect-pollinated plants have obvious flowers, combining both male and female organs, often developing at different rates in each flower to avoid self-fertilization. They provide a reward to attract pollinating insects—usually sugary nectar—and to access it, the insect must contact stamens that deposit pollen and a stigma that removes and uses any pollen from other flowers. Insects move between flowers of the same species, searching for the reward, and at the same time distributing the plants' genetic material. Some insect groups become specialized pollinators of particular flowers, guaranteeing a source of food, and at the same time ensuring the plants reproduce. Such insects often evolve structures that make them better pollinators, such as the fuzzy setae of bumble bees and flower chafer beetles that hold more pollen. This in turn increases populations of the plant on which they rely, so is an example of mutualism, a relationship between organisms where both benefit.

When we think of pollinators, we often think of bees and butterflies, but in the early Cretaceous when flowering plants first diversified, beetles were likely the first pollinators, just as they were, and still are, the primary pollinators of cycads and some other ancient plants. In modern ecosystems, beetles still play an important role in pollination, especially of flowering trees, and in tropical and arid environments. Beetle-pollinated flowers are often large or clustered, pale-colored, and may have a strong, sweet, sometimes even sickly scent. Examples include water lilies, arum lilies, magnolia, and hawthorn blossom. The fleshy petals of many of these, especially magnolia and water lilies, reflect an ancient association with beetles and protect the flowers from the beetles' chewing

LEFT | *Meligethes aeneus* (Nitidulidae)
A mass of tiny pollen beetles pollinate a yellow zucchini (courgette) flower in an English garden.

ABOVE | *Anchylorhynchus* (Curculionidae) South American palm-pollinating weevils—similar African weevils are used to pollinate commercial oil palm.

BELOW | *Eupoecila australasiae* (Scarabaeidae) A fiddler beetle pollinating an Australian eucalyptus. Although these beetles eat part of the flowers, the benefits outweigh the damage.

mouthparts. Some beetle pollinators damage the plant, eating the pollen and stamens, or developing as larvae inside the ovules, so the pollination service has a cost.

Pollinators are worth billions of dollars annually to agriculture. Some important crops have failed to thrive in parts of the world because of a lack of native pollinators (hand pollination is far too labor-intensive). A famous example is the introduction of West African oil palm to tropical Asia, which has only been possible due to the introduction of pollinating weevils (genus *Elaeidobius*). This is a bittersweet success story, because oil palm has been so destructive to Asia's rainforests.

BIOLOGICAL CONTROL OF WEEDS

As people traveled around the world they brought with them exotic plants, sometimes to remind them of home, or as crops, ornamentals, food for livestock, to modify the landscape in some way, or even by accident as seeds in animal feed or bedding. Some of these plants then established and proliferated in the new environment and became invasive weeds. Unchecked by the usual herbivores and competitors, these plants can grow faster and denser than usual, crowding out native habitats and becoming severe pests, to the extent that invasive species have been described as the second biggest threat to biodiversity after habitat destruction.

Often, when a plant is established in a new environment, controlling it by the usual methods becomes impossible, as it establishes a seed bank in the soil—and it is then that people generally resort to biological control. The object of biological control is straightforward. The invasive plant has become so successful because it has escaped the usual checks and balances that regulate its population in its native range, so scientists look at the wild population where the target plant originated, to seek specific herbivores and seed predators, and import them as well, in the hope that they might regulate the pest without affecting anything else in the environment. This has to be carefully managed, since the wrong "biocontrol agent" might become an invasive species in its own right, or switch hosts and attack a vulnerable native relative of the target plant. Nowadays, a lot of laboratory testing takes place before biocontrol agents can be released, and only agents shown to be host-specific to the target weed are selected, to reduce collateral damage to other plants. Beetles, as well as Lepidoptera (butterflies and moths), are most frequently selected against invasive plants, because many of them are very host-specific, feeding on only one genus or species of plant. Among beetles, weevils (Curculionoidea) and leaf beetles (Chrysomelidae) have been used most often. Successful examples include Thistle Weevil *Rhinocyllus conicus* (Curculionidae), introduced from Europe to Canada, and Gorse Weevil *Exapion ulicis* (Brentidae) from Europe to New Zealand.

LEFT | Larvae of *Oxyops vitiosa* (Curculionidae) An Australian weevil biocontrol agent for paperbark tree, an invasive pest tree in Florida's wetlands.

Biological control of plants has generally been much more successful than biological control of animals, because most plant feeders are much more specific in their diet than most predators. A notorious historical failure of biological control of animals was the introduction of the South American Cane Toad into Australia to control the sugarcane beetle *Dermolepida albohirtum*. The toad was a totally inappropriate biological control agent, since it feeds indiscriminately on a wide range of insects, arthropods, and even small mammals, reptiles, and amphibians. Furthermore, it is toxic, and therefore dangerous to native predators such as monitor lizards and snakes that try to eat it. It remains a serious invasive in Australia to this day; it was also not very effective at controlling the sugarcane beetle.

ABOVE | *Agasicles hygrophila* (Chrysomelidae) The Alligator Weed Flea Beetle was introduced to Florida to control the invasive alligator weed that was blocking waterways.

RIGHT | *Nanophyes marmoratus* (Brentidae) A European weevil successfully introduced to North America to control the flowering plant European purple loosestrife.

SOURCE OF FOOD

Insects have probably always formed part of the human diet, and still do in most parts of the world today. It is only in Europe and North America that people have generally turned their backs on "entomophagy," as the eating of insects is called. In the Bible Lands at the time of the writing of the Old Testament, the eating of certain insects was explicitly encouraged (while mollusks and crustaceans were considered unclean).

Probably in more northern countries, where insects are few, small, and seasonal, and thus difficult to harvest in quantity, while marine invertebrates such as shellfish, crabs, and lobsters are large and abundant all year round (and stay fresh longer in the cooler climates), these preferences were reversed, and now insect eating seems strange and unpleasant to many Europeans and North Americans who would not think twice about a plate of oysters or shrimp. However, insects breed rapidly, can be fed cheaply, require very little land, and produce very little carbon dioxide per pound of protein produced, so they represent a sustainable alternative to almost all other meat sources, and may have an important role to play in the future in feeding a growing human population.

LEFT | *Rhynchophorus ferrugineus* (Curculionidae) Palm weevil larvae fried with garlic and chili on a bed of rice, served as a bar snack in southern Thailand.

ABOVE | *Tenebrio molitor* (Tenebrionidae) Usually ground into flour, but here entire mealworm larvae are served as an alternative to meat.

As in most things, beetles feature largely in the list of edible insects, especially the larvae, which are generally bulkier than the adults, easier to collect in quantity, and lack the hard chitinous exoskeleton. The larvae of weevils (Curculionoidea) and scarabs (Scarabaeoidea) are among the most popular; they contain no noxious chemicals, can

BELOW | *Oryctes rhinoceros* (Scarabaeidae) Turning a pest into a meal. These large larvae destroy palm trees but are rich in protein. They look more appetizing after cooking.

be pests, and may occur in large numbers on agricultural land. In many tropical cultures, the pith of palm trees, such as sago, is used as a source of starch and carbohydrate, while the larvae of palm weevils (Curculionidae: *Rhynchophorus*), which develop in the same substrate and may be encountered while harvesting the sago, are used as a protein supplement. In other cultures, grubs of chafers (Scarabaeidae: Melolonthinae) that occur in the soil developing on the roots of crops may be collected in large numbers and either used to feed poultry or cooked and eaten directly, thus combining food foraging with pest control.

In Western countries, mealworm larvae (Tenebrionidae: *Tenebrio*) are grown in industrial quantities, not just as pet food but also to be ground up into "insect flour," which is used to make protein-rich breads or energy bars. Whole dried and spiced larvae may also be sold as an artisanal condiment, and recently we have seen a gradual normalization of insects as a food source in Western cuisine.

Adult insects are eaten less commonly, but in the night-markets of Southeast Asia, one can buy a large selection of flash-fried adult beetles straight out of a wok, which include water beetles (Dytiscidae and Hydrophilidae) and chafer beetles (Scarabaeidae: Melolonthinae), as a crunchy midnight snack. These are usually attracted to lights, gathered, and fried immediately.

ART

Since the dawn of representative art, people have drawn the objects and creatures with which they share their environment. While large prey animals dominate the earliest cave paintings and rock art, there are also some representations of insects, sometimes interpreted as beetles. Occasionally, beetles have featured in mythology, or have gained allegorical significance. A famous example, discussed on pages 72–73, is the ancient Egyptian veneration of scarab beetles, paintings and carvings of which adorn the pyramids and sarcophagi of the pharaohs.

There was a revival of such scarab imagery in the 1920s in Europe and the USA, when the discovery of Tutankhamun's tomb in 1922 led to a surge of interest in Egypt. The Art Nouveau and Art Deco movements incorporated stylized scarab motifs into art, jewelry, and architecture, and Egyptian-style scarab beetles, often with wings outstretched, are a common feature of buildings of that era. Today, visitors to London Zoo can see a much more realistic scarab sculpture, a modern bronze statue of a pair of *Kheper* (Scarabaeinae) with a dung ball, emphasizing the essential role dung beetles play in the African savanna.

Beetles feature prominently in still-life paintings of the Dutch Golden Age (1609–1713), particularly those of the Vanitas style, where symbolic objects remind viewers of their mortality and the fleeting nature of worldly goods and pleasures. Stag beetles *Lucanus cervus* were most frequently used, and receive a symbolism similar to that of the beetle's evening flight in literature, representing the end of day and, by extension, the end of life. An opulent table laid with food and drink was often juxtaposed with a single dead beetle, skull, or snuffed-out candle, as a *memento mori*. Stag beetles were probably popular because of their impressive size and menacing jaws, and it is consistent with the theme of the paintings that they were obviously dead.

Albrecht Dürer painted his famous stag beetle in 1505; at a time when nature was little valued, such a choice of subject was in the true spirit of the Renaissance. Although defiantly and vibrantly posed, the articulation is slightly unnatural, suggesting the model was dead. The use of actual dead beetles in art has a long history, especially in India and Indochina, where beetle elytra decorate hangings and muslin dresses. This inspired the

LEFT | Illuminated page from *Model Book of Calligraphy* (1561–96) by Bocskay and Hoefnagel, showing an accurate European rhinoceros beetle *Oryctes nasicornis*.

LEFT | A realistic bronze sculpture of dung beetles with a dung ball by Wendy Taylor delights children and entomologists at London Zoo.

BELOW | Albrecht Dürer's famous stag beetle, one of the earliest Renaissance works to choose a beetle, without allegory or symbolism, for a subject.

famous "Beetle Wing Dress" worn by Victorian actress Ellen Terry in her portrayal of Lady Macbeth (1888–89), now preserved at her home at Smallhythe Place, in Kent, UK. The same jewel beetles *Sternocera aequisignata* (Buprestidae) were used in large installations by Belgian artist Jan Fabre (born 1958), including "Heaven of Delight," where a whole room of a Brussels Palace, including the chandeliers, is encrusted with thousands of elytra. Another metallic green beetle often used in jewelry is the tortoise beetle *Polychalca punctatissima* (Chrysomelidae) from Brazil. These were popular in the 1920s and were often sold, in the spirit of the times but quite wrongly, as "scarabs." Sadly, they seem much rarer now. Many of the Atlantic coastal forests where they used to live have been destroyed.

LITERATURE

In his "Ode on Melancholy" (1820), the romantic poet John Keats urges the reader: "Make not your rosary of yew-berries, Nor let the beetle, nor the death-moth be, Your mournful Psyche." The admonition is not to indulge too freely in baleful associations of death. "Psyche," representing the human soul, is often depicted as a butterfly. The "death-moth," on the other hand, refers to a quite different and more nocturnal lepidopteran, the Death's Head Hawk Moth, a large insect with a pattern on its thorax that resembles a human skull, and which has long been a literary and artistic symbol of mortality. "Yew-berries" are deadly poisonous, and yew trees with their dark foliage are traditionally planted in churchyards. But why beetles? The noisy, bumbling, crepuscular flight of beetles such as Geotrupidae, Cerambycidae: Prioninae, and Lucanidae has long symbolized the end of the day and the beginning of the night, and they have become literary guardians of the darkness, like moths, inhabitants of the veil that separates the brightness of day from the darkness of night (and by extension, life from death). The same use of the beetle's flight is seen in the earlier "Elegy Written in a Country Churchyard" (1751) in which the poet Thomas Gray describes the evening: "Now fades the glimm'ring landscape on the sight, And all the air a solemn stillness holds, Save where the beetle wheels his droning flight." The beetle is the only thing breaking the graveyard's silence. Shakespeare's Macbeth (1606) uses the same image and other images of darkness to confess the murder he is planning: "Ere the bat hath flown His cloistered flight, ere to black Hecate's summons The shard-borne beetle with his drowsy hums Hath rung night's yawning peal, there shall be done A deed of dreadful note" (what he means is "before dark"). "Shards" refers to the

ABOVE | Bewitching splendor: Ellen Terry's famous Lady Macbeth dress was made from tropical Buprestidae elytra, slightly out of place in eleventh-century Scotland.

(continued...)

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