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GENERAL ZOOLOGY: Investigating the Animal World 2e

Dennis Holley

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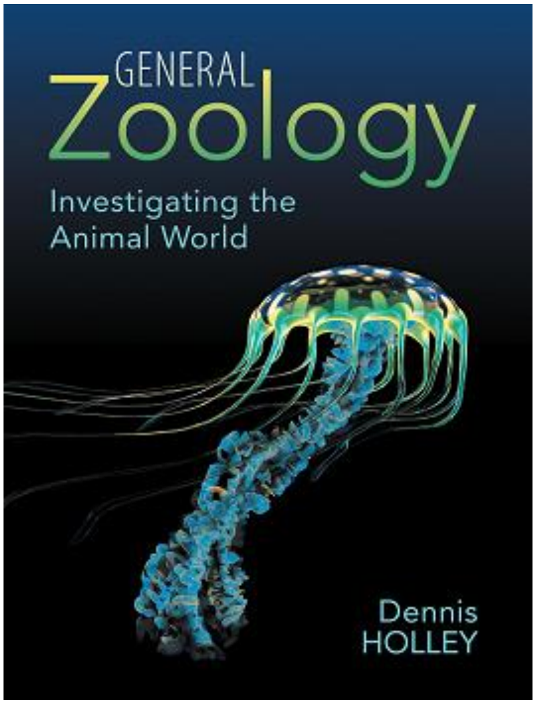

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- ***Research-based.*** This book is based on current educational research and best educational practices, not tradition.
- ***Understandable.*** This textbook is content (ideas) driven and not consumed with terms and terminology (definitions). Terms and scientific names are used when and where appropriate to illustrate and explain the concepts and ideas inherent in a particular chapter.
- ***Readable.*** Presented in a single column format, this book is written more similar to a magazine article than a dry, stilted entry in an encyclopedia. This allows for easier student reading which in turn increases reading comprehension.
- ***Appropriate level.*** Many, if not most, of the students that take introductory biology courses come with only a fair to poor biology background. This problem is compounded by college biology textbooks that are written at a higher technical level than they should be. This textbook, however, takes such student deficiencies into account as it is written at an appropriate technical level.
- ***Connected.*** Often students do not appreciate how they connect with animals directly or indirectly on a daily basis. In order to convey the importance of animals, each specific phylum chapter concludes with a detailed look at how the animals in that chapter connect to humans economically, ecologically, medically and even culturally.

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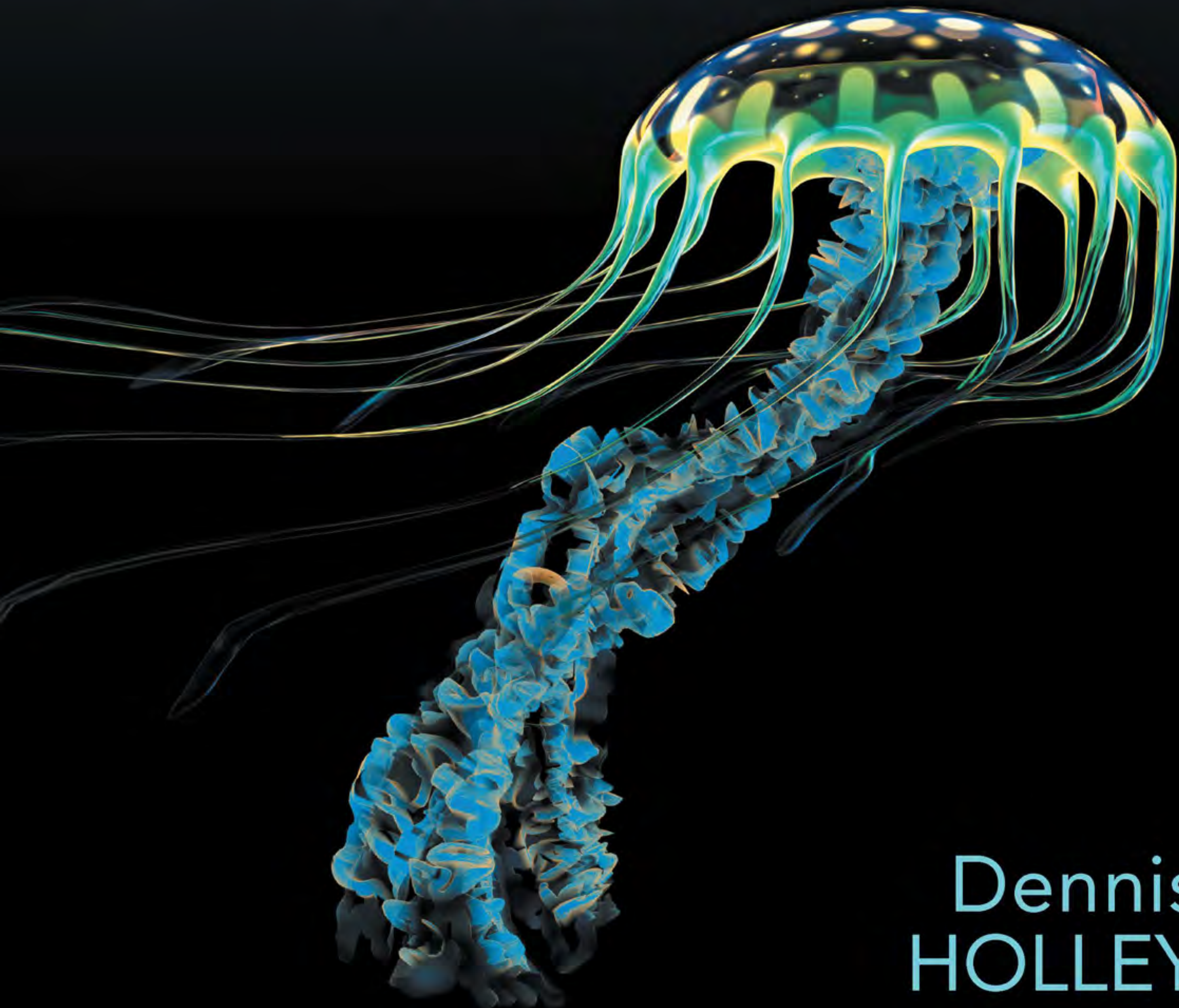

Dennis HOLLEY

GENERAL ZOOLOGY

Investigating the Animal World

Dennis Holley

PREFACE

Greetings zoology student and welcome to the always astonishing, sometimes strange, and occasionally even bizarre world of animals.

> *We patronize them for their incompleteness, for their tragic fate of having taken form so far below ourselves, And therein do we err. For the animal shall not be measured by man. In a world older and more complete than ours, they moved finished and complete, gifted with the extension of senses we have lost or never attained, living by voices we shall never hear. They are not our brethren. They are not our underlings. They are other nations, caught with ourselves in the net of life and time, fellow prisoners of the splendor and travail of the earth.*
>
> —Henry Beston

Zoology or any scientific endeavor should be thought of as consisting of two phases: the first being the *Investigation* and *Exploration* phase while the final is the *Accumulation* phase. Zoologists attempt to answer questions about the animal world by actively investigating animals through experimentation and by discovering new animal species through exploration. Investigation and exploration in turn lead to the accumulation of facts and information. These accumulated facts and information lead to even more questions that in turn lead to more investigation resulting in even more facts and information being accumulated. And the cycle continues.

In this course, you will confront the facts and concepts of zoology in your textbook (*Accumulation*). However, you will also be challenged to think, act, and work like a zoologist (*Investigation*) at certain points in your textbook, and especially in the laboratory segment of this course. As you investigate, you will use the same information, develop the same scientific skills, and employ the same scientific processes as do professional zoologists.

Science Process Skills

Organizing Information

- Classify
- Sequence

- Describe
- Summarize
- Explain
- Definition and proper use of terminology
- Accessing and using reference materials
- Reading comprehension

Critical Thinking

- Critical and creative thinking
- Observe
- Infer
- Compare and contrast
- Recognize cause and effect
- Formulate and use models

Experimentation

- Experimental design
- Formulate hypothesis/prediction
- Establish variables and controls
- Collect and organize data
- Accurate measurement
- Analyze data
- Draw reasonable conclusions

Graphics and Numbers

- Make and interpret graphs
- Construct and interpret tables
- Interpret scientific illustrations
- Calculate and compute

Communication

- Brainstorming
- Collaboration
- Communicating

Developing and using these skills effectively is very important if you are biology major, but even if you are not majoring in a scientific field, mastering these skills will help you function as a clear-thinking and scientifically literate citizen of a society that grows ever more science-based and technologically oriented.

Approach and Organization

Approach

Biology textbooks and related curricular materials at all levels have come under harsh but justified criticism by various scientific and educational groups in the past decade. From the inception of this text, it has been the goal to write a zoology program that acts on the criticisms and recommendations of those authorities and is based on current educational research. This textbook has been designed and written to be:

- **Readable and Interesting**. My goal has been to write a textbook in which the chapters read more like an interesting magazine or newspaper article and less like a dry and detailed technical entry from an encyclopedia. Increasing reader interest increases readability and to aid in that goal, I include out-of-the-ordinary things in each chapter that would not normally be found in zoology texts. I have also taken a different approach than other zoology books in that while I firmly believe that evolution is driving force and cornerstone of all things biological, I did not make the theoretical and often speculative aspects of origins and patterns of evolution the focal point of each chapter. Instead, I opted for a more concrete "here-and-now" approach in which our focus is mainly on animal systematics, phyla and class characteristics, and ecology. Hopefully, less emphasis on the theoretical translates into a work that is more relevant to you the student.
- **Understandable.** As I wrote this textbook I tried to avoid the "Huh? Factor" as much as possible. That is; students should not be obliged to reread a passage several times all the while armed with a biological dictionary to understand what they just read. The chapters of this textbook are centered on concepts and ideas. Specific facts, terms and terminology, and scientific names are used only when necessary and appropriate to illustrate and explain the concepts and ideas inherent in a particular chapter. This textbook is concept (idea) driven, not terminology (definitions) driven.
- **Connected.** Animals are all around us, on us and possibly in us, and they affect our daily lives directly and indirectly in ways we are continuing to uncover. In an attempt to connect you the reader directly to each animal group, each chapter concludes with a discussion on how the animals encountered in that chapter connect to humans economically, environmentally, medically, and even culturally.
- **Personable** Many textbooks are written by teams of writers, some of which are anonymous. As a result, the reader (student) lacks a personal connection with the author(s). Again, this text is different. First, this text was written in entirety only by the name you see stamped on the front of this book—Dennis Holley. Secondly, I have attempted to write each chapter in the tone of enthusiastic and passionate, but caring and concerned teacher speaking directly to you the student. Hopefully, I have succeeded. Lastly, personal notes will appear at the end of each chapter. In

these short conversations and dialogues, I may share an anecdote, look behind the headlines, or pose intriguing questions. You will encounter the first of these conversations and dialogues in this preface. Hopefully, you will find them interesting, thought-provoking and even amusing.

Organization

A quick glance at the table of contents reveals that what zoology is and how it works is detailed in Chapter 1. With this foundation in place, Unit One examines the place of animals in the bigger picture of the web of life. Unit Two delves into animal structure and behavior then investigates the possible origins of animals (phylogeny) as well as the system of organization (taxonomy) developed to bring scientific order to biologic chaos. In the remaining three units, we will voyage through the animal realm from the simplest life form—sponges to the most complex—humans. The progression of units is based on increasing morphological and anatomical complexity.

At the end of each chapter you will find both a set of *Review and Reflect* questions that will test your critical thinking skills while reviewing the main concepts of that particular chapter and a set of *Create and Connect* challenges that will help you develop and use important science process skills. Some or all of these questions and challenges may be assigned by the instructor as part of the assessment package for this course. In these assignments, you will be asked to write everything from formal scientific reports to essays to position papers to short stories. The exact format and details will be given with each assignment. Consult Appendix A—Scientific Writing for guidelines and suggestions for correct scientific writing.

I believe this textbook represents a major paradigm shift in the way college biology textbooks are written and presented because it was written by a teacher (not a research scientist) for students. I have labored to make this textbook accurate, understandable, and interesting so that you can and will read it. And if you do indeed bother to read it, I guarantee that you will gather not only a wealth of information, but also a never-ending respect for those amazing creatures we call animals.

A Personal Note from the Author

I am a biologist to the core, always have been, and always will be. My interest in all things living is broad and generic. If it's a living creature—plant, animal, or microbe—I find it fascinating. How did I get this way? Understanding parents and a nurturing habitat are to blame. My mother was constantly contending with tadpoles in jars, aquariums of fish, mice in cages, and occasionally rewashing the clothes she had just hung out to dry because my flock of pigeons flew too low overhead. She pretended to make a fuss but encouraged my every adventure. My father helped me build cages and traps and was quite adept at capturing and helping me rear the many kinds of small animals that constantly caught my attention and interest.

I was blessed with growing up in a very small rural village where my family's acreage was only several blocks from a meandering stream aptly known by the locals as "Muddy Creek." This brook was shaded by many huge overhanging trees and was full of snails, fish, frogs, turtles, and even beavers and muskrats. Many inquisitive hours were spent around and in that stream.

Two events sealed my fate and set me on my course. In my early high school years, my parents finally gave in to my pestering and bought me a small, simple microscope (which they couldn't afford even though it cost only around $30). This amazing black beauty came complete with a wooden box of slides and a few dissecting instruments. Once I dove into the microscopic world, I was hooked on all things biological. Later, I stumbled on Paul de Kruif's 1926 book, *Microbe Hunters* and was inspired to get the education that would allow me to become a professional biologist. At that point, I didn't know exactly what I wanted to do professionally, but I did know my future would have something to do with biology.

I eagerly devoured every biology course I could take in college, and while I flirted for a time with the idea of becoming a marine biologist, I eventually became an educator. For nearly forty years, high schools and universities have actually paid me for merely doing what I love—teaching biology and teaching others how to teach biology and science. I am a very inquiry-oriented, hands-on type of teacher whose philosophy as an educator is best and most simply articulated in the words of Louis Agassiz:

Study nature, not books.

My love of all things biological continues unabated to this day. As such, I would consider the day poorly spent were I not to stumble upon at least several biological "WOW! Moments" (*WoMos*) during the course of that day. Such moments are not hard to find for they are everywhere. You just have to be receptive to them. Stop, look, and appreciate the natural world around you.

It was my intent and it is my hope that through this zoology program, you will come to know and respect those amazing creatures we call animals and that you too will have many personal zoological *WoMos* as this course unfolds.

I would like to dedicate this book to my parents for their nurturing and understanding, my wife and family for their patience and support, and to my students—past and present—who have taught me more than they will ever know.

Dennis Holley

CHAPTER

13

PHYLUM ARTHROPODA: SOVEREIGNS OF THE TERRAN EMPIRE

If all mankind were to disappear, the world would regenerate back to the rich state of equilibrium that existed ten thousand years ago. If insects were to vanish, the environment would collapse into chaos.

—E. O. Wilson

Introduction

Arthropods have evolved to become the most abundant, most diverse, and most biologically successful animals on earth. Their biological prowess is demonstrated in species numbers that stagger the imagination. Of all the known and described species of animals, at least three out of every four is an arthropod. In fact, some studies indicate that as many as 80% of all known animal species are arthropods. (**Figure 13.1**) Some estimates place the total number of arthropods species at 5 to 10 million. Other studies suggest there may be as many as 6 to 9 million species of arthropods in tropical forests alone. Taxonomists can only speculate on the possible total number of extant arthropod species

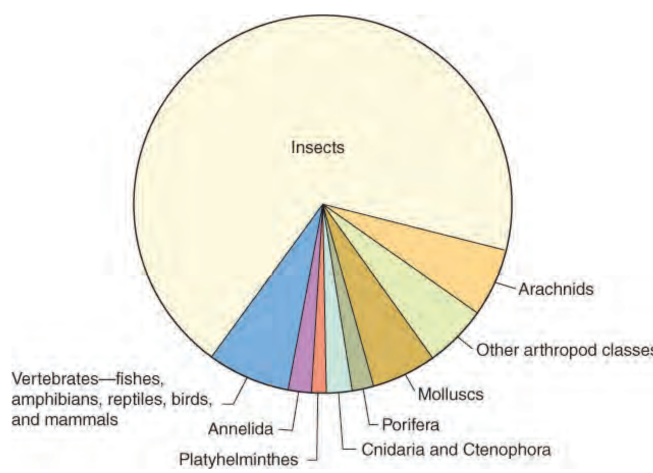

Figure 13.1 A biological nation unto themselves, the arthropods constitute far and away the largest and most diverse group of animals.

History of the Arthropods

The fossil record indicates that the first arthropods appeared in the primeval seas of the Precambrian over 600 million years ago. At some point in time and somewhere within in those ancient waters, the soft cuticle covering the segmented bodies of worm-like creatures began to harden as more proteins accumulated and the inert polysaccharide chitin was added. This developing cuticular exoskeleton offered its bearers a considerable number of benefits. A hardened cuticles offered more protection from predators; it allowed for jointed extensions on each segment to become appendages; it offered protection to joints, fostering strength in key muscle attachment areas, which, over time, became powerful levers, and it added great potential for speed of movement, including flight.

As natural selection drove the development of the exoskeleton, other changes took place in the bodies and life cycles of these protoarthropods in a process zoologists call "arthropodization." Today most zoologists judge that the modern arthropods resulting from this process represent the pinnacle of protostome development.

The phylogeny of the major extant arthropod subphyla had been an area of major interest and dispute and the validity of many of the arthropod groups suggested in earlier works is being questioned. **Figure 13.2** depicts the possible origin of the subphyla and classes comprising phylum Arthropoda as developed through a blending of traditional and cladistic interpretations.

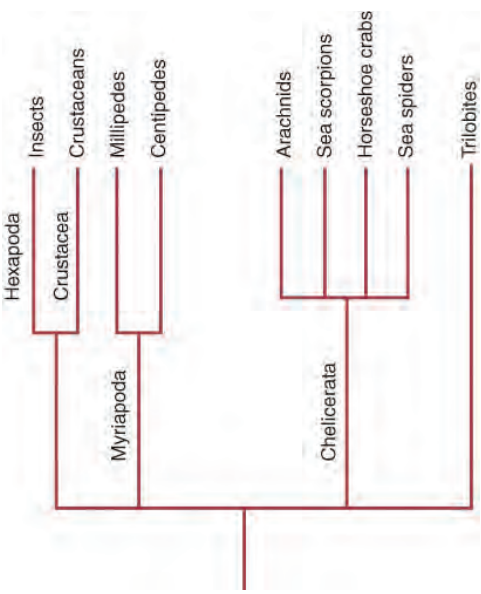

Figure 13.2 The possible origin of the subphyla and classes comprising phylum Arthropoda.

It has been long believed that the extinct Trilobitomorpha (trilobites) were ancestral to all other arthropods. Furthermore, the Crustacea have traditionally been considered as a monophyletic clade within the arthropods. The cladogram depicted in **Figure 13.3** represents this traditional view of arthropod phylogeny. Recent and ever-increasing data from molecular studies, developmental biology and new paleontological discoveries, however, have necessitated major revisions in our understanding of all things arthropod. As arthropod phylogeny is currently in a state of

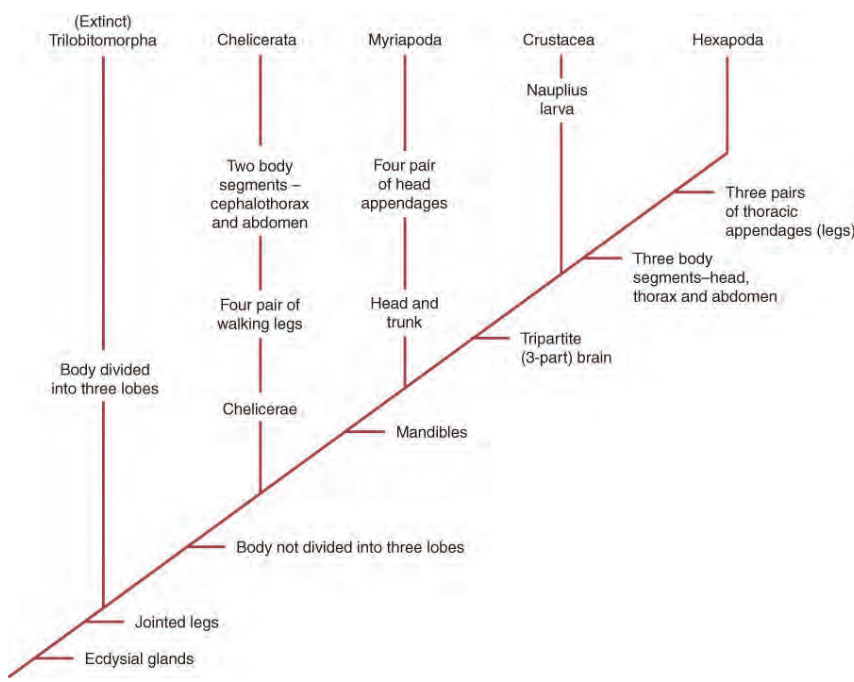

Figure 13.3 The possible phylogeny of the subphyla comprising phylum Arthropoda.

change and flux, we have opted to present a more traditional interpretation until such time as these matters become more settled.

Arthropods were some of the earliest animal forms to appear, and their lineage can be traced back to the Precambrian times some 600 million years ago. Interestingly, the earliest arthropod fossils from that time are similar to crustaceans, not trilobites as was originally hypothesized. It becomes increasingly clear that protocrustaceans and not trilobites were the ancestral stem from which other arthropods arose. If true, this means that the subphylum Crustacea is paraphyletic, not monophyletic.

Diversity and Classification

Currently, the number of identified arthropod species as listed in the literature varies from 874,000 to 1,170,000. Clearly, the total number of species of arthropods and the tremendous diversity of those species spurns our paltry attempts at classifying them. In our biological hubris we humans call the current era the age of mammals but the biological reality is that actually we live in the age of the arthropods. In a recent survey, zoologists identified over 2,000 species of insects on a *single tree* in the Amazon rain forest, many previously unknown to taxonomists. No other group of animals approaches this magnitude of species richness. It is in their individual numbers, however, that they are truly awe-inspiring. It has been suggested that if all the individual arthropods were placed in one gigantic heap and if in a single-file line all humans paraded past that pile with each human receiving their equal share of arthropods, each person would walk away with over 200 million individual arthropods. A simple calculation will yield an estimated number of total individual arthropods that defies comprehension.

In the past few decades, several specialists have suggested that arthropods are a polyphyletic group and that groups we herein consider as subphyla should each be raised to the rank of phylum. Our contention is that the evidence more strongly supports the view of Arthropoda as a monophyletic clade, and we retain its single-phylum status in this chapter.

Ignoring some minor taxa for clarity and considering only the taxa with extant members, we classify the arthropods as follows:

- Domain Eukarya
  - Kingdom Animalia
    - Subphylum Chelicerata
      - Class Arachnida—Spiders, scorpions, ticks, mites
      - Class Merostomata—Horseshoe crabs
    - Subphylum Myriapoda
      - Class Chilopoda—Centipedes
      - Class Diplopoda—Millipedes
    - Subphylum Hexapoda
      - Class Insecta—Insects
      - Class Entognatha—Springtails, bristletails, proturans

Subphylum Crustacea
- Class Malacostraca—Crabs, shrimps, lobsters, woodlice
- Class Branchiopoda—Brine shrimp, fairy shrimp
- Class Maxillopoda—Barnacles, copepods, fish lice
- Class Ostracoda—mussel shrimp

(A fifth subphylum—Trilobitomorpha—is represented only by several thousand species of extinct animals known as *trilobites*.)

Phylum Characteristics

Arthropods have successfully colonized virtually every habitat and exploited every imaginable life style and developmental strategy. They are adapted for life on land; in soil; in fresh, brackish, or salt water, and even in the air. Arthropods occur anywhere from heights of over 6,000 m (20,000 feet) on mountainsides to depths of over 9,000 m (30,000 feet) in the ocean and everywhere in-between.

They range in size from tiny mites and crustaceans less than 1 mm (0.04 inch) long, to the great Japanese spider crabs with leg spans exceeding 4 m (13 feet). And one species or another displays every type of symbiotic relationship and feeding mode known to biologists. Not only are they a morphologically large and diverse group, but environmentally they may be critical to the well-being of other living things around them, including humans. As the quote that opens this chapter indicates, it is quite possible and perhaps highly probable that the health of the worldwide web of life as we know it, at least terrestrially, depends on these magnificent armored animals.

The members of phylum Arthropoda exhibit the following general characteristics:

- Their segmented body is divided into **tagmata** (specialized body regions)
- The coelom is reduced to portions of the reproductive and excretory systems. Most of the body cavity consists of a **hemocoel** (sinuses or spaces within the tissues) filled with blood.
- They possess a cuticular **exoskeleton** composed of chitin, protein, and lipids. The chitinous skeleton is calcified in many groups. Growth occurs by the process of molting or **ecdysis** (Gr., *edkysis*, getting out) marked by the periodic shedding of the old exoskeleton and the formation of a new larger one.
- They possess jointed appendages from which their phylum name—arthropod (Gr. *arthros*, joint + *podos*, foot)—is derived. Ancestrally each true body segment bore a pair of jointed appendages but in modern arthropods, the number of appendages may be reduced, and they are often modified for specialized functions.
- They possess a complex muscle system attached to the exoskeleton for support and leverage. Functional cilia are absent.
- They possess a complete digestive system with mouthparts modified from ancestral appendages into structures adapted for different methods of feeding.
- The circulatory system is open with a dorsal heart, arteries, and hemocoel containing **hemolymph** (blood).

- **Coaxial glands** or **Malpighian tubules** serve as their excretory system. Coaxial glands are paired, and thin-walled spherical sacs bathed in the blood of body sinuses. Nitrogenous wastes are absorbed across the sacs, and excreted through long, convoluted tubules that empty at the base of the posterior appendages. Malpighian tubules are diverticula (pockets or pouches off the gut tract of arachnids adapted to dry environments). These tubules absorb nitrogenous wastes from the blood and then empty them into the gut tract where they are eliminated along with the digestive wastes.
- Gas exchange occurs through the body surface, gills, **tracheae** (air tubes), or **book lungs**. Tracheae are a series of branched, chitin-lined tubules that conduct gases to and from body tissues. This tubule system opens to the outside through holes called **spiracles** located along the ventrally or laterally along the abdomen. Some arachnids possess book lungs. These are paired invaginations of the ventral body wall that fold into a series of leaf-like **lamellae** (thin, flat plates or disks). Air enters the book lung through a slit-like opening and circulates between the lamellae. Respiratory gases diffuse between the blood moving among the lamellae and the air in the lung chamber.
- The nervous system is much like that of the annelids. It includes a dorsal brain made up of a ring around the gullet that attaches to a double nerve cord chain of ventral ganglia. Well-developed sense organs are present.
- The sexes are usually separate with paired reproductive organs and ducts and internal fertilization the norm; some types are capable of **parthenogenesis**. Development progresses through several stages in a process known as **metamorphosis**.

Subphylum and Class Characteristics

Each arthropod subphylum has evolved its own variations and modification on the basic theme.

Subphylum Chelicerata (Gr. *chele*, claw + keras, horn)

The following are characteristics of this subphylum:

- A body composed of two tagmata: the **prosoma** (cephalothorax) and the **opisthosoma** (abdomen). The cephalothorax represents a fusion of the head and thorax (trunk) and is often covered with a carapace-like dorsal shield. The abdomen is composed of up to 12 **somites** (sections) and a postsegmental **telson**. Antennae and wings are absent.
- **Uniramous** (unbranched) appendages attached to the cephalothorax including: **chelicerae** (anterior appendages of an arachnid often specialized as fangs.), **pedipalps** (specialized sensory appendages borne near the mouth), and four pairs (8) walking legs.
- An exoskeleton modified with projections, pores, and slits to accommodate a variety of mechanoreceptors and chemoreceptors (collectively known as **sensilla**), together with sensory and accessory cells. Vibration detectors are very important to spiders that use webs to trap prey as these detectors allow the spiders to determine both the size of the prey and its position on the web by

the vibrations the prey makes while struggling to free itself. The chemical sensitivity of arachnids is comparable to taste and smell in vertebrates. Arachnids also possess two or more pairs of eyes capable of detecting movement and changes in light intensity, and some hunting spiders have eyes capable of forming images.

Class Arachnida (Gr. *arachne*, spider)—spiders, scorpions, ticks, and mites.

The members of this class are some of the most misrepresented creatures in all the animal kingdom. Their reputation as grotesque and deadly creatures is vastly exaggerated. In truth, the majority of arachnids are either harmless or very beneficial to humans.

The arachnid body is divided into two tagmata (segments): cephalothorax (prosoma) and abdomen (opisthosoma). Attached to the cephalothorax are four pairs of legs, and around the mouth are cheliceras in the form of pinchers or fangs and a pair of pedipalps. The chelicerae serve to macerate food particles or inject poison and the leg-like pedipalps are adapted for prey capture, sensory detection, and reproductive functions depending on the species (**Figure 13.4**).

Spiders (Order Araneae) are the most familiar group of Arachnids. The cephalothorax (prosoma) of spiders bears chelicerae with poison glands and fangs and the characteristic four pair of walking legs. The pedipalps are leg-like and, in males, are modified for sperm transfer. A slender, waist-like **pedicel** attaches the cephalothorax to the abdomen, a trait that allows the spider to move the abdomen in all directions. The pedicel is the last segment (somite) of the cephalothorax and is lost in most other members of Arachnida.

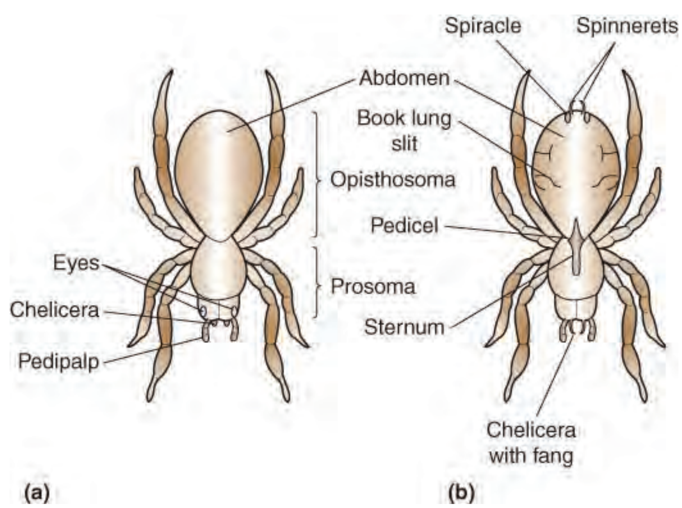

Figure 13.4 The Morphology of a Spider. (a) Dorsal view. (b) Ventral view

The abdomen has no appendages except for one to four modified pairs of conical telescoping organs called **spinnerets**, that produce **silk**. The protein that forms silk is stored as a liquid, but can be spun almost instantly into a solid thread without creating any clumps. The chemistry of this remarkable transformation are not completely understood but recent research in Germany and Sweden indicates that a high salt content and low acidity in the silk gland and spinning duct keeps the silk liquid, whereas reduced salt and higher acidity cause the proteins to link together rapidly during spinning.

All spiders possess spinnerets and make silk that they use for a wide variety of purposes: for safety draglines, for making durable egg cocoons, to line their homes, to trap their prey, and to immobilize their victims. In some species, males use silk to ritually immobilize the females before mating, and all male spiders make a special sperm-web or sperm-line that allows them to transfer the sperm from their genitals to their copulatory organs.

Spiders even use silk to fly. In a process of aerial dispersal known as **ballooning**, the newly hatched young (or spiderlings) of many large spiders, and the young and adults of some species can move to new areas via air currents. The spider first crawls to the top of vegetation or some other convenient launch pad, stands on "tiptoe" with abdomen pointing skyward and releases strands of silk from its spinnerets. When the breeze is judged sufficient, the spider lets go and as a wind surfer being towed by a speedboat, the spider becomes airborne. In this way, spiders may be carried for many, many miles. Spiders have been discovered over 4,500 m (14,000 feet) in the air and in the middle of the ocean 1,500 km (1,000 miles) from the nearest land. In 1839, Charles Darwin observed ballooning spiders aboard the H. M. S. Beagle when it was more than 60 miles off the coast of South America.

Flying in this manner, however, carries the risk of being eaten by insectivorous birds, such as swallows, or landing in the ocean or a lake. Nevertheless, large numbers of ballooning spiders manage to survive these risks as evidenced by their rapid colonization of fresh habitats such as freshly planted farm fields or newly formed volcanic islands.

Spider silk floating on the wind is known as **gossamer**. Gossamer can be seen on certain warm days late in the fall, when glinting in the sun, the sparkling threads wafting through the air present an almost magical scene. Gossamer has enthralled humans since ancient times. Pliny the Roman historian described a year in which it "rained wool" and over 200 years ago Charlotte Smith in her Sonnet LXIII appropriately entitled *The Gossamer* penned:

O'er faded heath flowers spun or thorny furze,
The filmy Gossamer is lightly spread:
Waving in every sighing air that stirs,
As Fairy fingers had entwined the threads.

Spiders are the largest group of arachnids, and they occur in greater numbers than most people realize. An undisturbed meadow, for example, may support as many as 2,250,000 spiders per acre (roughly the size of a football field). Spiders range in size from less than 0.5 mm (0.02 inch) in body length to a body length of 9 centimeters (3.6 inches) and leg spans as great as 25 cm (10 inches) in the case of some tarantulas.

Spiders are found all over the world, from the tropics to the poles and from the tops of mountains to underwater silken domes they supply with air. Found in ponds in Europe, northern Asia, and parts of Africa, the diving bell spider, *Argyroneta aquatica*, spends its entire life underwater. Because it must breathe air, this spider constructs a silk entrapment for a large bubble of air. The spider forms the initial bubble and replenishes the air in it periodically by rising abdomen first to the surface. There it traps a thin layer of air in the dense hairs on its abdomen and legs. It then dives back down transporting this trapped air to its larger bubble bell. This spider hunts small invertebrates, tadpoles, and frogs underwater, biting its prey to immobilize it and then swimming its prize back up and into the bell where it finishes devouring its meal.

Figure 13.5 Hidden behind a camouflaged flap, a trap door spider awaits the chance to explosively pounce on passing prey.

Most spiders feed on insects and other arthropods although a few, such as the tarantulas or "bird spiders," feed on small vertebrates as well. Spiders have an amazing array of prey catching strategies ranging from simple ambush to complex silk snares and

Figure 13.6 The golden orb spider (*Argiope*) patiently awaits for prey to blunder into its gossamer snare.

webs. Ambush hunters (or *mygalomorph spiders*) may leap from burrow entrances in the ground, in logs, or in tree trunks to capture passing prey. Some burrow dwellers lurk behind trapdoors, but others, like tarantulas and funnel-webs, will forage on the surface in the vicinity of the burrow at night (**Figure 13.5**). A few make sheet or curtain-like webs at their burrow entrances that impede both prey and predators. Others have silk or twig trip-line radiating out from the burrow entrance to alert the occupants to prey walking nearby. Others live as vagrants in leaf litter using vibration and touch to sense and ambush prey. Web-based hunters (or araneomorph spiders) construct webs from spider silk proteins (**Figure 13.6**).

Box 13.1
Spin Me a Tale, Weave Me a Web

Who has not reveled in the beauty of a spider web dripping with dew backlit by the early morning sun or recoiled fearfully when walking into an unexpected web? Those geometrically precise silky wonders we call spider webs rank among the most amazing constructs in the entire animal world. Spider webs are as diverse as they are beautiful:

Gum-footed webs. These webs consist of an irregular upper silk network with a closely woven, thimble-like retreat. From this upper network, vertical sticky catch threads run down to ground attachments ("gum feet"). These vertical lines are not only sticky, but they also provide strength and are under tension. When prey blunders into the array of sticky threads, its struggle breaks the lines at their weakest attachment points, and the lines contract upwards, lifting the prey off the ground. The spider then races down to deliver a quick bite and cover the struggling prey in loops of sticky capture silk.

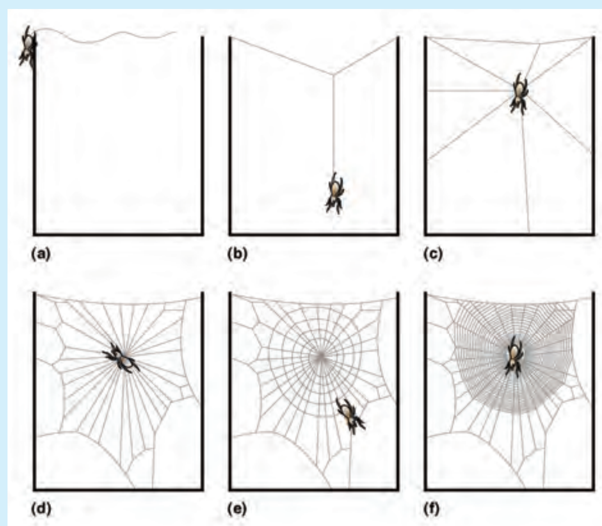

Figure 13.7 How does an orb spider spins its web?

Platform webs. These webs are constructed with a network of threads above a silk sheet (the "platform"). When insects fly into this network of threads, they are knocked down and fall through onto the silk sheet below where they are seized by the spider. In the center of the knockdown network, the spider will often place a loosely woven retreat constructed from curled leaves or some leaf fragments.

Orb webs. These webs are the familiar large, planar (flat, two-dimensional) catching surfaces we associate with spider webs. They are sticky, elastic, and virtually invisible to flying insects, especially at night (**Figure 13.7**). The spider first releases an initial silk line extruded from the spinnerets allowing air currents to carry it across a gap in the foliage to entangle twigs or leaves on the other side (Figure 13.7a). The spider moves back and forth across this bridge line laying down more silk each time gradually strengthening the line. It then drops from the center of the bridge line to attach a vertical line to the ground (Figure 13.7b). This basic Y-shaped framework provides the scaffolding on which the supporting outer frame-lines and the radial lines (the "spokes") are laid (Figure 13.7 c-d). The spiral lines are then added (Figure 13.7 e-f). A non-sticky, temporary spiral line is laid down first, starting from the center and running outwards. This temporary spiral gives the spider a working platform from which it then lays down the more closely spaced, permanent, sticky spiral starting from the periphery toward the center or hub. The spider removes, rolls up, and eats the temporary spiral as it lays down the sticky spiral. Not every web is constructed in precisely this same manner; variations exist.

The web of a typical orb weaver spider contains 6-18 m (20-60 feet) of silk and takes anywhere from 30 minutes to several hours to build, yet it only lasts one night. Each morning, the spider eats and processes the silk from the old web and sets about spinning another.

The largest orb webs in the world are spun by spiders in the genus *Nephila.* These amazing constructs may be 2 m (6 feet) in diameter and are capable of catching small birds and bats. And not only are these webs sticky and elastic, they are incredibly strong. A spider web absorbs the proportionally equal impact of a jet Figurehter plane slamming in for a landing on an aircraft carrier every time a small insect flies full speed into it.

Horizontal line webs. A number of unrelated spiders use these simplest of webs to catch their prey. Line webs consist of a single sticky line strung either horizontally or at an angle. The spider sits in wait with a front leg holding the line. Small insects, especially flies, either hit or attempt to land on the sticky line and become stuck. The spider then pounces.

Bolas webs. At night, the bolas spiders (Araneidae) emerge to hunt male moths, which is their only prey. To do this, they sit on a horizontal line and spin a short, single vertical line with a large dollop of sticky silk on its free end (the bolas). This line hangs from a leg down into an open space among the foliage. (This is so similar to the way we hold the line over our fingers when fishing to feel for fish bites that these spiders are also commonly called angling or fishing spiders.) While the spider sits and waits, it is exuding an air-borne scent (pheromone) that mimics that used by female moths to attract males. When male moths fly in towards the spider attracted by this false scent, the spider senses the vibrations of their wing beats through long sensitive hairs. The spider then starts to swing the bolas in a circle beneath it. The moth is hit by the bolas and covered in sticky silk. Like a fisherman "playing" the moth, the spider releases coiled reserve silk from within the bolas to prevent the line from breaking. Soon the spider reels the moth in, bites it, and begins feeding upon it. Taking this practice one step further the spiders in the genus *Caelenia* in Australia do not even bother with a bolas. Instead, they simply hang from a thread (presumably emitting pheromones) legs and jaws at the ready, and the moths fly straight into them.

Net webs. *Dinopis guatemalensis*, commonly known as the ogre-eyed spider because they have huge eyes that are extremely sensitive, hunts at night. These spiders build a small platform of strands they can hang from, and then they make a small silk net. They hold the net open and hang quietly waiting for a passing insect. If an insect passes on the ground, they will see it and throw the net over it, tugging it a few times to make sure the prey is well entangled. If an insect flies past, however, the spider can detect the vibrations caused by its flight and will throw the net upwards to catch it.

Knowing this, perhaps the next time you see a spider's web you will view it with a more appreciative eye for what you are seeing is among the most amazing of nature's constructs.

Adapted from Spiders. 2002. Retrieved from http//www. austmus.gov.au>.

Other araneomorph spiders no longer build snare webs. Such spiders also have a surprising range of prey-catching strategies. Many are ambush hunters like the flower or crab spiders (Thomisidae). These spiders sit in the open, on foliage, flowers, or bark actively adjusting their body colors to conceal them from both predator and prey (**Figure 13.8**). Using well-developed sight, vibration, and tactile senses, they target flies, bees, and butterflies alighting or walking nearby. A tropical species has gone about things a little differently. Its body color and shape resemble a drop of bird dung. To enhance its disguise, the spider also secretes a chemical scent that makes it smell like dung as well. This scent attracts unsuspecting dung-feeding flies and butterflies to these unusual spiders where they are summarily dispatched. Water spiders (Pisauridae) hunt along streams and pond banks. With their legs extended into the water film, they can sense vibrations caused by fallen insects or small fish and tadpoles. The assassin spiders (Mimetidae) are spider hunters that invade the webs of other spiders and use the fangs on their elongate and slender jaws to spear their spider prey.

Figure 13.8 Small insects beware. Danger in the form of a yellow crab spider *(Misumena vatia*) lurks in the beauty of a flower.

Spiders immobilize their prey in two ways: by biting and injecting paralyzing venom, and by silk swathing and wrapping. Most hunting spiders simply grab and hold their prey in the pedipalps and front legs while biting it. Many web builders use bands of swathing silk thrown over and around the entangled prey, often before biting it (although large web builders tend to bite first). Securely wrapped and immobilized prey is sometimes stored in the web to be eaten later.

Spider venom causes paralysis in the victim and helps with the chemical breakdown of prey tissues. When feeding, the spider regurgitates enzyme-rich stomach fluids over and into its prey. This external digestion by venom and stomach chemicals, often aided by the grinding, masticating action of the fangs and toothed jaw bases and maxillae, reduces the prey's body and tissues to a chitinous soup. This liquid is sucked up through the spider's tube-like mouth, aided by the action of the pumping stomach, leaving only the hard parts of the prey behind. Spiders are also capable of digesting their own silk, and as a result, many spiders eat their used webs. When a spider drops down on a single strand of silk and then returns, it will rapidly consume the strand of silk on its way back up. In fact, many nocturnal orb spinners destroy and eat their webs as dawn approaches and then rebuild them again each night. This recycling process is very efficient as it returns the silk protein to the silk glands where it is processed into new silk.

Mating of spiders involves elaborate rituals that include chemical, tactile, and/or visual signals to allow partners to identify each other and to allow the male to approach and inseminate the female without triggering a predatory response. Females may deposit pheromones on their webs or bodies to attract males whereas males may attract a female by plucking the strands of the female's web. The pattern of plucking is species specific and helps identify the gentleman caller as a potential mate and not a possible meal.

Once a male spider has matured, he leaves his web or burrow, charges his pedipalpal mating organs with sperm and wanders off on his nomadic search for a female. Seemingly random, male wandering is usually directed by the presence of silk or air-borne pheromones put out by the female.

Having found a female, the male must first establish his identity as a mate rather than ameal. Most do this through various forms of courtship, which can involve vibrational, chemical, tactile, and visual cues. Web builders tweak the female's web in a very specific pattern; wolf spiders drum the ground; keen-sighted jumping spiders "dance," providing a visual display to the female; funnel web spiders tap the burrow entrance silk and stroke the female's legs: male flower spiders also tap and stroke but take the additional precaution of tying the female down with a few silk lines. Despite these efforts, unreceptive females will react aggressively and chase the male away, nip off the odd leg or even capturing and eating the male in some instances.

Once identities have been established, and consent given, mating occurs. Sperm transmission is accomplished by the male inserting one or both palps into the female's genital opening, known as the **epigyne**. He then transfers his seminal fluid into the female by expanding the sinuses in his palp(s). Once the sperm is inside her, the female stores it in a chamber and only uses it during the egg-laying process when the eggs come into contact with the sperm for the first time. Once fertilized, the eggs are deposited into a silk cocoon that the female then hides or carries with her.

It is a common belief that male spiders, which are usually significantly smaller than the females will be killed after or even during mating. Males are sometimes killed by females but in at least some of these cases it is likely that the males are simply mistaken as prey. The risk of this happening is greater if the female is hungry. To counter this, some male spiders offer a "bribe" to the female in the form of a prey animal, prior to mating. Even in some species of black widow, which are named exactly for this belief of inevitable post-mating doom, the male may live in the female's web for some time without being harmed.

Harvestman or daddy long legs (Order Opiliones) are often confused with spiders. Harvestmen, however, lack the narrow waist of the spider with their cephalothorax and abdomen being so broadly joined as to appear as one oval structure (**Figure 13.9**). The body typically does not exceed 7 mm (0.25 inch) even in the largest species. The signature legs of harvestmen are exceedingly long and slender given the size of their body and can exceed 160 mm (6-7 inches) in span.

Harvestmen are omnivores feeding on small insects and all kinds of plant material and fungi; some are scavengers on dead animals and fecal matter. They have neither silk glands nor poison glands. They are mostly nocturnal and dark-colored, but there are a number of diurnal species are vividly colored in patterns of yellow, green, and black with varied reddish and blackish mottling. Mating involves direct copulation rather than the deposition of a spermatophore, as is the case with spiders.

Figure 13.9 Appearance can be deceiving as the harvestman (Opiliones) known commonly as daddy longlegs is not a true spider.

Mites and ticks (Order Acarina) are typically small in stature but of all arachnids, acarines have had the greatest impact on human health and welfare. Most acarines are minute being only about 0.08 to 1.00 mm (0.0003 to 0.04 inch), but some ticks and red velvet mites may reach lengths of 10 to 20 mm (0.4 to 0.8 inch). Acarines are specialists that live in practically every conceivable habitat, including the anuses of turtles, the digestive system of sea urchins, the lungs of snakes, the trachea of bees, the shafts of feathers, the fat of pigeons, and the eyeballs of fruit bats to name only a few. Aquatic mites live mostly in lakes, ponds, and puddles, often in densities of hundreds of thousands per cubic centimeter.

Mites are so small that a dozen of them could dance on the head of a pin. They are more likely, though, to dance on your face, which they do at night before they mate, before crawling back into your follicles by day to eat.

—Rob Dunn

In mites, the cephalothorax and abdomen are fused and covered by a single carapace. An anterior projection known as the **capitulum** carries the mouthparts. Chelicerae and pedipalps are variously modified for piercing, biting, anchoring, and sucking. Most adults have four pairs of legs, like other arachnids, but some species have fewer (**Figure 13.10**).

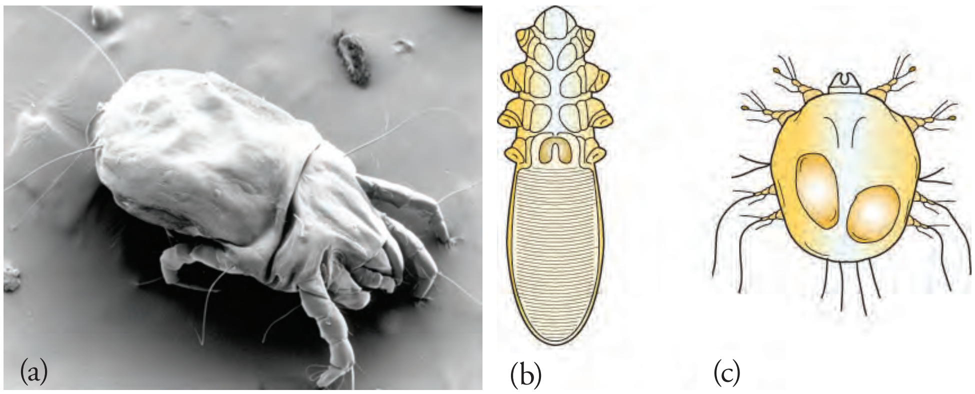

Figure 13.10 The Realm of Mites. (a) The household dust mite is a cosmopolitan inhabitant of mattresses, carpets, furniture, and bedding where they feed on flakes of shed human skin. Every gram of household dust contains nearly 200 of these tiny acarines. These mites are so ubiquitous that they have even been found on the space station. (b) Follicle mite (*Demodex*) displaying its characteristic stumpy legs. (c) A mange mite (*Sarcoptes scabiei*).

Free-living mites may be herbivores or scavengers. Scavenging mites are among the most common animals in soil and leaf litter. These mites include some pest species that feed on flour, dried fruit, hay, cheese, and animal fur. Predatory mites may be found in the soil. These monsters of the mite world have mouthparts resembling the various tools in a Swiss army knife. Some have smooth blades that snap together with tremendous force; others have jaws with sharklike teeth; still others stab and pierce with deadly sharp sabers.

Parasitic mites usually do not permanently attach to their host, but feed only a few hours or days and then drop to the ground. One mite, the notorious chigger or red bug (*Trombicula*) is a parasite during one of its larval stages on all groups of terrestrial vertebrates. The larval mite enzymatically breaks down its host's skin causing local inflammation and intense itching at the site of attack. The chigger larva drops from the host and then molts first into an immature nymph and then finally into an adult. Both nymphs and adults feed on insect eggs.

A few mites are permanent ectoparasites. The follicle mite, *Demodex folliculorum*, is a common (but harmless) inhabitant of mainly the facial hair follicles of most humans (including you, dear reader). Unlike the follicle mite, the human itch mite, *Sarcoptes scabies*, is more than a benign passenger on our bodies. Like a mole in your lawn, these mites tunnel through the epidermis of human skin releasing irritating secretions that cause intense itching. Females lay about 20 eggs each day. Such an infestation, known as **scabies**, may be acquired by contact with an infected individual.

Ticks are ectoparasites during their entire life cycle. Ticks may be up to 3 cm (1.2 inch) in length but otherwise are similar to mites (**Figure 13.11**). Hooked mouthparts are used to attach to their hosts and to feed on blood. Copulation occurs on the host, and after gorging with blood, females drop to the ground to lay eggs.

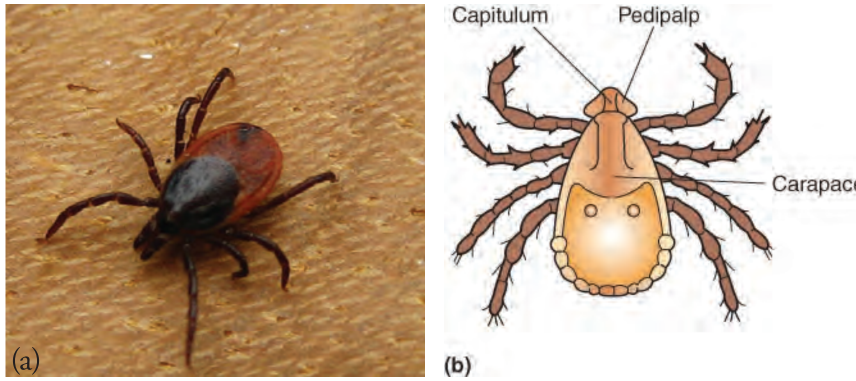

Figure 13.11 The Tick. (a) Magnified view of a tick on human skin. This tick has not yet implanted. (b) General morphology of a tick (*Dermacentor*).

Scorpions (Order Scorpionida) are characterized by a long tail (**metasoma**) comprising six segments bearing the sting (**aculeus**) at the end. The sting has a bulbous base that contains venom-producing glands and a hollow, sharp, barbed point (**Figure 13.12**). A few species of scorpions possess venom that is highly toxic to humans. The abdomen's front half, the **mesosoma**, is also made up of six segments. The first segment contains the sexual organs; the second segment bears a pair of featherlike sensory organs known as the **pectines**; the final four segments each contain a pair of book lungs. The chelicerae are short and used for grinding food. The pedipalps are extraordinarily large, and the last segment has been modified into grasping pinchers (**chela**).

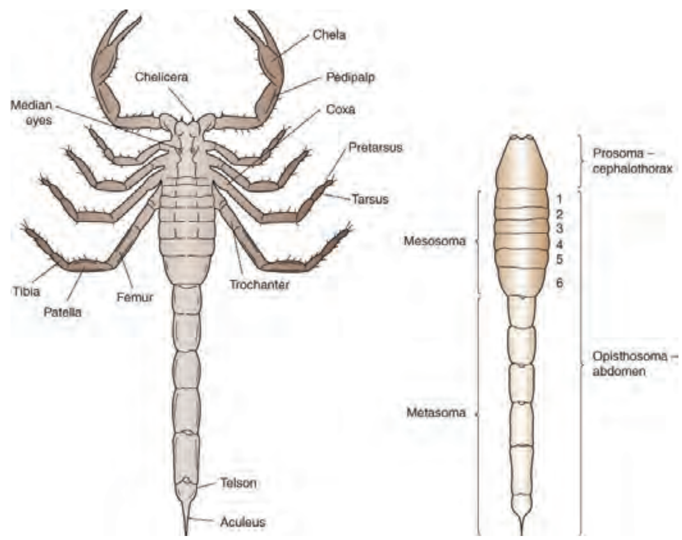

Figure 13.12 Morphology of a Scorpion-Dorsal View

Considered to be among the most ancient terrestrial arthropods and the most primitive arachnids, all the known species of scorpions today are terrestrial predators. These largest of arachnids reach lengths of about 18 cm (7 inches) and inhabit a variety of environments, particularly, deserts and tropical rain forests where some arboreal species occur. They are notably absent from colder regions of the world.

Scorpions are nocturnal opportunistic predators of small arthropods. They use their chela (pinchers) to catch their prey initially. Depending on the toxicity of their venom and the size of their claws, they will then either crush the prey or arch the metasoma up over their back and drive the sting into the prey injecting it with venom (**Figure 13.13**).

Figure 13.13 Emperor Scorpion *(Pandinus imperator)*. Stinger aside, scorpions superficially resemble crustaceans. The pinchers of a scorpion, however, are elongated and highly modified mouthparts, while the pinchers of a lobster or crayfish are modified legs.

Most arthropods are **oviparous**; females lay eggs that develop outside the body. Many scorpions and some other arthropods are **ovoviviparous**; development is internal, although large yolky eggs provide all the nourishment for development. Some scorpions, however, are **viviparous**, meaning that the mother provides nutrients to directly nourish the embryos. Development may take 1.5 years with 20 to 40 young being brooded inside the female's body. After being born one by one, the young are carried about on the mother's back until the young have undergone at least one molt.

Class Merostomata (Gr. *meros*, thigh + *stoma*, mouth)

This ancient class of arachnids known commonly as horseshoe crabs (Order Xiphosura) is represented by only four living species. One species, *Limulus polyphemus*, is widely distributed in the Atlantic Ocean and Gulf of Mexico (**Figure 13.14**). Scavenging sandy and muddy substrates for annelids, small molluscs, and other invertebrates, horseshoe crabs display a body form that has remained virtually unchanged for over 200 million years.

Figure 13.14 Dorsal view of two horseshoe crabs in shallow water. To see horseshoe crabs in such a setting is to literally peer back in time several hundred million years.

A hard, horseshoe-shaped carapace covers the prosoma of horseshoe crabs. The chelicerae, pedipalps, and first three pair of legs have pinchers and are used for walking and food handling (**Figure 13.15**). The fourth legs have leaf-like plates at their tips and are used for locomotion and digging.

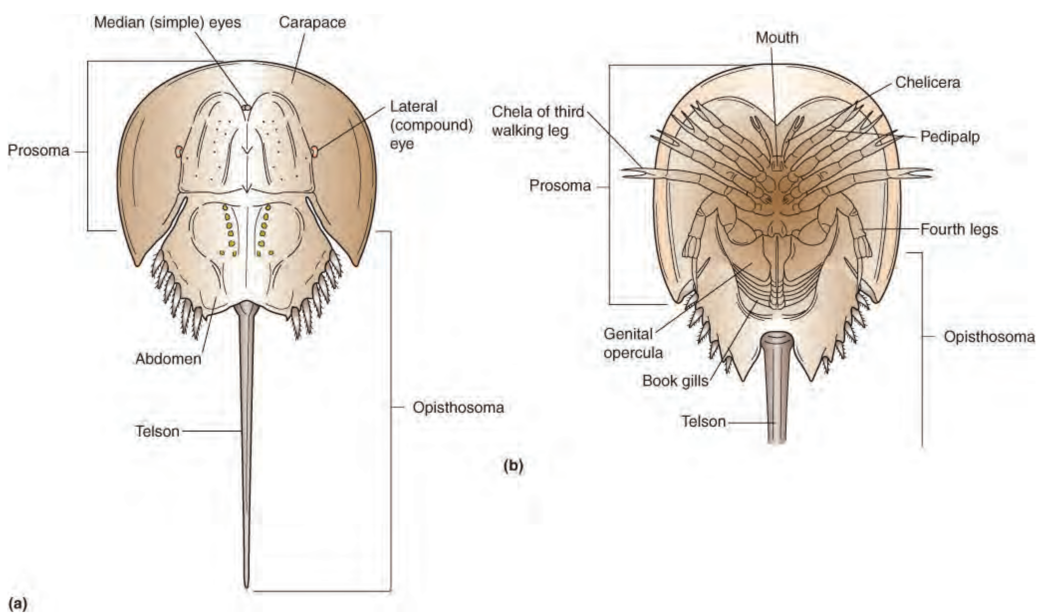

Figure 13.15 Morphology of a Horseshoe Crab (*Limulus polyphemus*). (a) Dorsal view. (b) Ventral view.

The opisthosoma of a horseshoe crab includes a long, unsegmented telson. If wave action flips a horseshoe crab over, the telson may be used to right the animal. The first pair of opisthosomal appendages called

genital opercula, covers the genital pores. The remaining five pairs of appendages are **book gills**. The name is derived from the resemblance of these plate-like gills to the pages of a closed book.

Horseshoe crabs are dioecious. During reproductive periods, males and females congregate, often in large numbers, in intertidal areas. The male mounts the female and grasps her with his pedipalps. The female excavates shallow depressions in the sand, and as she sheds eggs into the depressions, the male fertilizes them. Fertilized eggs are covered with sand and left to develop unattended.Although not detailed here, subphylum Chelicerata also includes the whip scorpions, sea spiders, pseudoscorpions, and a few others.

Subphylum Myriapoda (Gr. *myriad*, ten thousand + *podus*, foot)

This group consists of arthropods possessing:

- A body of two tagmata: head and trunk (abdomen). No carapace or wings present.
- A long and cylindrical abdomen consisting of many segments.
- Uniramous appendages.
- One or two pair of walking legs per segment.
- One pair of articulate (jointed and movable) antennae attached to the head segment.
- A few to many clustered ocelli (simple eyes) on the head segment.
- Mouthparts consisting of **mandibles** (jaws), **maxillules** (first maxillae), and **maxillae** (second maxillae). The second maxillae are fused into a single flap-like structure called the **labrum**.
- A gas exchange system composed of tracheae and spiracles.

Class Chilopoda (Gr. *cheilos*, lip + *podus*, foot)—centipedes (L. *centum*, hundred + *pede*, foot)

Centipedes are fast-moving venomous, predatory arthropods that have long bodies and many jointed legs (**Figure 13.16**). Mainly nocturnal, centipedes of the largest size and in most numbers are found in tropical climes, but their smaller kin are widely distributed in temperate zones as well.

Figure 13.16 The red centipede (*Scolopendra polymorpha*) is an agile predator. Centipedes are generalist predators and large varieties have been observed eating small amphibians, reptiles, birds, and mammals.

Centipedes range in size from 10-270 mm (0.4-10.6 inches) in length. The giant redheaded centipede (*Scolopendra heros)* is the largest North American species at about 153 mm (6 inches) long but the giant of the class is the Amazonian giant centipede (*Scolopendra gigantea*) measuring in at over 30 cm (12 inches). This goliath is known to eat rodents, spiders, and even bats that it catches in midflight.

The body of a centipede is dorsoventrally flattened and consists of 15 to 173 segments with one pair of walking legs per segment. The last pair of legs is usually modified into long sensory appendages. The first anterior trunk segment has been modified into a pair of venomous poison fangs (**maxillipeds**) that are used both for defense and for capturing and paralyzing prey.

The head has a pair of jointed antennae, jaw-like mandibles, and other characteristic mouthparts (**Figure 13.17**).

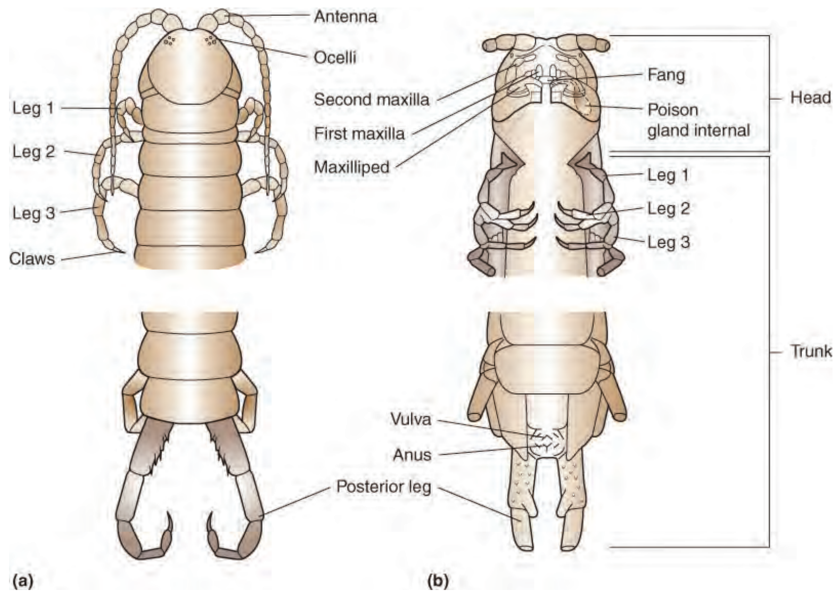

Figure 13.17 Morphology of a Centipede. (a) Dorsal view. (b) Ventral view.

Centipedes are fast and agile predators feeding on small arthropods, earthworms, and snails. The poison claws kill or immobilize prey. The poison claws, along with mouth appendages, hold the prey as mandibles chew and ingest the food. Some species are highly venomous and can produce very painful bites but only a few human deaths have ever been recorded from the bite of a centipede. The bite of a small centipede such as those found in temperate areas may be similar to a bee sting, but the bite of a large tropical species is excruciatingly painful.

Centipede reproduction may involve courtship displays in which the male lays down a silk web using glands at the posterior tip of the body. He places a spermatophore in the web, which the female picks up and introduces into her genital opening. Eggs are fertilized as they are laid. A female may brood and guard the eggs by wrapping her body around them, or they may be deposited in the soil.

Class Diplopoda (Gr. *diplos*, twofold + *podus*, foot)—Millipedes (L. *milli*, thousand + *pede*, foot).

Millipedes are relatively common leaf litter and soil animals that occur in most parts of the world (**Figure 13.18**).

Millipedes range in size from 2 mm to 300 mm (0.08-12 inches) in length. *Paeromopus paniculus*, the largest North American millipede measures in at about 160 mm (6.3 inches). Each segment of a millipede is two segments fused together resulting in two pairs of walking legs per segment. Most millipedes normally have only 100 to 300 total legs, not a thousand as their name would suggest. *Illacme plenipes*, first identified in 1926 but rediscovered recently inhabiting a tiny patch of San Benito County, California, can possess up to 750 legs or 375 pairs. Although their many legs are individually small, as a group they are powerful allowing millipedes to literally bulldoze their way through soil, leaf litter, and rotting wood.

The head of a millipede has two sections of ocelli, two antennae, two mandibles, and two maxillae (**Figure. 13.19**). The antennae are relatively short being composed of only eight segments. They have between 4 and 90 ocelli depending on the species, but some types have none and are totally blind. The millipede mouth consists of a pair of mandibles that are armed with a few blunt teeth and a lower jaw-like plate known as a **gnathochilarium**. Usually nocturnal, millipedes feed on decaying plant matter using their mandibles in a chewing or scraping fashion. A few millipedes have mouthparts adapted for sucking plant juices.

Figure 13.18 This red and black millipede (*Aphistogoniulus sp)* is a slow-moving detritovore in the Madagascar rain forest.

Millipedes roll into a ball when threatened with desiccation or when disturbed. This balling strategy alone, however, is not enough to deter the many predators seeking to dine on millipedes. To further protect themselves, millipedes have armed themselves with **repugnatorial glands** that produce defensive secretions that are foul tasting and sometimes either poisonous or sedative in nature depending on the species. Interestingly, lemurs have been observed intentionally irritating millipedes in order to rub these defensive chemicals on themselves to repel insects, and possibly produce a psychoactive effect (getting "high"?). As far as humans are concerned, this chemical brew is fairly harmless usually causing only minor effects—discoloration, pain, itching, and blisters—on the skin. Eye exposure causes general eye irritation and potentially more serious effects, such as conjunctivitis and keratitis. Many millipedes are quite docile and may safely be kept as pets and handled without risk of injury. With the proper caging and feeding, some pet millipedes can live up to seven years and grow to be as long as 38 cm (15 inches).

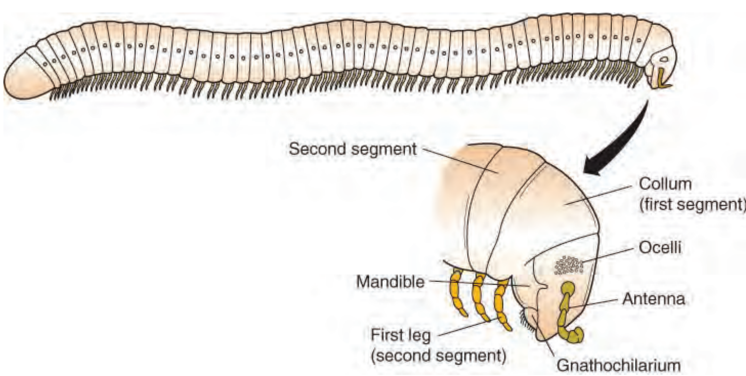

Figure 13.19 Morphology of a millipede showing an enlarged lateral view of the head.

Male millipedes transfer sperm to the female with modified trunk appendages, called **gonopods**, or in spermatophores. Female millipedes make an underground nest into which they lay their eggs. The nest is made by excreting soil they have eaten and using anal folds to shape it as required. The eggs are fertilized as they are laid.

Although not detailed here, subphylum Myriapoda also contains class Symphyla (symphylans) and class Pauropoda (pauropodans).

Subphylum Hexapoda (Gr. *hexa,* six + *podus*, foot)

Characteristics of this subphylum are:

- A body of three tagmata: head, thorax, abdomen without a carapace.
- Uniramous appendages.
- Three pairs of walking legs attached to the thorax. Wings are present in many species.
- A head bearing a single pair of jointed antennae, mouthparts consisting of mandibles, maxilla, labium, and labrum, and compound eyes. Some groups possess ocelli as well.
- A gas exchange system consisting of tracheae and spiracles.
- An excretory system consisting of Malpighian tubules.

Class Insecta (L. *insectus*, to cut up)

One of the grandest groups of animals on the planet must surely be the insects. They exist in numbers that defy comprehension and their diversity of forms staggers the imagination.

> *We hope that when the insects take over the world, they will remember with gratitude how we took them along on all our picnics.*
>
> —Bill Vaughn

Over a million insect species have been catalogued—more than all other animal groups combined. Recent studies indicate that there may be anywhere from six to ten million additional insect species awaiting discovery. This multitude of species is organized into approximately 32 orders, far too many for us to examine each separately (**Figure 13.20**).

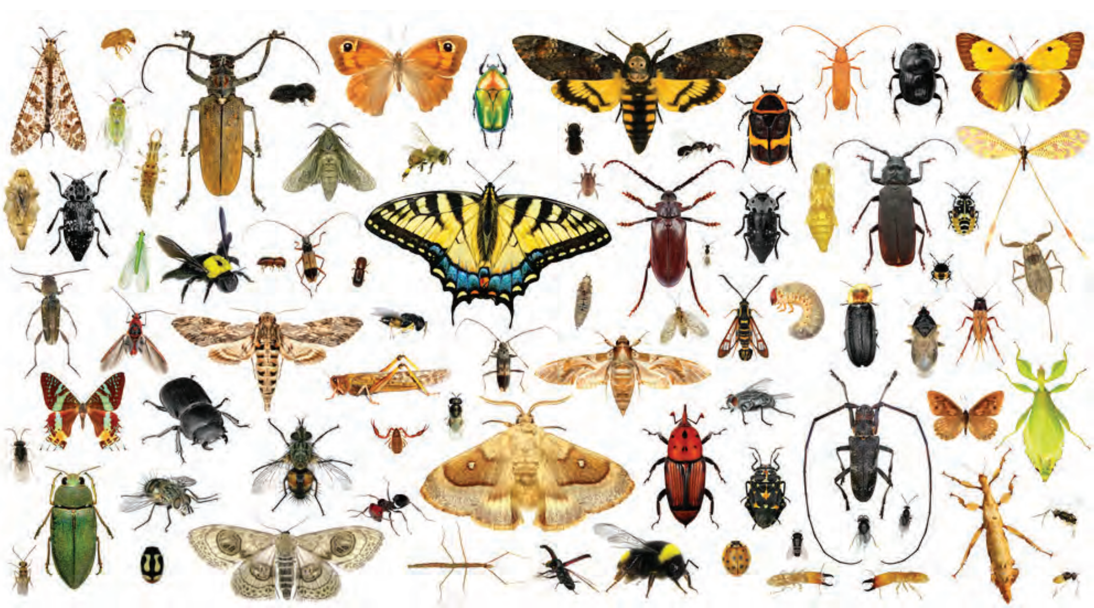

Figure 13.20 A few representatives of the 32 orders of insects. There are more species of insects than all other species of animals combined.

A spectacular explosion of evolutionary radiation has equipped the insects to inhabit nearly every conceivable nook and cranny of terrestrial and freshwater aquatic systems, although none is considered truly marine. They even populate the air. In fact, studies have revealed the existence of "aerial plankton" consisting of minute insects and other arthropods, extending to altitudes as high as 4,267 m (14,000 feet). Insects have become so environmentally successful and so vitally intertwined into the fabric of life in nearly all habitats that their removal might possibly result in collapse of those systems.

Insects range in size from the fairyfly (*Dicopomorpha echmepterygis*) at 0.139 mm (0.0055 inch) long and able to fly through the eye of a needle to the stick insect (*Phobaeticus serratipes*) at 55.5 cm (22 inches). The heaviest larva belongs to the Goliath beetle (*Goliathus goliatus)* at 115 gr (4.1 oz) whereas the heaviest adult insect recorded so far has been a female Little Barrier Island Weta (*Deinacrida heteracantha*) at 71 gr (2.5 oz). It is likely, however, that the adult elephant beetles (*Megasoma elephas* and *Megasoma actaeon*) that commonly exceed 50 gr (1.7 oz) could reach a larger weight.

The body of an insect is divided into three tagmata: head, thorax, and abdomen (**Figure 13.21**). The head segment bears one pair of antennae, one pair of large compound eyes and zero, two, or three ocelli as well as mouthparts. The thorax consists of three segments that from anterior to posterior are the **prothorax**, the **mesothorax**, and the **metathorax**. One pair of walking legs is attached to each thoracic segment. Wings, when present, attach dorsolaterally to the margin between the mesothorax and the metathorax. The thorax also contains two pairs of spiracles opening into the tracheal system. Most insects have 10 to 11 abdominal segments, each of which has a pair of spiracles. The abdomen also houses most of the digestive, respiratory, excretory, and reproductive organs.

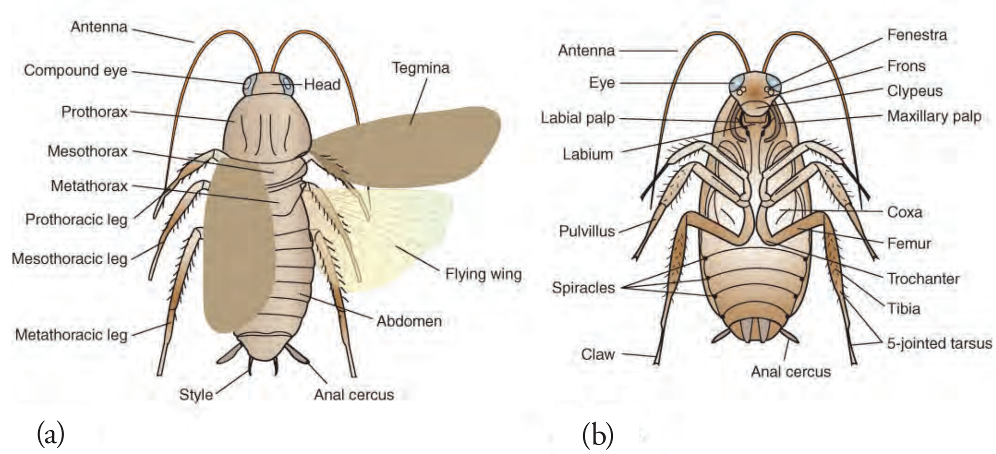

Figure 13.21 Morphology of a common insect—the cockroach. (a) Dorsal view. (b) Ventral view.

Adaptation to a multitude of different habitats and lifestyles has resulted in many variations on basic arthropod mouthparts plus the challenges of competition have resulted in every conceivable kind of diet being exploited by insects. The herbivores grind and chew plants and suck their juices whereas the carnivores rip, tear, and suck the life out of other small animals. Many labor as scavengers in rotting and putrid offal whereas others have adapted to a symbiotic existence on, in, or around other creatures.

Most insects lead short lives as adults and congregate only to find suitable partners and mate or possibly perform some other survival function. The **social insects** live together in large, ordered groups known as **colonies**, however, through a phenomenon known as **eusociality**. In a eusocial society, sterile members of the species (**worker caste**) carry out specialized tasks, effectively caring for the **reproductive caste** (queens and drones). Eusociality in insects is found in the orders Hymenoperta—ants (all species), bees (few species), and wasps (few species)—and Isopetera—termites(all species)—and to a lesser extent Homoptera—aphids and thrips. The different castes within the society are often modified from each other anatomically and structurally as well as behaviorally so as to perform the survival tasks inherent with their caste (**Figure 13.22**).

Some primal termite knocked on wood
And tasted it, and found it good!
And that is why your Cousin May
Fell through the parlor floor today.
—Ogden Nash

Some large colonies of social insects may contain as many individuals as there are people in a large human-constructed city. How are all these individuals to be controlled and coordinated? In a word—biochemistry. The queen produces pheromones that attendant workers pick up as they lick and groom the queen. As these workers then lick other workers and so on the chemical instructions issued by the queen quickly spread through the colony. It is the many chemical nuances of the pheromones produced by the queen coupled with the genetic programming of each individual that keep the colony humming along, almost as if it were one single organism.

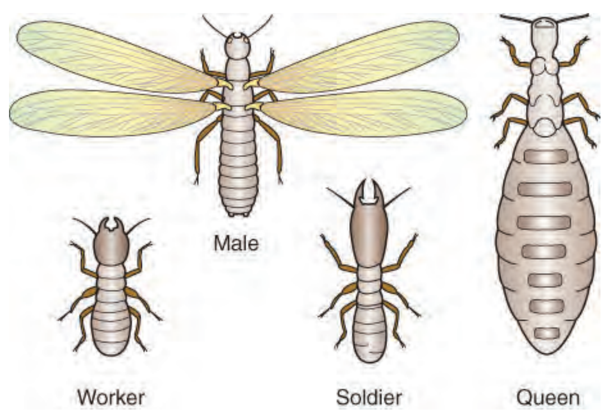

Figure 13.22 Castes of the eastern subterranean termite (*Reticulitermes flavipes*) the most common North American termite.

Insect societies demonstrate a number of peculiarities:

- *Slavery*. Slavery is wide-spread among ants. Ant slavery is biological in nature and unique because it is usually between species, unlike human slavery in which we enslave only own species doing so for cultural and/or economic gains. Invading parties of ants will seek out the colonies of other ants in an attempt to capture their larvae and pupae. Captured immatures are carried back to the invaders' nest where they acquire the nest odor eventually developing into adults that act as workers for their adopted colony. Some slaver species have become so dependent on their slave that they are no longer able to collect food or feed themselves or their immatures and would thus perish without the slave workers to perform these tasks for them.
- *Warfare*. Waging war against their own and other species, some ants engage in restless aggression, territorial conquest, and genocidal annihilation of neighboring colonies. As an example, consider the interplay between the introduced non-native Fire Ant, *Solenopsis invicta* and the native wood-

land ant, *Pheidole dentata*. The fire ants have colonies hundreds of times larger than the woodland ant and whenever they discover a woodland colony they completely destroy it. Yet woodland ant colonies are abundant around fire ants. Whenever a woodland worker discovers a fire ant scout, woodland soldiers are so rapidly deployed that the fire ant scout rarely makes it back alive to its own colony. The woodland soldiers rely on large mandibles to cut their fire ant opponent to pieces. Woodland ants, however, are no match for fire ants en masse so if their nest is discovered, the woodland soldiers fall back to form a short perimeter around the nest and sacrifice themselves in battle in an attempt to keep the fire ants at bay temporarily while the colony evacuates the nest. After the battle and the fire ants have departed, the woodland ants will return and reclaim their nest.

The evolution of social behavior involving many individuals leaving no offspring and sacrificing individuals for the perpetuation of the colony has puzzled evolutionists for many years. It may be explained by the concepts of kin selection and altruism.

- *Ranching and Farming*. Some species of ants will herd aphids like livestock. The ants will place the aphids on plants and protect the aphids as they feed on plant juices. The ants then "milk the cows" by stroking the aphids with their antennae. This stimulates the aphids to release a drop of sweet and nourishing honeydew from the tip of their abdomen. The ants will ingest the honeydew and carry it back to the colony to feed others through regurgitation.

  Leaf cutter ants and some termites are gardeners. The workers collect plant material that they bring back into the nest. This plant material is not eaten directly but instead serves as compost for growing a type of fungus that is the actual food for the colony.
- *Ventilation and Temperature Regulation*. In arid tropical savannas, termites construct extremely large and complex concretions that house their colonies. Standing anywhere from 6 to 9 m (20 to 30 feet) tall, these mounds are exposed to blazing sun and low humidity, conditions that spell nearly instant doom to soft-bodied termites and the fungi gardens they depend upon for food. If one sends miniature sensors down into these mounds, however, the temperature and humidity levels within are ideal for termite survival, and they remain so often varying only ±1° C over the course of 24 hours. Opening these mounds reveals not a haphazard pile of dirt, but a complicated internal architecture: a capricious central chimney from which radiates a complex network of passages.

  The mound is not the actual habitation for the millions of termites that build it. Their residence is in a nest below the mound, a spherical underground city about 2 m (6-7 feet) in diameter. These mounds represent an enormous expenditure of energy and time; a mound contains, on the average, about five cubic yards of soils and takes a mature colony about one year to build. The secret lies with the wind. By building the mound upward into stiffer breezes higher off the ground, the termites harness the wind to drive air movements in the mound's tunnels. The flow of the wind pushes air through the porous soil on the windward side and out on the leeward side, allowing the nest atmosphere to mix with fresh air from the outside. Bees also collectively regulate the hive temperature. When the weather is cold, they cluster into compact balls and shiver, warming the hive. When the weather is hot, workers fan their wings at the entrance of the hive, cooling it.

- *Communication*. Command and coordination do not always come from the queen in the form of chemical messages. Visual cues can also play a role in certain situations as exemplified by the **waggle dance** of the honeybee (Figure 5.15). First translated and understood by Austrian ethologist Karl von Frisch, the waggle dance is a peculiar Figure-eight movement performed by successful foragers through which they share with their hive mates information about the direction and distance to patches of flowers yielding nectar and/or pollen and to water sources. A waggle dance consists of one to 100 or more Figure-eight circuits, each of which consists of two phases: the waggle phase and the return phase. The direction and duration of waggle runs are closely related with the direction and distance of the patch of flowers being advertised by the dancing bee. Flowers located directly in line with the sun are represented by waggle runs in an upward direction on vertical combs, and any angle to the right or left of the sun is coded by a corresponding angle to the right or left of the upward direction of the waggle runs. The farther the target, the longer the waggle phase, with a rate of increase of about 75 milliseconds per 100 meters. Amazingly, waggle dancing bees that have been in the hive for an extended time adjust the angle of their dance to accommodate the changing direction of the sun. Therefore, bees that follow the waggle run of the dance are still correctly led to the food source even though its angle relative to the sun has changed.

One of the main reasons for the tremendous environmental success enjoyed by insects is their tremendous reproductive potential. The life of the adult insect is geared primarily to reproduction. For instance, in her lifetime, a single queen honeybee is capable of laying over 1 million eggs whereas the queens of some African termite species are reputed to lay over 30,000 eggs a day!

Insects are dioecious and most often fertilize their eggs internally. For reproduction to occur, however, the two parties must first find each other. In butterflies, the color of the female in flight can attract a male of the same species. In mayflies and certain midges, males dance in swarms to provide a visual attraction for females. In certain beetles, such as fireflies and glowworms, parts of the fat body in the female have become modified to form a luminous, glowing organ that attracts the male. Male crickets, grasshoppers, cicadas, and katydids attract females by their chirping songs, and the male mosquito is lured to the sound emitted by the female in flight. However, the most important element in mate attraction is odor. Depending on the species, the male and/or the female secrete odorous pheromones that serve as specific attractants to the opposite sex.

Males most often place their sperm into their mate's vagina during mating. In some insects, however, sperm are contained within spermatophores (packets) allowing for either direct placement at copulation or substratum placement for later collection by the female. For example, male silverfish leave a spermatophore on the ground that the female then takes into her body via her ovipositor to fertilize the eggs. It is most common for female insects to store enough extra sperm in their seminal receptacle to fertilize multiple batches of eggs. Eggs are fertilized as they leave the female and are usually laid near or on the food supply. Tiger moths, for example, will search out pigweeds on which to lay their eggs whereas the monarch butterfly prefers milkweed plants, and the sphinx moth tomato or tobacco plants. Females may use structures known as **ovipositors** to place their eggs into or on some substrate. The ichneumon wasp uses her extraordinarily long ovipositor to inject her eggs into the larva of other insects where they develop into parasites devouring the host from within. Her favorite targets are the larvae of the wood wasp or wood-boring beetles. The fact that these larvae live inside twigs and branches does not deter the female ichneumon wasp. With unerring accuracy and precision, she uses her long ovipositor to penetrate 1 to 2 cm (0.4 to 0.8 inch) of wood to find a host larva and inject her eggs into it.

Most insects experience a metamorphosis (change) at the postembryonic development stage. Insect development results in a divergence of immature and adult body forms and habits. Immature stages are a time of growth and accumulation of reserves for the transition to adulthood. The mature stage, on the other hand, is associated with reproduction and dispersal. The degree of divergence between immatures and adults can be classified into three (sometimes four) categories.

In insects that display **ametabolous metamorphosis** (Gr. *a*, without + *metabolos*, change), the primary differences between adults and larvae are body size and sexual maturity. Both adults and larvae are wingless and unlike most other insects, molting continues after sexual maturity. Silverfish (order Thysanura) exhibit ametabolous metamorphosis.

Hemimetabolous (incomplete) **metamorphosis** (Gr. *hemi*, half) is characterized by a species-specific number of molts or **instars** between egg and adult stages, during which immatures gradually take on the adult form. The external wings develop, adult body size and proportions are attained, and the sexual organs develop during this time. Immatures are called **nymphs** (**Figure 13.23**). Grasshoppers (order Orthoptera) and chinch bugs (order Hemiptera) exhibit hemimetabolous metamorphosis. When immature stages are aquatic, they often have gills (e.g. mayflies [order Ephemeroptera}and dragonflies, [order Odonata]) and are called **naiads**.

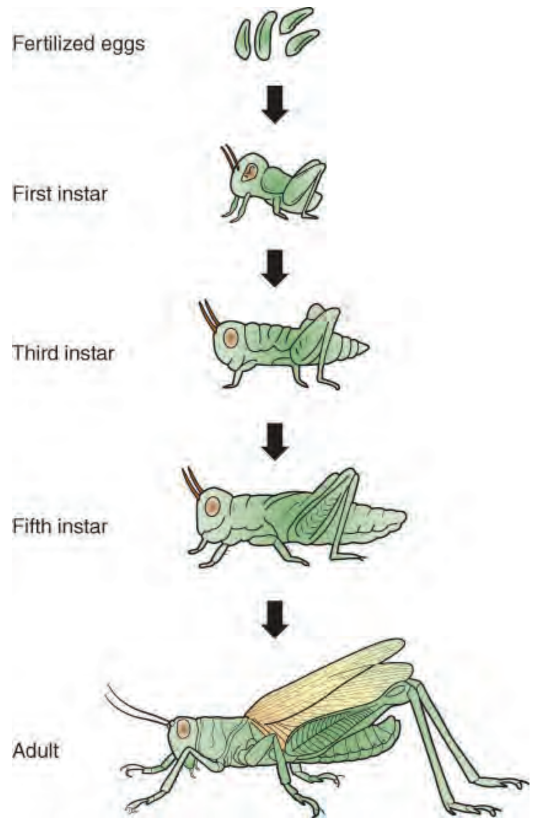

Figure 13.23 Hemimetabolous development (incomplete metamorphosis) in the grasshopper. Each development stage is referred to as an instar.

In **holometabolous** (complete) **metamorphosis** (Gr. *holos*, whole), the immatures are very different from the adults in body form, behavior, and habitat (**Figure 13.24**). The number of larval instars is species-specific, and the last larval molt forms the **pupa**. The pupa is a time of radical cellular change, during which all characteristics of the adult insect develop. A protective case may enclose the pupal stage. Some moths (order Lepidoptera) spin a silken **cocoon** around the pupa whereas the **chrysalis** of butterflies (order Lepidoptera) and the **puparium** of flies (order Diptera), are the last larval exoskeletons and are retained through the pupal stage. The final molt to the adult stage usually occurs within the cocoon, chrysalis, or puparium, and the adult, known as an **imago**, then exits.

Metamorphosis in insects is controlled and regulated by a complex interaction of hormones produced in glands and neurosecretory cells located in the prothorax and brain. **Neurosecretory cells** secrete hormones that stimulate the neurohemal **corpus cardiac** organs to release **prothoraciotropic hormone** (PTTH). Carried in the hemolymph, PTTH in turn stimulates the **prothoracic glands** to release **ecdysteroids** (molting hormones). The ecdysteroids trigger a cascade of physiological events that culminate in molting (ecdysis). All the while the neurohemal **corpora allata** organs, also regulated by neurosecretory cells, secrete **juvenile**

hormone (JH) during larval or nymphal instars, inhibiting the transition to adulthood, then reactivating once the insect is sexually mature and ready for reproduction.

When the molting hormone **ecdysone** initiates a molt in an early larval instar, the accompanying concentration of juvenile hormone is high. Such a high concentration ensures a smaller larva-to-larger larva molt. After the last larval instar is reached, the corpora allata ceases to secrete juvenile hormone. Low concentrations of juvenile hormone result in a larva-to-pupa molt. Finally, when the pupa is ready to molt, juvenile hormone is absent altogether from the hemolymph, and this deficiency leads to a final pupa-to-adult molt.

A number of insect groups, particularly those living in seasonally changing environments will undergo a process known as **parthenogenesis** (Gr. *parthenos*, virgin + *genesis*, creation or birth). Parthenogenesis is a form of asexual reproduction in which females produce eggs that can develop without fertilization. In some groups (e.g., honeybees and aphids), fertilized eggs develop into females, and unfertilized (parthenogenetic) eggs develop into males.

Subphylum Crustacea (L. *crustaceus*, hard shelled)

This subphylum is characterized by arthropods possessing:

- Sixteen to 20 segments, with some forms having 60 segments or more.
- An exoskeleton that is more pronounced and generally thicker and heavier than other taxa of arthropods.
- Two or three tagmata: cephalothorax with a shield-like carapace and abdomen or head, thorax, and abdomen.
- **Biramous** (branched) appendages.
- Head appendages consisting of two pairs of antennae, a pair of mandibles, two pairs of maxillae, and one pair of compound eyes.
- Both simple ocelli and compound eyes are often elevated on stalks.
- Gas exchange typically occurs across gills.
- Excretion by true nephridial structures.
- A developmental stage known as a **nauplius larva** that is characterized by the presence of three pair of head appendages.

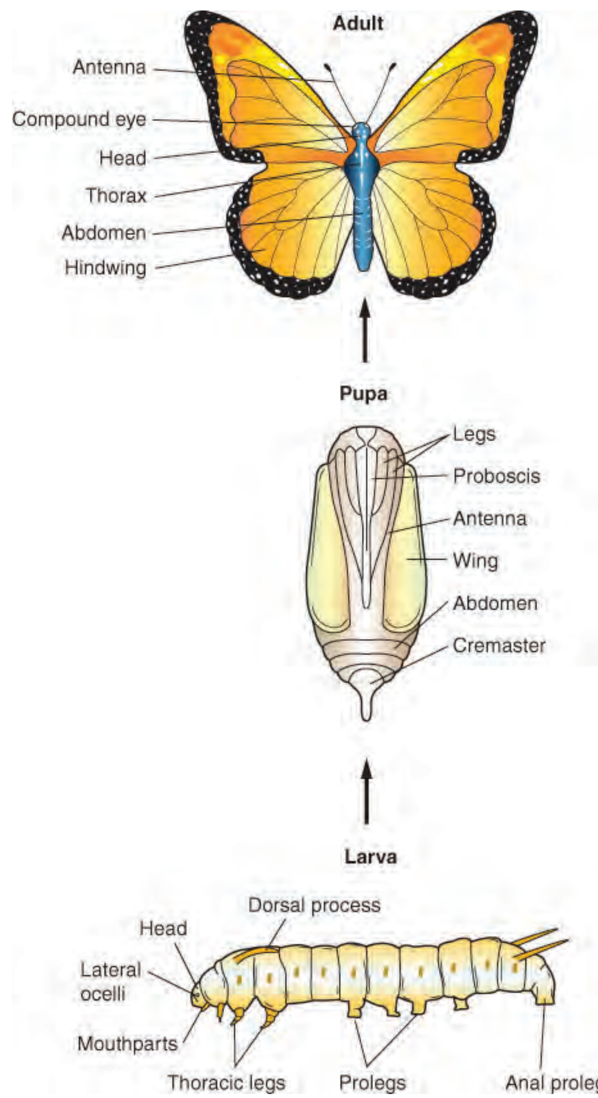

Figure 13.24 Holometabolous development (complete metamorphosis) in a butterfly. The pupa is encased in a chrysalis which is attached to a leaf or a twig by the cremaster.

Because crustaceans exist in large numbers and demonstrate a range of morphological diversity that exceeds even insects, crafting a satisfactory description of the group is difficult.

> *Creatures of such unsuspected importance and numbers stir our imagination and invite us to find out more about them. But let us beware of lightly following our curiosity in this matter. The attempt to obtain a clear-cut definition of the class Crustacea has left many a student bewildered.*
>
> —Waldo L. Schmitt

Crustaceans are found at all depths in every marine, brackish, and freshwater environment known; they are so pervasive in marine habitats in particular that they are often referred to as "insects of the sea." Some, however, such as terrestrial crabs and isopods, have adapted to at least a semiterrestrial life, and a few taxa, collectively known as "crustacean lice," are parasitic.

Although the insects still rule in terms of numbers, the crustaceans are the most diverse in terms of form. The largest of the crustaceans include the giant Japanese spider crab (*Macrocheira kaempferi*) with its four-meter (13 foot) leg span, and the American lobster (*Homarus americanus*) at an impressive 20 kilograms (44 pounds) in weight. On the other end of this spectrum are tiny interstitial and planktonic forms that never grow larger than 0.25 mm (0.01 inch), even as adults. Although certain varieties move along the bottom, others burrow, and some, such as barnacles, are sessile, spending their life attached head down. Swimming upright or upside down, microscopic crustaceans float along in both salt and fresh water environments. The tiny, delicate members of the copepod genus *Calanus* are among the most abundant animals in the world.

Crustaceans take on many different habits and adaptations in their feeding. Those that practice suspension feeding filter plankton, bacteria, and detritus from the water whereas the predatory forms consume larvae of all types, worms, other crustaceans, snails, and fishes, and scavengers eat dead plant and animal material. Numerous types can alter the way in which they feed as their environment and availability of food change. A crayfish routinely captures and devours small invertebrates, worms, and fish, browses on water plants, or consumes decaying matter in the course of its daily survival.

Among crustacean predators, none is more heavily armed than the colorful mantis shrimp (order Stomatopoda). At about 17 cm (7 inches) long and neither true mantis nor true shrimp but superficially resembling both, these crustaceans are armed with specialized forelimbs called **raptorial claws**. These highly modified appendages are either spear-like and armed with spiny appendages topped with barbed tips for stabbing and snagging prey or club-like for bludgeoning and smashing a potential meal (**Figure 13.25**). To attack, the mantis shrimp latches the limb so it cannot move. It then contracts the muscles as much as possible storing an amazing amount of energy in a special saddle-shaped spring that due to its shape, can distribute huge loads over its surface without buckling (similar to a coiled jack-

Figure 13.25 This female mantis shrimp (*Odontodactylus scyllarus*) has emerged from her hole in shallow tropical waters. Note the club-like raptorial claws that are cocked and ready to bludgeon any prey that wanders within range.

in-the-box). When the latched limb and spring are freed, the stored energy is released with blinding speed and the claw lashes out to smash or spear the hapless prey. It has been calculated that this combination spring and muscle conFigureuration can generate 470,000 watts of power per kilogram of muscle, orders of magnitude higher than the fastest-moving muscles alone can deliver. This tremendous amount of nearly instantaneous energy can propel the claw at speeds of 23 m/s (51 mph). Furthermore, because the strike is so rapid, the claw generates cavitation bubbles between the appendage and the striking surface. The collapse of these cavitation bubbles produces measurable forces on the prey in addition to the instantaneous forces of 1,500 newtons (337 pound-force) caused by the impact of the claw. Thus, the prey is hit twice by a single strike, first by the claw and then by an even greater force from the collapsing cavitation bubbles that immediately follow. Even if the claw misses the prey, the resulting shock wave can be enough to kill or stun the prey. Captive mantis shrimp have managed to shatter double-paned aquarium glass with a single blow from this weapon.

Specialists recognize six classes of crustaceans. In this section, we will examine the four most familiar ones.

Class Malacostraca (Gr. *malakos*, soft + *ostreion*, shell)

Crabs, lobsters, shrimp, prawns, crayfish, krill, isopods, and amphipods. Malacostraca is the largest group of crustaceans and includes three subclasses, 14 orders, and many suborders. We confine our attention to a few of the most familiar orders.

Order Decapoda (Gr., *deka,* ten + *podos*, foot) As their order name implies, the crayfish, lobsters, crabs, prawns, and shrimp that comprise this order have five pairs of walking legs, the first of which is modified in many to form pinchers (**chelae**). Crayfish, lobsters, and shrimp have a body consisting of two regions: a cephalothorax and an abdomen. The cephalothorax is derived from the fusion of sensory and feeding tagmata (the head) with a locomotor tagmata (the thorax). The exoskeleton extends over and around the cephalothorax to form a shield-like carapace. A laterally compressed muscular abdomen with a "tail" extends from the cephalothorax. Decapods bristle with appendages on the head, thorax and abdomen (**Figure 13.26**).

A crab's body differs from that of other decapods in that it is dorsoventrally flattened and oval in shape. The abdomen of a crab is not apparent as it is greatly reduced and folded up under the cephalothorax (**Figure 13.27**).

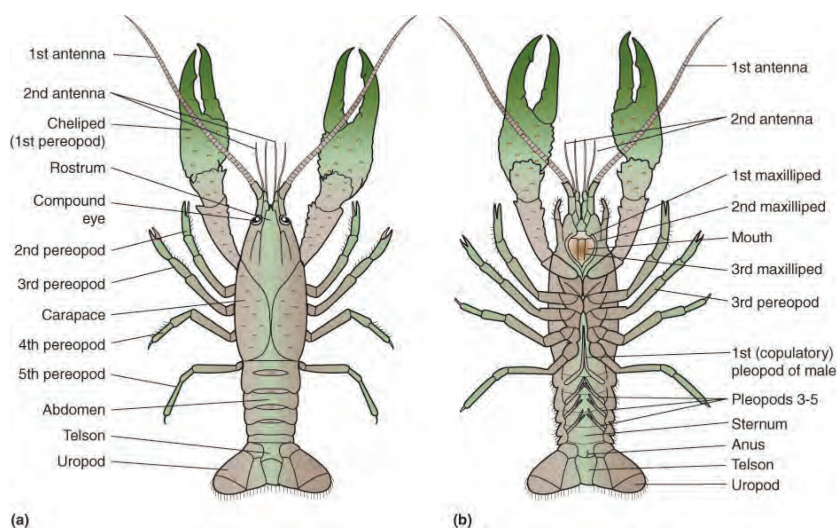

Figure 13.26 Morphology of a Male Crayfish. (a) Dorsal view. (b) Ventral view. In female crayfish the 1st pleopod is greatly reduced resembling pleopods 3-5.

If we live out our span of life on earth without ever knowing a crab intimately we have missed having a jolly friendship. Life is a little incomplete if we can look back and recall these small people only as supplying the course after soup and with the Chablis.

—William Beebe

Order Isopoda (Gr., *iso*, equal + podos, foot) Isopods are one of the few crustacean groups to have successfully invaded terrestrial habitats in addition to freshwater and seawater environments. Isopods are dorsoventrally flattened and lack a carapace. Common land forms are the scavenging sow bugs (*Porcellio*), or pill bugs (*Armadillidium*) that live under rocks and logs and in leaf litter (**Figure 13.28**).When threatened, pill bugs can roll into a tight ball for protection. Freshwater types are found under rocks and among aquatic plants whereas marine forms scurry about on the beach or rocky shore. Some are parasite externally or internally of fish or other crustaceans. The strangest of these isopod parasites (and perhaps the strangest invertebrate parasite of all) is *Cymothoa exigua*. This isopod parasite attaches itself at the base of the tongue of a fish with the claws, on its front three pairs of appendages, and extracts blood (Figure 2.11). As the parasite grows, less and less blood is able to reach the fish's tongue and eventually the organ atrophies from lack of blood. The parasite then replaces the fish's tongue with its own body by attaching to the muscles of the tongue stub. The fish is able to use the parasite as a functional tongue, and it appears that the parasite does not cause any other damage to the host fish. This is the only known case of a parasite functionally replacing a host organ.

Figure 13.27 Morphology of the blue crab (*Callinectes sapidus*). Dorsal view (right) shows no abdomen. Ventral view (left) reveals the abdomen folded up under and attached to the carapace.

Figure 13.28 These wood lice (*Oniscus asellus*) are residents of the damp shadowy world found beneath leaf litter and fallen branches.

Order Amphipoda (Gr., *amphis*, on both sides + *podos*, foot) Members of this order have a laterally compressed body that gives them a shrimplike appearance. Amphipods move by crawling or swimming on their sides. Some species are modified for burrowing, climbing, or hopping. Most amphipods are marine; although a small number of species are freshwater or terrestrial, and they are primarily scavengers with some predatory and a few parasitic types.

Class Branchiopoda (Gr., *branchio*, gill + *podos*, foot)

Fairy shrimp, brine shrimp, water fleas, and tadpole shrimp. Found primarily in fresh water, all branchiopods possess flattened, leaf-like appendages used in respiration, filter feeding and locomotion (**Figure 13.29**). Fairy shrimp (order Anostraca) usually live in vernal pools and temporary ponds that rains and runoff form in early spring. Embryos that have lain dormant perhaps for years revive and grow quickly to adults, racing to secure another generation of embryos before their pool once again dries to dust. Brine shrimp (order Anostraca) also form resistant embryos, but they are adapted to survive the high salinity of salt lakes and ponds such as those around the Great Salt Lake in Utah.

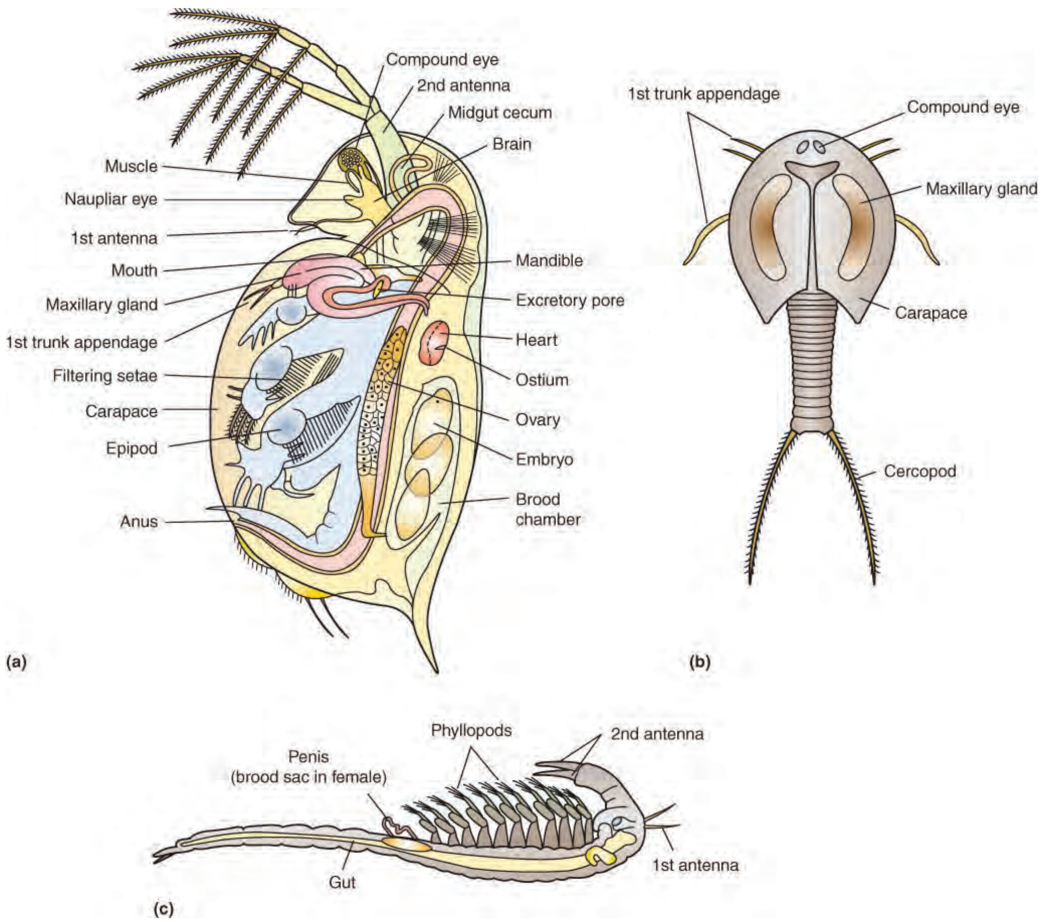

Figure 13.29 Representative Branchiopods. (a) A female water flea (*Daphnia pulex*). (b) A tadpole shrimp (*Triops*). (c) A fairy shrimp (*Branchinecta*).

Water fleas (order Cladocera) are covered by a large carapace over their bodies, and they swim by repeatedly thrusting their second antennae downward to create a jerky, upward motion. Female water fleas are seasonally parthogenetic in the spring and summer and can quickly populate a pond or lake. In response to decreasing temperatures, changing photoperiod, or decreasing food supply, females produce eggs that develop parthenogenetically into males. Sexual reproduction ensues and a generation of resistant "winter eggs" is produced to hatch in the spring.

Class Maxillopoda (L., *maxilla*, the jawbone + *podos*, foot)—copepods and barnacles

With the exception of the barnacles, members of class Maxillopoda are small and sometimes bizarre crustaceans that are recognized by their short bodies and the unique combination of five head, six thoracic, and four abdominal segments, plus a telson ("tail"). Copepods (subclass Copepoda) are so abundant in both marine and freshwater habitats that they dominate the primary consumer level of aquatic communities. Copepods have a cylindrical body with the first antennae (and the thoracic appendages in some) modified for swimming whereas the abdomen is free of appendages. Most copepods are planktonic and use their second maxillae for filter feeding. A few types live on the substrate; a few are predatory, and others are commensals or parasites of marine invertebrates, fishes, or marine mammals.

At first glance, barnacles (subclass Cirripedia) appear more molluscan than crustacean because as adults, their body is surrounded by a shell of calcareous plates and they are totally sessile as adults. One must look internally to discern their true nature. Although their head is small, and they exist without an abdomen or eyes, they do possess long, jointed thoracic **cirri** with hair-like setae. The cirri grow out of a crevice between the calcareous plates (**Figure 13.30**). Their function is to separate small, unwanted matter from desired food and discard it. All barnacles are marine, and they will attach head down by means of adhesive glands in their first antennae to almost anything, including rock outcroppings, ship bottoms and pilings, and even whales. Attachment to the substrate is direct (e.g. acorn barnacles) or by a stalk (e.g. gooseneck barnacles).

Barnacles that colonize ship bottoms reduce both speed and fuel efficiency. Much time, effort, and money have been devoted to research on keeping ships and other surface free of barnacles. In the past, coatings of toxic levels of heavy metals and chemicals were applied to ships. These paints were cheap and effective but leached easily into the surrounding environment where they caused many problems. Recently paint polymers mixed with relatively harmless pharmacological substances, such as dopamine antagonists, have shown good results in preventing the release of adhesives by barnacle larvae, thus inhibiting them from attaching.

Some barnacles have become parasites. *Sacculina* (order Rhizocephala) are highly modified to parasitize crabs in a most unusual fashion. Their first form in life is as a nauplius larva. Later, upon location of a host crab, they metamorphose into a **kentrogon**, injecting parasitic cells into the hemocoel of their host crab. Eventually, root-like absorptive structures of the parasite develop in the same location as would the crab's egg mass (if the crab had an egg mass, which it doesn't). The host crab, however, believes the parasite to be its own egg mass protecting, ventilating, and grooming it. This level of care includes well-timed spawning behavior that assists the parasite in its own reproduction. Strangely, if this parasitic barnacle infects a male crab, there is a castration effect whereby the male host crab becomes a female in its structure and behavior.

Figure 13.30 Barnacles such as these goose barnacles (order Pedunculata) encrust anything in ocean water—rocks, pilings, ship hulls, and even whales and turtles.

Class Ostracoda (Gr., *ostrakodes*, having a shell)—mussel shrimp

Wrapped in a bivalve-like chitinous or calcareous carapace ("shell") only 0.25 to 30 mm (0.01 to 0.12 inch) long, these crustaceans resemble tiny clams or mussels, thus the common name "mussel shrimp." (**Figure 13.31**) Ostracods consist of little more than a head bearing five pairs of appendages. Trunk segments have been fused and thoracic appendages number either two or zero. The head appendages are the principle force for both feeding and mobility.

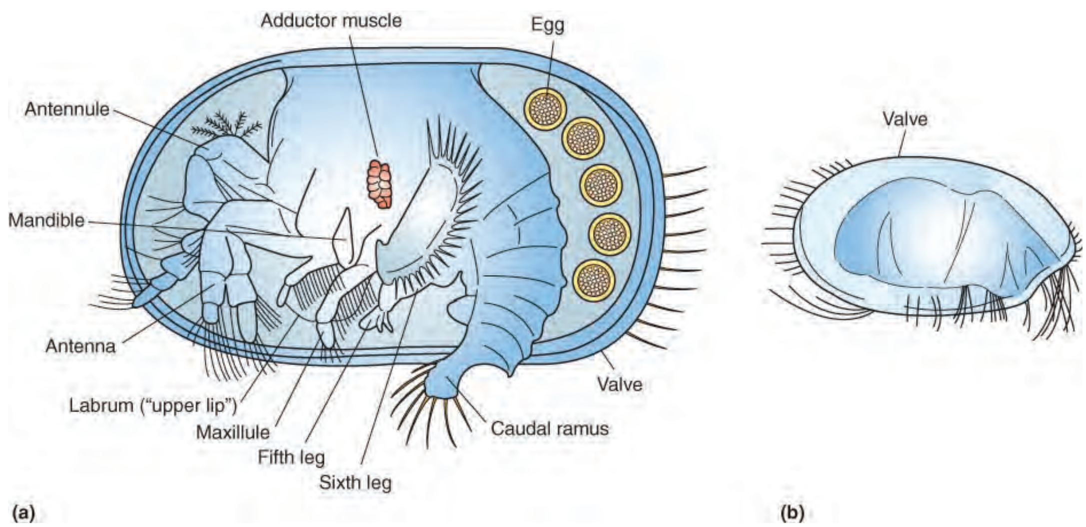

Figure 13.31 Morphology of an Ostracod. (a) The ostracod *Cytherella sp* with the left valve removed for clarity. (b) An intact ostracods showing the position of the body within the valves.

Ostracods have a worldwide distribution in the ocean where they may be planktonic or most commonly, part of the benthos, living on or in the upper layer of the sea floor. Many ostracod species are found in fresh water, and some are found in moist forest soils. They feed on varied diets; from particle, plant, and carrion feeders to predators of different types of prey. Fossil ostracods in some rock strata are often key indicators of oil deposits.

The Arthropod Body Plan

Although arthropods are the most morphologically diverse group of animals on the planet, they all share an assemblage of unifying characteristics: a tough, chitinous exoskeleton, a segmented body specialized into tagmata and jointed appendages. Ancestral arthropods may have been worm-like but an annelid encased in a rigid exoskeleton is not what arthropods came to be. In conjunction with the development of the exoskeleton, the arthropods evolved a suite of highly successful adaptations, referred to as **arthropodization**:

1. The problem of locomotion was solved by the development of flexible joints and regionalized muscles in the body and the appendages. Muscles became organized as intersegmental bands

associated with the individual body segments and appendage joints, whereas circular muscles were lost almost entirely

2. With the loss of peristaltic (squeezing) capabilities as a result of a now rigid body and the absence of circular muscles, the coelom became useless as a hydrostatic skeleton. Loss of the coelom led to the formation of an open circulatory system and the use of the body cavity as a hemocoel or blood chamber in which the internal organs are bathed directly in body fluids. Large body size, however, still demanded some sort of pumping organ for moving blood around the hemocoel, hence arthropods retained the annelid-like dorsal blood vessel but evolution modified it into a highly muscular pumping structure—a heart.
3. Instead of the open metanephridia typical of annelids, excretory organs became enclosed internally, thereby preventing the blood from being drained from the body.
4. A whole set of surface sense organs evolved with various devices for transmitting sensory impulses to the nervous system in spite of the hard exoskeleton.
5. A number of different gas exchange structures evolved to overcome the barrier of the cuticle. This makes a high metabolic rate possible which in turn allows for periods of intense activity.
6. The arthropod body itself has undergone various forms of regional specialization (tagmosis) to produce segment groups or tagmata such as the head, thorax, cephalothorax, and abdomen.
7. The process of periodic molting (ecdysis) evolved to allow the exoskeleton to be shed to make room for an increase in body size.

Such evolutionary plasticity of form and structure has been of paramount importance in establishing the diversity and dominant position of the arthropods.

Body Wall and Exoskeleton

The body wall is composed of the complex, layered **cuticle** secreted by the underlying **hypodermis**. This nonliving exoskeleton covers all body surfaces and supports a variety of functions: protection from injury and predators, preventing water loss, offering structural support, and providing a system of levers for muscle attachment.

The exoskeleton has two layers (**Figure 13.32**). Outermost is the **epicuticle**. Hard and slick because of its waxy lipoprotein composition, the epicuticle is impermeable to water and a barrier to microorganisms and natural or human-produced chemicals. Beneath the epicuticle and comprising the bulk of the exoskeleton is the **procuticle**. The procuticle is composed of chitin, a plastic-like saccharide, and several kinds of proteins. The procuticle hardens through a process known as **sclerotization** in which layers of protein are chemically cross-linked with one another resulting in hardening and darkening of the exoskeleton. (Crustaceans

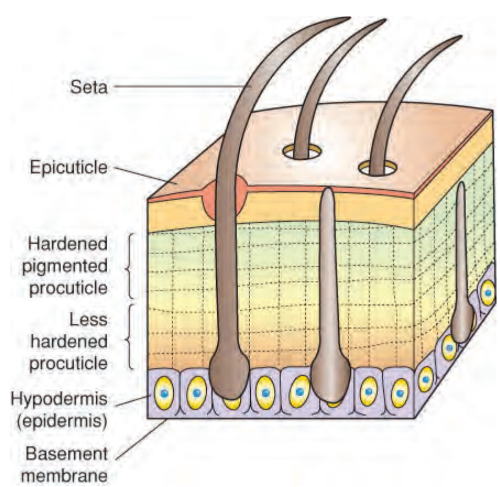

Figure 13.32 A Section of Arthropod Cuticle. The hypodermis secretes the entire skeleton. Calcium carbonate deposits and/or sclerotization harden the outer layer of the procuticle.

also incorporate calcium carbonate into their exoskeleton during sclerotization.). To retain the flexibility needed for running, jumping or flying, the innermost part of the procuticle does not fully harden.

In general, each body segment (somite) is enclosed by four exoskeletal plates, or **sclerites**: a dorsal **tergite**, two lateral **pleurites**, and a ventral **sternite** (**Figure 13.33**). Numerous variations among taxa exist, however, as the result of fusion, fragmentation, and loss of sclerites.

Molting and Growth

Although an exoskeleton endows its bearer with many advantages, it has one serious drawback. How is growth to occur? Growth by the standard gradual increase in external body size is impossible, so arthropods are forced instead to periodically shed their old exoskeleton and form a new, larger one. The process by which this shedding occurs is known as molting or ecdysis.

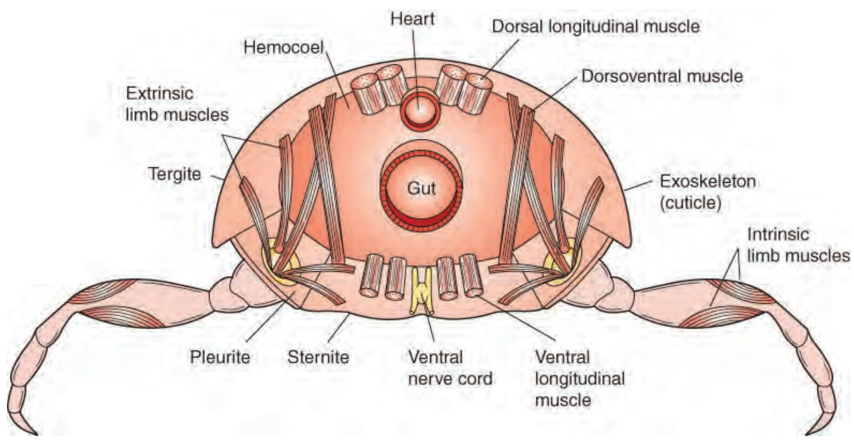

Figure 13.33 Generalized anatomy of an arthropod as seen in cross section.

Ecdysis involves shedding the old exoskeleton, forming a new exoskeleton, and then inflating the body with air before the new exoskeleton hardens. Controlled by the nervous and endocrine (hormone) systems, ecdysis proceeds through four basic stages:

1. **Preecdysis**. In preparation for ecdysis, the arthropod often hides and becomes inactive for a period of time and undergoes **apolysis**, a process in which hormones secreted by glands in the hypodermis begin to digest the old procuticle.
2. As the old exoskeleton begins to detach, the space between the hypodermis and the old exoskeleton begins to fill with a fluid known as **molting gel**.
3. The hypodermis begins secreting a new exoskeleton.
4. The arthropod takes in air or water and as its body swells; the old exoskeleton splits open along predetermined lines. The arthropod then wriggles out of the old exoskeleton.

An arthropod usually remains hidden and inactive as the new exoskeleton hardens fully by sclerotization and/or calcium carbonate deposition. In addition, color pigments are deposited in the outer layers of the procuticle.

Support and Locomotion

The arthropods have largely abandoned the hydrostatic skeleton of their coelomate ancestors. As a result, they lack discrete coelomic spaces (except for small cavities around the gonads and sometimes the excretory structures) and the associated muscle sheets that act upon them. Instead, arthropods rely on the exoskeleton for support and maintenance of body shape. Sheets of muscle are not compatible with an exoskeleton. Therefore, arthropod musculature consists of short bands of muscle that extend from one body segment to the next or across the joints of appendages and other regions or articulation (Figure 13.33).

Life inside a rigid exoskeletal box is not possible. Hence, part of the evolution of the exoskeleton included the formation of various joints where the skeleton might be articulated (moved). In contrast to most of the exoskeleton, joints between body and limb segments are bridged by very thin flexible cuticle in which the procuticular layer is much reduced and somewhat soft. Each joint is bridged by one or more pair of **antagonistic muscles**. One set of muscles, the **flexors,** bend the body or limb at the articulation point whereas the opposing set of muscles, the **extensors**, serve to straighten the body or appendage. The legs of spiders have flexor muscles, but no extensor muscles. Extension is accomplished by hydrostatic pressure from the blood. When a spider dies, blood volume decreases and the flexor muscles contract, causing the legs to bend and close in a characteristic death pose.

Some arthropod joints articulate in only a single plane as do your elbows and knees; others are constructed to allow movement in more than one plane similar to the ball-and-socket joint of your hip, and occasionally two adjacent joints will articulate at 90 degrees to one another, forming a gimbal-like arrangement that facilitates movement in two planes.

Arthropods have evolved a plethora of appendage mechanisms and contraptions for locomotion on land, through water, and in the air. Movement through the water can be accomplished in a number of different ways, smooth paddling of shrimp, jerky stroking of certain insects and small crustaceans, and the startling backward jetting propelled by the tail flexon of crayfish and lobsters. Those moving across the land walk, creep, bound, crawl, or run. Based on relative speed (body lengths per sec), the fastest arthropod is the Australian tiger beetle (*Cicindela hudsoni*) that has been clocked at 2.5 meters per second or 5.6 miles per hour. A comparable relative speed for a 6-foot human would be 1026 feet per second or 720 miles per hour, nearly the speed of sound at sea level. Moving at that rate of speed a human could cover a mile in 4.3 seconds.

Others jump and glide, whereas some, such as the flea, simply jump. To merely state that fleas jump is to dismiss the dramatic fashion through which they accomplish their jumps. Muscles in the flea's legs distort the skeleton, and a special catch mechanism locks the cocked legs in place. When the catch is released, the energy stored by distorting the skeleton explosively extends the legs catapulting the flea a distance that often exceeds 100 times its body length. A comparable relative leap for a human would be jumping the length of two football fields from a standing start!

Arthropods move in ways that are nearly as diverse as they are. The insects, however, evolved a mode of locomotion possessed by no other group of invertebrates (protostomes)—the ability to fly. In fact, insects were the first animal group to take to the air. Two different modes of flying evolved in insects—direct (synchronous) flight and indirect (asynchronous) flight. **Direct** or **synchronous flight** is accomplished when muscles acting on the bases of the wings contract to produce a downward thrust, and muscles attaching dorsally and ventrally on the exoskeleton contract to produce an upward thrust (**Figure 13.34**). Butterflies, grasshoppers, and dragonflies are examples of insects that employ a synchronous flight mechanism.

Other insects employ an **indirect** or **asynchronous flight** mechanism. In this case muscles act to change the shape of the exoskeleton on both the upward and downward wing strokes. Dorsoventral muscles pulling the dorsal exoskeleton (tergum) downward produce the upward wing thrust. Downward thrust results when longitudinal muscles contract and cause the exoskeleton to arch upwards. The flexibility and energy-storing properties of the exoskeleton enhance the power and velocity of these thrusts. Flies and wasps are examples of insects with an asynchronous flight mechanism.

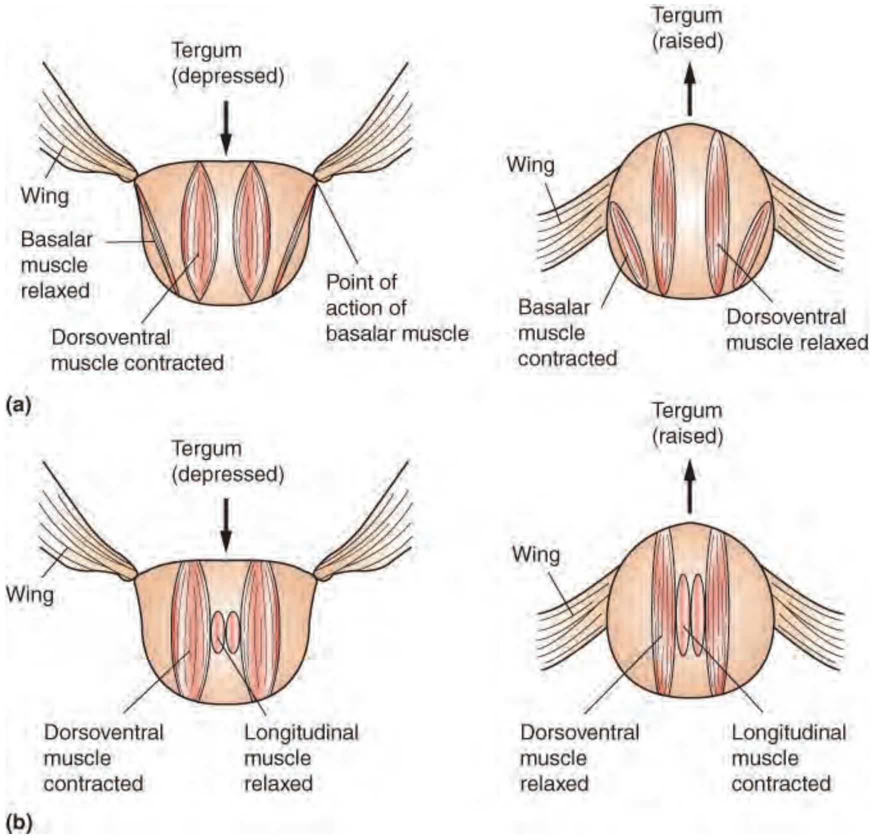

Figure 13.34 The Action of Insect Flight Muscles. (a) Muscle arrangements for the direct or synchronous flight mechanism. Note the muscles responsible for the downstroke attach at the base of the wings. (b) Muscle arrangement for the indirect or asynchronous flight mechanism. Muscles change the shape of the thorax causing the wings to move up and down.

Nerve impulses trigger muscle contractions in both types of flight. In synchronous flight, there is a one-to-one correspondence between nerve impulses and wing beats, but in asynchronous flight a single nerve impulse can result in approximately 50 cycles of the wing. Thus, rapid firing of a nerve can produce tremendous wing speeds (cycles). For instance, frequencies of 1,000 cycles per second (cps) have been recorded for some midges. High wing speeds creates the buzzing sound we associate with small insects such as mosquitoes.

Simply flapping the wings is not enough for controlled flight. The tilt of the wing must be adjusted to provide lift and forward propulsion. In most insects, such control is established through muscles that attach to sclerotized plates at the base of the wing.

Flight speeds vary tremendously. Sphinx moths and horse flies are capable of speeds up to 48 km (30 miles) per hour, while dragonflies can reach 40 km (25 miles) per hour. Other insects can partake in lengthy, nonstop flights. Migrating monarch butterflies, *Danaus plexippus*, for example, are known to fly many thousands of miles at roughly 10 km (6 miles) per hour in their annual migration—an amazing feat of endurance for such a small animal.

Appendages

Arthropod appendages are moveable outgrowths of the body wall equipped with extrinsic (connecting limb to body) and intrinsic (wholly within the limb) muscles that move the various limb segments or pieces called **podites**. Beyond this general plan, however, the variations in arthropod limbs and the myriad of terms associated them can be overwhelming to both student and experts alike.

Arthropod appendages may be categorized as **uniramous** (with only a single branch or **ramus**) and **biramous** (Y-shaped with two rami). Spiders and their kin, centipedes, millipedes, and insects possess uniramous appendages (**Figure 13.35**) whereas crustaceans bear both biramous and uniramous appendages.

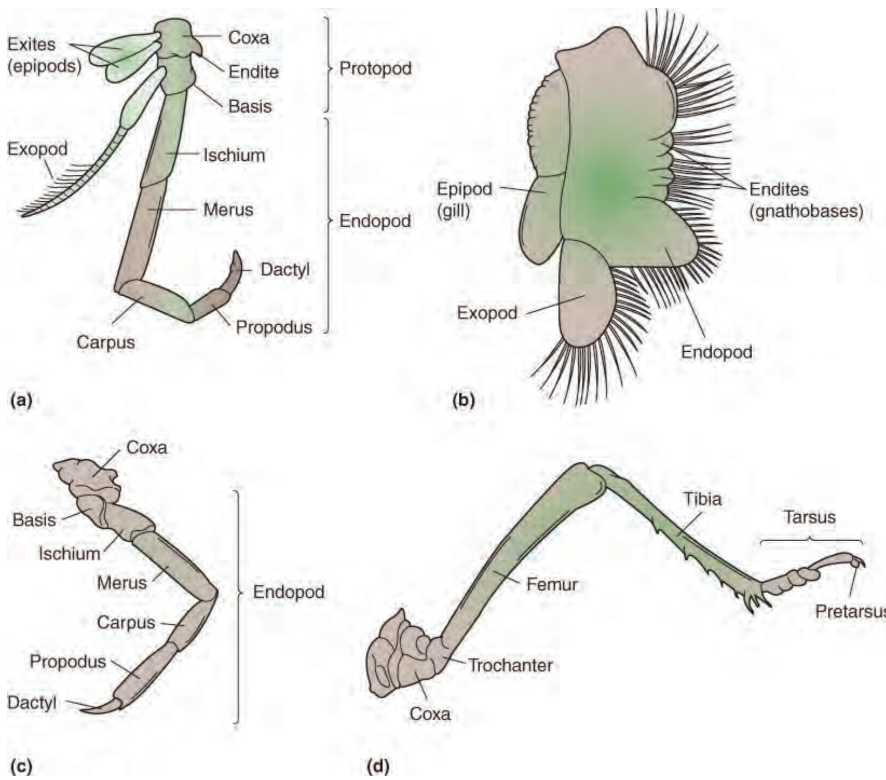

Figure 13.35 Arthropod Trunk Appendages. (a) Generalized biramous limb of a crustacean. (b) Generalized biramous phyllopodal limb of a crustacean. (c) Crustacean uniramous walking leg (stenopod). (d) Uniramous walking leg (stenopod) of a grasshopper.

The uniramous limbs of spiders and insects are typically ambulatory (walking) in function. They are long and thin, and thus are often called **stenopodia** (Gr., *steno*, narrow + *podia*, feet). Some biramous limbs of crustaceans may also be used for walking; in these limbs the inner branch is long and thin and used for walking, whereas the outer branch is greatly reduced. The swimming limbs of some crustaceans are greatly expanded and flattened and are known as **phyllopodia** (Gr., *phyllo*, leaf-shaped + *podia,* feet).

To varying degrees, arthropods have the capacity to regenerate lost appendages. In all arthropods, regeneration is associated with molting. Regenerating appendages develop within the enveloping cuticle and do not become functional until their sheath is shed at the next molt. Metamorphosis into the adult stage marks the end of molting in insects, and accordingly, adults do not regenerate amputated appendages.

Crustaceans, however, are the exception as they tend to molt and grow throughout life. Therefore, crustaceans never lose the ability to grow back a missing appendage.

Digestive System

The great diversity among arthropods is reflected in the multiplicity of their feeding strategies, mouth structures, and appendages. The only real constraint on arthropods in regards to modes of feeding is the absence of external, functional cilia that allow for filter feeding in many animal types. Many arthropods, however, have managed to overcome even this limitation and suspension feed by other means. We have already discussed specific feeding strategies in each section on specific arthropod taxa so here we generalize only about the basic structure and function of the arthropod digestive system.

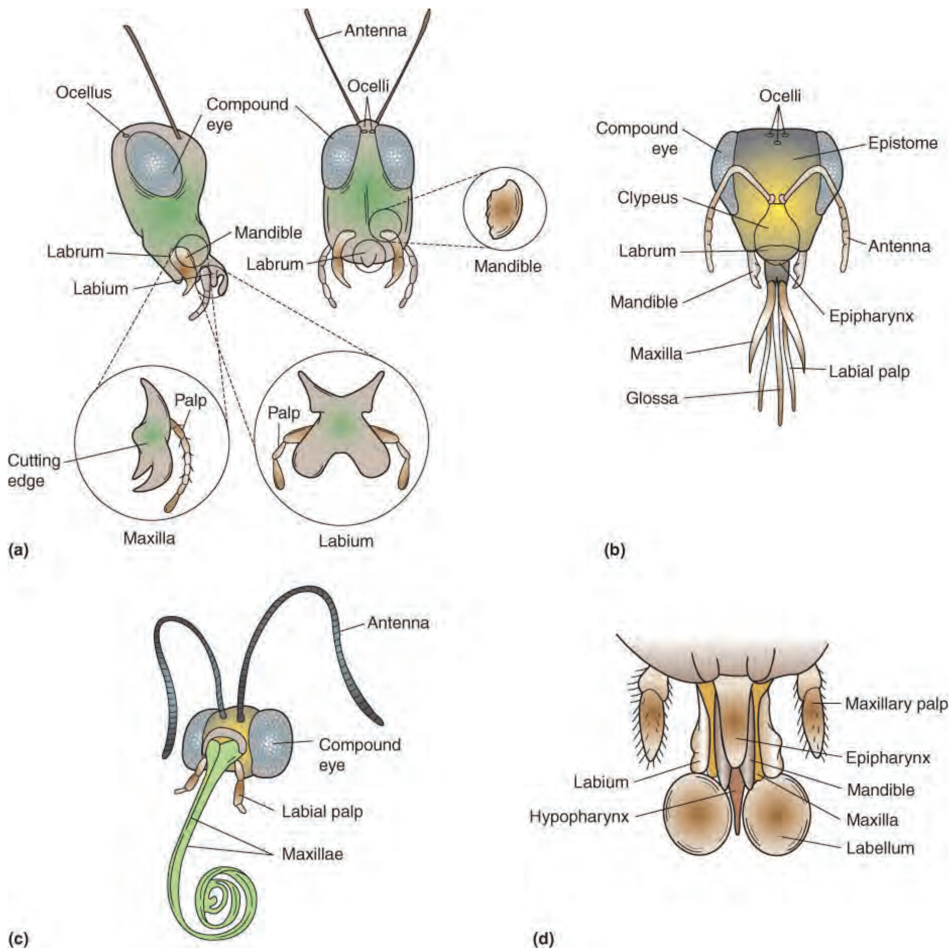

Figure 13.36 Arthropod Mouth Appendages. (a) The biting/grinding mouthparts of a grasshopper. The labrum is a sensory upper lip and the labium a sensory lower lip. The mandibles are hard and used for tearing and grinding. The maxillae have cutting edges and a sensory palp. (b) The piercing/sucking mouthparts of a honeybee. (c) The sucking mouthparts of a butterfly. (d) A close-up view of the sponging/lapping mouthparts of a housefly.

Different feeding modes require different mouthparts (**Figure 13.36**). Once food is ingested it moves into the digestive tract. The digestive tract of arthropods is complete and usually straight, extending from a ventral mouth on the head to a posterior anus. In nearly all cases there is a well-developed cuticle-lined **foregut** and **hindgut**, connected by a **midgut** (**Figure 13.37**). In general, the foregut serves for ingestion, transport, storage, and mechanical digestion of food; the midgut for enzyme production, chemical digestion, and absorption; and the hindgut for water absorption and preparation of fecal material. The midgut typically bears one or more evaginations in the form of **digestive ceca** (often referred to as the **digestive gland**). The exact number of ceca and the arrangement of other gut regions varies among the different groups of arthropods,

Various terrestrial arthropods have evolved structures associated with (although not necessarily derived from) the gut. For example, excretory structures called Malpighian tubules develop from the mid-or hind-guts of insects and arachnids. Many unrelated taxa have special repugnatorial glands that produce noxious substances designed to deter predators. Modified salivary glands are common silk-producing organs, but silks are also sometimes secreted by the digestive tract.

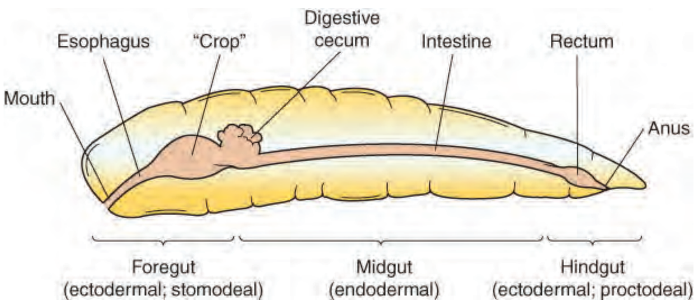

Figure 13.37 The gut regions of an arthropod.

Circulation and Gas Exchange.

The body cavity is an open hemocoel with the organs being bathed directly in **hemolymph** (blood). Without a muscular, flexible body wall to augment blood movement, the elaboration of a muscular heart in arthropods became a necessity. The result is a system wherein the blood is driven from the heart chamber through short vessels and into the hemocoel, where it bathes the internal organs. The blood returns to the heart via a noncoelomic **pericardial sinus** and perforations in the heart wall called **ostia**.

The hemolymph of many kinds of small arthropods may be colorless but most larger forms contain a copper-based respiratory pigment, **hemocyanin**, that is blue when oxygenated, thus giving arthropod blood a blue color rather than the red color of vertebrate blood. Unlike the red hemoglobin in our blood, blue hemocyanin is not carried on blood cells but rather is dissolved in the plasma so that it colors not only the blood but permeates all tissues as well. If you squish an insect, you will see green hemolymph ooze out of the mangled corpse. Insect blood is green because yellow xanthophylls pigments in the leafy diet of an insect mix with the blue hemocyanin to produce a hemolymph that appears green.

As one might expect, arthropod gas exchange structures have taken one form in aquatic groups and quite another in terrestrial types. Most larger crustaceans have evolved various types of gills for exchanging gases with the water surrounding them. These gills are in the form of thin-walled cuticular evaginations. Gills are usually branched or folded, providing large surface areas.

The terrestrial insects and arachnids have evolved gas exchange structures in the form of invaginations of the cuticle. By folding the cuticle inward, the gas exchange structures are kept moist allowing oxygen to enter solution for uptake. Many arachnids possess highly folded invaginations called **book lungs** (internal gills in a sense) whereas insects possess inwardly directed branching tubules called **tracheae** that open externally through pores called **spiracles**.

Excretion and Osmoregulation

Arthropods possess nephridia, but a hemolytic circulatory system demands that they be quite different than those found in the annelids. The open nephridia of annelids would be functionally untenable in arthropods as they would drain the blood directly from the open hemocoel to the outside. Instead, arthropods are equipped with closed nephridia, and there has been a reduction in the number of nephridia as well.

In most adult crustaceans, only a single pair of nephridia persists, and these are usually associated with particular segments of the head such as the antennae (**antennal glands**) and maxillae (**maxillary glands**). In arachnids, there may be as many as four pairs of nephridial opening at the bases of the walking legs (**coxal glands**).

Another type of arthropod excretory structure exists in many terrestrial forms (e.g. arachnids and insects). These structures, known as Malpighian tubules, arise as blind tubules extending into the hemocoel from the gut wall.

The inner ends of the nephridia absorb fluid from the hemocoel that is generally similar to the blood itself, but as it passes along the plumbing system of the nephridium, a good deal of selective reabsorption occurs, particularly of salts and nutrients such as glucose. Thus, the urine exiting the nephridial pores is a concentration of nitrogenous waste products.

Malpighian tubules accomplish the same processes, but they must rely on assistance from the gut. Malpighian tubules uptake from the hemocoel is nonselective, and thus this "primary urine," emptied directly into the gut, contains nutrients, salts, water, and so on. The hindgut is mostly responsible for concentrating the urine by reabsorbing the nonwaste components.

Nervous System and Sense Organs

The arthropod brain comprises several bundles of fused ganglia. The **supraesophageal ganglion** lies in the head and is composed of the **protocerebrum**, the **deuterocerebrum**, and the **tritocerebrum**. The posterior portion of the tritocerebrum forms circumenteric (looping) connectives around the esophagus attaching the brain to the **subesophageal ganglion** that lies beneath the esophagus. From the subesophageal ganglion, a ventral nerve cord runs back to the anus. This ventral nerve cord contains a fused ganglion in each segment (**Figure 13.38**).

Possessing an exoskeleton certainly shields the bearer against the outside world, but how is an animal so clad to receive critical sensory input from the surrounding environment? Arthropods have compensated by evolving numerous cuticular processes—setae, hairs, bristles, pores, or slits—collectively known as **sensilla** that serve as mechanoreceptors and chemoreceptors.

Tactile(touch/hearing) reception. Most arthropod tactile receptors (mechanoreceptors) are movable bristles or setae. When the cuticular projections are touched, that movement is translated into a deformation of a nerve ending which in turn initiates a nerve impulse to the brain.

Sensitivity to environmental vibrations ("hearing"), pressure waves, and air currents is similar to tactile reception. Sensilla in the form of fine hairs or setae are mechanically moved by external vibrations or waves and impart that movement to underlying sensory neurons. At the base of the antennae of most insects are **Johnston's organs**, long setae that vibrate when certain frequencies of sound strike them. Vibrating setae move the antennae in its socket, stimulating sensory cells. Sound waves in the frequency range of 500 to 550 cycles per second (the range of sounds female wings produce) attract and elicit mating behavior in the male mosquito *Aedes aegypti*. **Tympanic organs** are located in the legs of crickets and katydids (order Orthoptera), in the abdomen of grasshoppers (order Orthoptera), and in the abdomen or thorax of moths (order Lepidoptera). These organs consist of a thin, cuticular membrane covering a large air sac. Sound waves resonate the air sac which in turn vibrates the membrane and stimulates the sensory nerves below. Grasshopper tympanic organs can detect sounds in the range of 1,000 to 50,000 cps. (The human ear can detect sounds between 20 and 20,000 cps.) Bilateral placement of tympanic organs allows insects to discriminate the direction and origins of a sound.

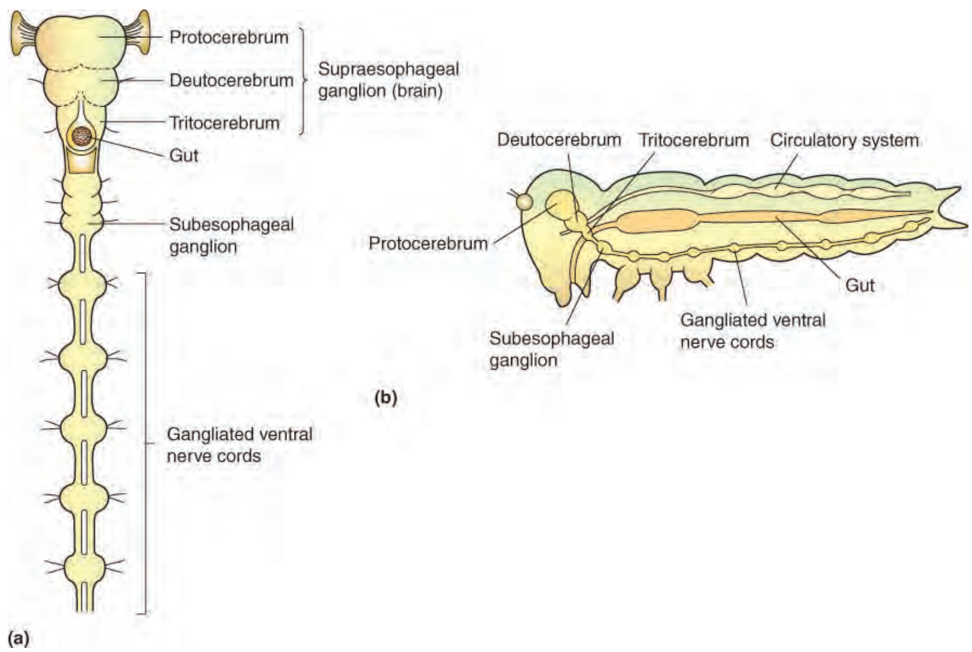

Figure 13.38 Generalized Structure of an Arthropod Nervous System. (a) Dorsal view. (b) Lateral view.

Chemical (smell/taste) reception. Chemoreceptors are usually abundant on the mouthparts, antennae, legs, and ovipositors, and take the form of hairs, pegs, pits, and plates that have one or more pores leading to internal nerve endings. Chemicals diffuse through these pores and bind to and excite sensory nerve endings. Arthropods use chemoreceptors in feeding, species identification, selection of egg laying sites, mate location, and social organization. The pheromones produced by many receptive female types must surely be among the most powerful scents in the arthropods group, and males are champions at detecting these odors. Male Chinese silkworm moths (order Lepidoptera) have been known to home in on and find perfuming females from as far away as seven miles. Odor is also a very reliable cue when it comes to arthropod feeding because it is more constant than color and shape. Some flies are so attuned to the odor of death that they can be found on the carcass of a dead animal only minutes after the animal's demise.

Photo (sight) reception. Many arthropods are capable of detecting light and use this capability for orientation, navigation, feeding, and other functions. Light is detected either through ocelli, compound eyes, or a combination of both. Ocelli consist of 500 to 1,000 receptor cells beneath a single cuticular lens. Compound eyes are much more complex and are usually well developed in most adult insects. Compound eyes consist of a few to 28,000 receptors, called **ommatidia**, that fuse into a multifaceted eye (**Figure 13.39**). The outer surface of each ommatidium is a lens. Below the lens is a crystalline cone. The lens and cone are the light-gathering structures. Certain cells of the ommatidium called **retinula cells** have a special light-collecting area known as the **rhabdom**. The rhabdom converts light energy into nerve impulses. Pigment cells surround the crystalline cone, and sometimes the rhabdom, prevent light that strikes one rhabdom from reflecting into an adjacent ommatidium.

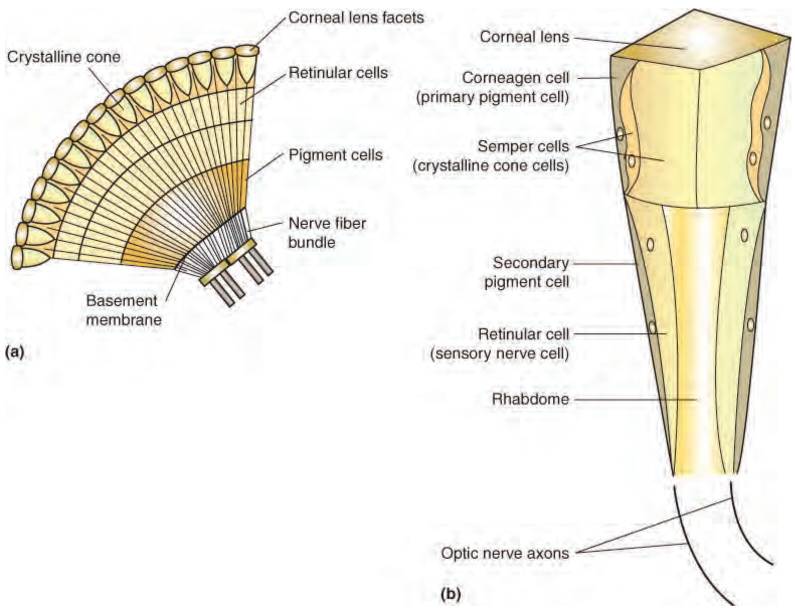

Figure 13.39 The Structure of the Compound Eye of Insects. (a)Compound eye of an insect in cross-section. (b) A single ommatidium from a compound eye.

Although compound eyes may form a fuzzy image of sorts, they are much better suited for detecting movement. In fact, movement of a point of light less than 0.1 degrees can be detected. For this reason, bees are attracted to flowers blowing in the wind, and predatory insects select moving prey. Compound eyes can detect wavelengths of light that the human eye cannot perceive, especially in the ultraviolet end of the spectrum. Some insects are also able to detect polarized light, an extremely useful adaptation for navigation and orientation. Mantis shrimp (Stomatopoda) have the most sophisticated visual system in the animal kingdom. Each eye contains 16 different types of photoreceptors. They can perceive both ultraviolet and polarized light, and discriminate up to 10,000 different colors (10 times greater than the human eye).

Arthropods are also capable of detecting changes in temperature, pressure due to increasing or decreasing depth, humidity, the position of their appendages, and even the magnetic field of the earth itself. Furthermore, research has indicated that insects are capable of some learning and have at least a limited memory.

Reproduction and Development

Arthropods are the most biologically successful group of animals on the planet, and one of the keys to their environmental dominance is their high reproductive potential (**fecundity**). Adult arthropods are reproductive machines that have the capability of reproducing their way around any obstacle—natural or human-made—they encounter. This is especially true of insects. A single Australian ghost moth (Hepialidae) female laid 29,100 eggs, and when it was dissected, 15,000 eggs still remained in the ovaries. It has been calculated that a single pair of flies beginning reproduction in April could be the progenitors of 191,010,000,000,000,000,000 flies by the end of August (assuming optimal conditions and that no flies die). Aphids may have the shortest generation time (from egg-laying adult to egg-laying adult) at only 5 days whereas the longest life cycle (from egg to reproducing adult) under normal conditions belongs to the periodical cicada (*Magicicada*). These insects require 17 years to complete nymphal development underground. The life spans of most arthropods range from a few hours to several years. However, the wood-boring beetle, *Eburia quadrigeminata*, may have its development so delayed by the poor nutritional quality of dead wood that a specimen was found emerging from a birch bookcase 40 years old.

With few exceptions, arthropods are dioecious. Sperm are commonly transferred to the female within sealed packets known as spermatophores. In this mode of delivery, the sperm are not dilute by water nor do they suffer rapid desiccation on land. Either the female is attracted to the spermatophore chemically or the deposition of the spermatophore occurs during the course of a nuptial dance, and the male afterward maneuvers the female into a position to take up the spermatophore within her genital opening. Many arthropods, such as some crustaceans, millipedes, some insects, spiders, and some mites, transfer free sperm through direct copulation and insemination.

The fertilized eggs are usually externally deposited in safe or hidden places (oviparous). The females of some arthropods, however, retain the eggs in their body but rely on the yolk within the eggs to nourish the developing young (ovoviviparous), and subsequently give birth to live young.

The eggs of many crustaceans hatch into a nauplius larvae which have fewer segments and appendages than adults (**Figure 13.40**). Additional segments and appendages then appear at regular intervals with molting. The **zoea** stage larva usually follows the nauplius stage, however, due to their accelerated development, the zoea is the first larval stage in decapods such as crabs and shrimps. There are several advantages of larval stages in the development of aquatic arthropods: less yolk is required in the eggs, and currents dispersing the larvae, allow the species to colonize new areas without planktonic larvae having to compete with benthic adults.

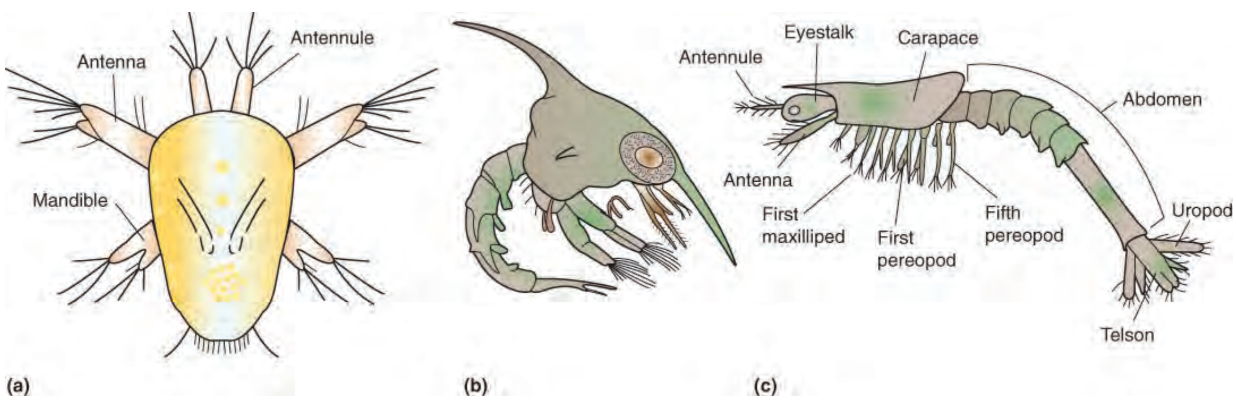

Figure 13.40 Laval Stages of Aquatic Arthropods. (a) A newly hatched copepod nauplius larva. (b) Zoea larva of a crab. (c) Zoeal stage larva of a shrimp.

The young of most arachnids are similar to the adult. The female scorpion gives birth to her young, which immediately crawl on her back. Unlike other arachnids, mites and ticks hatch as six-legged larvae, acquiring their fourth pair of legs at a later molt.

As discussed earlier, insects metamorphose from larva to adult either gradually through incomplete (hemimetabolous) metamorphosis or radically in only a few stages through complete (holometabolous) metamorphosis. Beneficially, larvae inhabit different environments and eat different foods than their parents, thus reducing competition.

Arthropod Connection

Economically

Spider silk is one of the great wonders of the natural world. That a small animal can produce an amazing substance that we humans with our technological prowess are unable to duplicate is yet another humbling reminder of how we pale in comparison to nature's works. Spider silk has a **tensile strength** (amount of force a material can withstand without breaking) greater than Kevlar (which in turn is stronger than steel). Furthermore, spider silk is highly elastic as well as waterproof. In an attempt to develop artificial spider's silk, researchers have used molecular techniques to sequence the genes coding for spider silk and have placed these genes into host organisms, including bacteria, plants, and goats. Silk proteins have been produced by these host organisms. Imagine the usefulness of a thread that is stronger than Kevlar and steel, yet elastic and biodegradable. Potential uses include body armor, parachutes, fishing nets, extremely fine sutures for microsurgery, artificial ligaments and tendons, and even personal clothing that would be nearly indestructible and never wear out. Furthermore, as anyone who wanders afield in the early morning can attest, spider webs can collect remarkable amounts of water. Artificial webs constructed in similar design could be used to harvest water from mist.

Crustaceans have been highly regarded as delectable gourmet fare since ancient times and our taste for them continues to this day as evidenced by the fact that nearly 10,700,000 tons of crabs, lobsters, crayfish, prawns, and shrimp were consumed worldwide in 2007. Over 70% by weight of all crustaceans caught for consumption are shrimp and prawns and over 80% of those are produced in Asia, with China alone producing half the world's total. Although krill have one of the greatest biomasses on the planet, these small crustaceans are not widely consumed by humans, with only about 130,000 tons caught for that purpose yearly. It takes up to seven years for a lobster to grow to 1 pound, the smallest size legal for trapping. "Big George," a lobster caught off the coast of Cape Cod in 1974, weighed in at hefty 17 kg (37.4 pounds) and was over 0.6 m (2 feet) in length. More recently, a 20 pound lobster that was caught and eventually released was estimated by experts to be over 140 years old. A quick calculation reveals that "Big George" was probably over 250 years old when he was captured.

Other arthropods provide everything from the ingredients for fabric dyes and wood preservatives to medicines. Insects, however, have the most impact on each and every one of us directly and indirectly. The economical dark side of this connection is the tremendous destruction and damage yearly to our food, clothing, and property by weevils, cockroaches, ants, moths, termites, and beetles, as well as to our pets and domestic livestock by arthropod pests and parasites. The annual lost revenue from insect damage to crops in the field and storage or insect-transmitted plant diseases in the United States alone is approximately $5 billion! As humans, we exhaust countless resources in agriculture and forestry as well as in the housing and food industries in our efforts to lessen the negative impact of insects. Termites cause around $2 billion annually in structural damage to our homes and other wooden structures, and other insects such as bark beetles, spruce budworms, and gypsy moths wreak economic havoc as well. Since 1980, the introduced gypsy moth has defoliated close to a million acres of trees a year. In 1981, a record 12.9 million acres (an area larger than Rhode Island, Massachusetts, and Connecticut combined) were defoliated.

Only about 0.5% of known insect species adversely affect human health and welfare and most contribute enormously to the richness of human life. Many others have provided valuable services and commercially valuable products, such as wax, honey, and silk, for thousands of years. Insects are responsible for the pollination of approximately 65% of all plant species, including many that we rely upon for food. In the U.S. alone, bees are annually responsible for the pollination of nearly $20 billion worth of produce, not including crops dedicated for livestock. Soil-dwelling insects play important roles in aeration, drainage, and turnover of soil, and they promote decay. It is estimated that cattle ranchers save $380 million a year because burying beetles dispose of cow dung. Another consideration is the $50 billion that would disappear from hunting, fishing, and bird-watching activities were it not for insects at the bottom of the food chain. And if it weren't for insects eating each other, we would have to spend an additional $4.5 billion in agricultural pest control.

Many new applications of arthropod chemicals are currently being investigated. For example, chitin could be sprayed onto fruit and frozen food to prevent spoilage and to preserve flavor. The natural adhesive that barnacles use to attach themselves permanently to rocks and other substrates could be useful in a number of application ranging from dentistry to underwater construction and repair. And chemicals in spider venom are being tested as potential natural pesticides.

In addition, insects are widely used in teaching and research, and have contributed to advances in genetics, population ecology, and physiology. The chemical that makes fireflies glow, for example, is used in medical tests and as a marker in genetic engineering.

Ecologically

From an ecological standpoint, the most important role arthropods play is in the composition of both aquatic and terrestrial food webs. Krill, copepods, and other planktonic crustaceans are the primary consumer foundation upon which oceanic and freshwater food chains are built whereas insects fill essentially the same role in terrestrial schemes. In short, arthropods of some sort and some size serve as food for every group of animals on the planet from protists to carnivorous plants (that actually rely on them for the mineral content of their bodies, not as actual food) and from sponges to mammals, including humans. Conversely, arthropods leave their mark on the environment as eaters. Herbivorous arthropods, especially insects in large adult swarms or as individual larva, eat tremendous amounts of plant material, including human-grown crops, fruits, vegetables, and flowers daily. The larvae of one insect—the European corn borer, *Ostrinia nubilalis*—causes $7 billion dollars in damage to one crop—corn—in the United States each year. Plagues of the desert locust, *Schistocerca gregaria*, have periodically threatened agricultural production in Africa, the Middle East, and parts of Asia for centuries. Each locust is capable of consuming its own weight (2 gr [0.07oz]) in green vegetation—leaves, flowers, bark, stem, fruits and seeds—daily. Singularly they pose no threat, but rolling swarms of these insects can contain tens of millions of individuals and are thus capable of laying waste to entire landscapes, including human agriculture and economies.

Predatory arthropods eat other animals of all types. Worms, other arthropods, and small vertebrates from fish to amphibians and even birds and mammals are eaten in large numbers by hungry arthropods. An undisturbed meadow may contain as many as 2,250,000 spiders per hectare alone. If each spider caught and consumed only one insect per day, the cumulative biomass consumed by just that one type of arthropod in just that one small area is astounding. In fact, the weight of insects eaten every year by spiders is estimated to be greater than the total weight of the entire human population.

The interactions of arthropods with other creatures are not limited to eating or being eaten, however. Arthropods form a number of different symbiotic relationships with other organisms. Some plants live more intimately with arthropods than merely being pollinated by them. Occupying hollow thorns on the bull-horn acacia tree, *Acacia cornigera*, colonies of stinging ants, *Pseudomyrmex ferruginea*, fiercely guard the tree against ravaging herbivorous insects and browsing mammals. The ants even go so far as to prune away vines and the leaves of other plants that may shade the acacia. In reward for their services, the tree provides shelter and food in the form of carbohydrate-rich nectar emanating from glands on its leaf stalk and protein-rich Beltian bodies from its leaf tips. Consider also the mutualistic relationship between cleaner shrimp and the fish who allow this bite-sized crustacean to crawl over them and even into their mouths unharmed in the search for parasites and bits of dead tissue. By allowing the cleaner shrimp to go unharmed, the fish gets a good cleaning of annoying parasites, and the shrimp gets a meal.

Many arthropods are important agents of decay and recycling and burrowing soil insects help aerate and loosen the soil and aid in soil formation.

Medically

The bites (venom delivered via mouthparts) and stings (venom delivered via a stinger usually at the tip of the abdomen) of some arthropods may be irritating, painful, or itchy but they are seldom harmful. Case in point, it would take 1, 120,000 mosquito bites to drain the average size human of blood. There are those, however, that can inject dangerous toxins to which many people are highly allergic. Bee and wasp stings, innocuous to most people, can be fatal to those highly allergic. Bee and wasp stings cause 30-120 deaths yearly in the United States. In contrast, fewer than four fatalities a year are caused by snake bite.

North Americans are fortunate in that we face few native arthropods that are individually dangerous to us. Two of the most potent are spiders, the black widow (*Latrodectus*) (**Figure 13.41**) and the brown recluse (*Laxoceles*), (**Figure 13.42**) and it is important to be able to identify them and to understand the threat they may pose to us.

Figure 13.41 A female black widow spider displays the characteristic red or orange hourglass design on the ventral side of the abdomen. Males are gray or brown.

The term "black widow" is almost universally recognized and feared. The name is apt for these distinctively-marked arachnids as only the female bites. The black widow's venom is a neurotoxin that blocks the nerve impulses to the victim's muscles resulting in cramps, excruciating muscle spasms, rigidity, and, in extreme cases, paralysis. These symptoms are temporary, and rarely result in death. If you are bitten, remain calm and seek medical assistance with the peace of mind that comes from knowing that there is an anti-venom for black widow bite and that prior to the development of this anti-venom in 1943, only 32 of the 578 cases reported in the 200 years before that resulted in death. Widow spiders are more common in warm and dry climates but do occur throughout North America.

The brown recluse is smaller than the black widow, and they are often found in human structures such as drawers in a garage workbench or the heating ducts of your home. The distribution of the brown recluse is limited to the south central United States making them far less prevalent than most people believe. The brown recluse's venom is much nastier than that of the black widow. Recluse venom is a necrotic toxin. Instead of affecting the victim's nervous system, it acts directly on the skin and musculature to kill the tissues immediately surrounding the bite. The dead tissues heal slowly, if at all. Death is unlikely, however; since 1896, fewer than 10 of 130 or more brown recluse cases recorded in the United States have resulted in death. In severe cases, necrosis may lead to gangrene and possible amputation.

Figure 13.42 Though quite small as the comparison indicates, the brown recluse spider (*Loxosceles reclusa*) possesses a neurotoxic venom more potent than that of the black widow.

Although most species of tarantulas are not native to North America, *Aphonopelma chalcodes*, the Desert tarantula is native to southwestern deserts and can be found in Arizona, New Mexico and southern California. Tarantulas are increasingly being kept as pets. Although the bite of a tarantula may be painful, they are not considered to be venomous spiders. The greatest health risk with these spiders is the fact that when aggravated or alarmed, they can release fine hairs from their legs and abdomen. These hairs, equipped with tiny barbs, can lodge in the eyes and nasal cavities where they can be very irritating.

Only one species of scorpion in North America has venom potent enough to be dangerous to human beings. The Arizona bark scorpion (*Centruoides sculpturatus*) is found primarily in Arizona and northern Mexico. The venom of this scorpion can cause severe pain and swelling at the site of the sting, numbness, frothing at the mouth, respiratory difficulties, muscle twitching, and convulsions. Symptoms are more pronounced in the very young or very old, but death is rare.

As with some other invertebrates, researchers ply the possibility of developing drugs from the toxins of various arthropods. Scorpion venom, for example, shows potential as an immune system suppressor that may prove useful in treating autoimmune diseases or preventing the rejection of transplanted organs. On the other hand, the poison of the funnel web spider, *Hololena curta*, stimulates the immune system and could possibly prevent brain damage caused by short bouts of oxygen loss. That bee venom warms the body, reduces inflammation, and boosts the immune system may soon translate into medicines that will help relieve the pain of arthritis, reduce inflammation, and treat allergies.

Other chemicals derived from arthropods may have useful medical applications as well. An extract of horseshoe crab blood, for example, is used to test the purity of medications, and the chitin extracted from crustacean exoskeletons is used to dress wounds and produce thread for surgical stitches.

Medically, arthropods are most significant as the **vectors** (carriers) of diseases such as malaria, yellow fever, dengue fever, west Nile virus, and elephantiasis (via mosquitoes), African sleeping sickness (via tsetse flies), typhus fever (via lice), bubonic plague (via fleas), and Rocky Mountain spotted fever and Lyme disease (via ticks). The worst of these is malaria. Approximately 300 million people worldwide are infected with the malarial parasite and between 1 and 1.5 million people die from it every year.

Although fly maggots (larvae) may not be your idea of a modern medical treatment, more and more doctors believe they do have a place in modern medicine, and that place is inside open wounds. **Maggot debridement therapy** involves mixing live fly larvae into a wound's dressing and then covering the area with gauze. The maggots, which will only eat dead (**necrotic**) tissue, feed on decaying flesh and leave the underlying healthy tissue untouched. In the process, the maggots also excrete an ammonia-like anti-microbial agent that helps cleanse the wound as well. Because of the decreased circulation and **neuropathy** (degenerative changes to nerves) associated with the disease, maggot debridement therapy has proven most useful in cleansing wounds on the feet and legs of people with diabetes.

As previously discussed, bees and other pollinators are critically important in the production of many of our crops and fruits. In fact, worldwide pollination supports about 35 percent of Earth's agricultural production by weight. Less known, however, is the link between pollination and human nutrition and health. Pollination insures crops that produce essential micronutrients—vitamins, minerals, and trace elements that human health depends on.

Researchers found that in regions of Argentina, Australia, India, Iran, Mexico, Thailand, Romania, and the U.S., vitamin A availability was up to 50 percent dependent on pollination. In addition, certain hotspots in African countries, Brazil, China, and Mexico iron and folate reliance reached 15 percent. Such studies may help target hotspots for pollinator conservation efforts. Unfortunately, bees and other pollinators are dwindling due to disease, intensive land use, and wide-spread pesticide use.

A Closing Note
Backyard Battlefields and Mystery Shrimp

Beneath our feet and beyond our sight is a world of tiny things every bit as dynamic as our larger world. As a young lad, I would often take my trusty magnifying lens and crawl about the yard seeing what I could find. One day I happened upon a battle, which for its scale size, would rival anything in our larger realm. A column of black ants was marching on a nest of red ants. The red ants fought bravely but to no avail and soon the black ants were streaming into the red ants' nest. Shortly, many black ants emerge bearing the captive larva and pupa of the red ants. I followed these black kidnappers as they returned to their nest some distance away. Checking on the red ant nest the next morning, I found the entrance torn open and the ground littered with the bodies of dead red worker ants. Animals were first to develop many of the things humans now take credit for, and warfare seems to be one of them.

For many years, I taught biology in a small community surrounded by cornfields. In those days, the corn was irrigated from ditches of water called laterals running perpendicular to the rows of corn. In late spring when irrigation would commence, I would invariably have students bring in crustaceans that just mysteriously appeared overnight in the irrigation laterals (and they just as mysteriously disappeared when irrigation season was over). What they collected were the ancient-looking tadpole shrimp (*Triops*). Hatching from winter resistant eggs laid by the previous generation in the mud of the last summer's irrigation, these creatures hatched, mated, laid the next generation of mystery shrimp eggs, and then vanished as quickly as they came. Just another example of how the animal world is always with us, surrounding us and all other life forms in ways we may never fully understand, but should always appreciate.

In Summary

- The ancestors of arthropods first appeared in the appeared in the primeval seas of the Precambrian over 600 million years ago. Today most zoologists judge that the modern arthropods represent the pinnacle of protostome development.
- Arthropods have evolved to become the most abundant, most diverse, and most biologically successful animals on earth. Of all the known and described species of animals, at least three out of every four is an arthropod.
- Arthropods may be classified into four subphyla and ten classes:

    Subphylum Chelicerata
        Class Arachnida—Spiders, scorpions, ticks, mites
        Class Merostomata—Horseshoe crabs
    Subphylum Myriapoda
        Class Chilopoda—Centipedes
        Class Diplopoda—Millipedes
    Subphylum Hexapoda
        Class Insecta—Insects
        Class Entognatha—Spring tails, bristletails, proturans
    Subphylum Crustacea
        Class Malacostraca—Crabs, shrimps, lobsters, woodlice
        Class Branchiopoda—Brine shrimp, fairy shrimp
        Class Maxillopoda—Barnacles, copepods, fish lice
        Class Ostracoda—Mussel shrimp

- The characteristics of phylum Arthropoda:

    1. Their segmented body is divided into tagmata (specialized body regions). The coelom is reduced to portions of the reproductive and excretory systems. Most of the body cavity consists of a hemocoel (sinuses or spaces within the tissues) filled with blood.
    2. They possess a cuticular exoskeleton composed of chitin, protein, and lipids. The chitinous skeleton is calcified in many groups. Growth occurs by the process of ecdysis (molting) periodically shedding the old exoskeleton and forming a new larger one.
    3. They possess jointed appendages. Ancestrally each true body segment bore a pair of jointed appendages but in modern arthropods, the number of appendages may be reduced and they are often modified for specialized functions.

4. They possess a complex muscle system attached to the exoskeleton for support and leverage. Functional cilia are absent.
5. They possess a complete digestive system with mouthparts modified from ancestral appendages into structures adapted for different methods of feeding.
6. Their circulatory system is open with a dorsal heart, arteries, and hemocoel containing blood.
7. Coaxial glands or Malpighian tubules serve as an excretory system. Coaxial glands are paired, thin-walled spherical sacs bathed in the blood of body sinuses. Nitrogenous wastes are absorbed across the sacs, and excreted through long, convoluted tubules that empty at the base of the posterior appendages. Malpighian tubules are diverticula (pockets or pouches off the gut tract of arachnids adapted to dry environments). These tubules absorb nitrogenous wastes from the blood and then empty them into the gut tract where they are eliminated along with the digestive wastes.
8. Gas exchange occurs through the body surface, gills, tracheae (air tubes), or book lungs. Tracheae are a series of branched, chitin-lined tubules that conduct gases to and from body tissues. This tubule system opens to the outside through holes called spiralces located along the ventrally or laterally along the abdomen. Book lungs are paired invaginations of the ventral body wall that fold into a series of leaf-like lamellae (thin, flat plates or disks). Air enters the book lung through a slit-like opening and circulates between the lamellae. Respiratory gases diffuse between the blood moving among the lamellae and the air in the lung chamber.
9. Their nervous system is similar to that of annelids with a dorsal brain connected by a ring around the gullet to a double nerve cord chain of ventral ganglia. Well-developed sense organs are present.
10. The sexes are usually separate with paired reproductive organs and ducts and internal fertilization the norm; some types are capable of parthenogenesis. Development progresses through several stages in a process known as metamorphosis.

- Subphylum Chelicerata is characterized by:

1. A body composed of two tagmata: the prosoma (cephalothorax) and the opisthosoma (abdomen). The cephalothorax represents a fusion of the head and thorax (trunk) and is often covered by a carapace-like dorsal shield. The abdomen is composed of up to 12 somites (sections) and a postsegmental telson. Antennae and wings are absent.
2. Uniramous appendages (single and unbranched) attached to the cephalothorax including: chelicerae (anterior appendages of an arachnid often specialized as fangs.), pedipalps (specialized sensory appendages borne near the mouth of an arachnid), and four pairs (8) walking legs.
3. An exoskeleton modified with projections, pores, and slits to accommodate a variety of mechanoreceptors and chemoreceptors (collectively known as sensilla), together with sensory and accessory cells.

- Subphylum Myriapoda is characterized by:

  1. A body of two tagmata: head and trunk (abdomen). No carapace or wings present.
  2. The abdomen being long and cylindrical and consisting of many segments.
  3. Uniramous appendages.
  4. One or two pair of walking legs per segment.
  5. One pair of articulate (jointed and movable) antennae attached to the head segment.
  6. A few to many clustered ocelli (simple eyes) on the head segment.
  7. Mouthparts consisting of mandibles (jaws), maxillules (first maxillae), and maxillae (second maxillae). The second maxillae are fused into a single flaplike structure called a labrum.
  8. A gas exchange system composed of tracheae and spiracles.

- Subphylum Hexapoda is characterized by:

  1. A body of three tagmata: head, thorax, abdomen without a carapace.
  2. Uniramous appendages.
  3. Three pairs of walking legs attached to the thorax. Wings are present in some species.
  4. A head bearing a single pair of jointed antennae, mouthparts consisting of mandibles, maxilla, labium, and labrum, compound eyes, and several ocelli.
  5. A gas exchange system consisting of tracheae and spiracles.
  6. An excretory system consisting of Malpighian tubules.

- Subphylum Crustacea is characterized by:

  1. Sixteen to 20 segments, with some forms having 60 segments or more.
  2. An exoskeleton that is more pronounced and generally thicker and heavier than other taxa of arthropods.
  3. Two or three tagmata: cephalothorax with a shield-like carapace and abdomen or head, thorax, and abdomen.
  4. Biramous (branching) appendages.
  5. Head appendages consisting of two pairs of antennae, a pair of mandibles, two pair of maxillae, and one pair of compound eyes.
  6. Both simple ocelli and compound eyes often elevated on stalks.
  7. Gas exchange typically across gills.
  8. Excretion by true nephridial structures.
  9. A developmental stage known as a nauplius larva that is characterized by the presence of three pairs of head appendages.

- Arthropods

    1. Have a body wall composed of a complex, layered cuticle or exoskeleton secreted by the underlying epidermis.
    2. Rely on the jointed exoskeleton for support and as attachments sites for the muscles that move the animal.
    3. Bear many limb segments or pieces called podites. Arthropod appendages may be categorized as either uniramous (with only a single branch or ramus) or biramous (Y-shaped with two rami). Spiders and their kin, centipedes, millipedes, and insects possess uniramous appendages whereas crustaceans bear biramous appendages.
    4. Possess a digestive tract that is complete and straight, extending from a ventral mouth on the head to a posterior anus. In nearly all cases, there is a well-developed cuticle-lined foregut and hindgut, connected by a midgut.
    5. Have a body cavity that functions as an open hemocoel with the organs being bathed directly in hemolymph (blood). The blood is driven from the heart chamber through short vessels and into the hemocoel, where it bathes the internal organs. The blood returns to the heart via a noncoelomic pericardial sinus and perforations in the heart wall called ostia.
    6. Exchange gas through gills in the crustaceans and through invaginations in the cuticle in insects and arachnids.
    7. Possess nephridia for filtering wastes but a hemolytic circulatory system demands that they be quite different than those found in the annelids. In contrast to the annelids, arthropods are equipped with closed nephridia, and there has been a reduction in the number of nephridia as well.
    8. Have a brain that comprises several bundles of fused ganglia. From the brain a ventral nerve cord runs back to the anus. This ventral nerve cord contains a fused ganglion in each segment.
    9. Have astonishingly high reproductive rates (fecunidty).
    10. With few exceptions, are dioecious. Sperm are commonly transferred to the female within sealed packets known as spermatophores. Once the eggs are fertilized the mode of development varies greatly with the subphylum.

- Arthropods connect to humans in ways that are important economically, ecologically, and medically.

Review and Reflect

1. ***What's My Job?*** Imagine you run an employment agency. Prospective employers have requested you find specific arthropods to fill the following job descriptions:

    - Athlete—a high jumper
    - Army—a combat soldier

- Construction—a bulldozer
- Construction—a plasterer
- Athlete—a weight lifter
- Recycling—a wood disassembler

Explain what specific arthropod you would select to fill each of the positions listed and why you selected them for that position. Your instructor may add additional jobs to be filled.

2. ***Walk a Mile in My Shoes*** If you had to be reincarnated as an arthropod, which specific arthropod would you choose to become and why?
3. ***A Giant Nightmare*** You and a group of your friends have just come out of a movie where three-story spiders battled giant ants as long as a football field. One of your friends turns to you and says, "Why don't real arthropods grow to be at least as large as elephants or whales?" How would you respond? (HINT: Fossils show that dragonflies with wingspans over 1 m (3 to 4 feet) did exist at one time but during that time it is believed that the concentration of oxygen in the atmosphere was much higher than it is today.)
4. ***The Nightmare Continues*** The movie about giant arthropods has given you bad dreams. In your dream, you are standing in a park when a giant predatory insect approaches you. What would be your best strategy—run like the wind or freeze motionless? Defend your choice.
5. ***Away We Grow*** **Figure 13.43** depicts the generalized growth pattern of a vertebrate, such as a koi fish in my pond, and an insect, such as an ant in my yard. Which line represents each type of animal? Explain how you arrived at your decision.

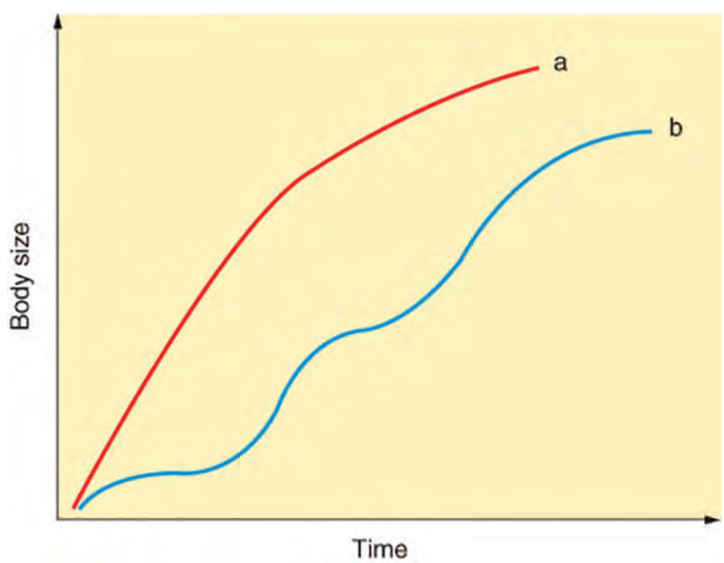

Figure 13.43 A generalized growth graph comparing the growth of an arthropod with the growth of a vertebrate.

6. ***A Sweet Set of Data*** Dr. Buzz Drosophila has been researching the relationship between the length of life in fruit flies and the amount of sugar they receive in their diet. His data is listed in **Table 13.1**. Graph the data from the table and use the graph to answer the following:

Table 13.1

Percentage of Sugar	Time of Survival
0	50
0.125	75
0.500	100
0.750	150
1.000	225
2.500	200
5.000	475
10.00	480
20.00	600
30.00	580
50.00	500
80.00	400
90.00	225
95.00	195
100	100

A. Exactly what information does the graph show?
B. What percentage of sugar provides for the longest life in fruit flies?
C. Theorize why the survival longevity went down as the percentage of sugar went up.

7. ***A Sticky Situation*** Why don't spiders get stuck in the own web? Investigate and explain.
8. ***Those Pesky Bugs*** You wander over to your neighbor's garden and find him sticking grasshoppers head down into a bucket of water. Seeing the strange look on your face, he replies, "These darned grasshoppers are eating up my garden, but I don't want to spray chemical insecticides so I am going to drown the little buggers." How would you respond?
9. ***A Bug-Proof Garden?*** Several days later your gardening neighbor knocks at your door. He gathered some information from the Organic Gardening Society and he shows you the information they sent him (**Table 13.2**). Unfortunately, he lost all the information other than the table itself. As you study the table he asks:

Table 13.2

Number of Caterpillars	Plant Type
105	Green bean
62	Pea
47	Tomato
4	Onion

A. What information is presented in this table?
B. Why might there be fewer caterpillars on the onion?
C. What good is this information? How can I use it? Help your neighbor draw up a garden plan for planting an organic garden that makes use of the information in the table.

10. ***A Call to Arms*** People who squash an annoying hornet are often unpleasantly surprised to find themselves suddenly under attack by dozens of hornets. Explain this phenomenon.

Create and Connect

1. ***More Bad Dreams*** Strange things happen in the laboratory. In fact, just this past week my assistant, Igor, spilled a beaker of secret formula onto a stack of zoology textbooks. This secret formula changes humans into arthropods. Unfortunately, the textbook you are now touching is from that pile, and you will change into an arthropod shortly. Science fiction writers have concocted stories about this very thing as the short piece below illustrates:

> *As Gregor Samsa awoke one morning from a troubled dream, he found himself changed in his bed to some monstrous kind of vermin (beetle). He lay on his back, which was as hard as armour-plate, and, raising his head a little, he could see the arch of his great brown belly, divided by bowed corrugations. The bed cover was slipping helplessly off the summit of the curve, and Gregor's legs, pitiably thin compared with their former size, fluttered helplessly before his eyes.*
>
> —Frank Kafka, *The Metamorphosis*

Write a short story in which you imagine what it would be like to be an arthropod.

Guidelines:

A. Specifically what type of arthropod you have changed into.
B. What you look like (diagrams and/or pictures would be appropriate).
C. How do you breathe, how and what do you eat, and how do you see, feel, and hear.
D. Set your story up in the following format:

- Appropriate Title
- Catchy Beginning. Catch and hold your reader's attention.
- Understandable Middle. Don't muddy up the middle.
- Believable Ending. Give believable (but not necessarily happy) closure.

E. The instructor may provide additional details or further instructions.

2. ***Keeping in Touch***. Despite being encased in an exoskeleton, arthropods are remarkably in touch with the physical aspects of the environment around them. Light, sound, temperature and humidity changes, and possibly even the magnetic field of the earth itself can be sensed by arthropods. Design an experiment to test the problem question: *Do mealworm larvae respond to magnetic fields*?

   Guidelines:

   A. Your design should include the following components in order:

   - The *Problem Question*. State exactly what problem you will be attempting to solve.
   - Your *Hypothesis*. Although this is a fictitious experiment, word your hypothesis as realistically as possible.
   - *Methods and Materials*. Explain exactly what you will do in your experiment including the materials necessary to accomplish the task. Be specific, take nothing for granted, and do not expect people to read your mind as they read your work.
   - *Collecting and Analyzing Data*. Explain what type(s) of data will be collected and what statistical tests might be performed on that data. It is not necessary to concoct either fictitious data or imaginary observations.

   B. Assume you have access to everything necessary to conduct your experiment. Within reason, money is no object.

   C. Your instructor may provide additional details or further instructions.

3. ***What's in a Quote?*** In his book, *The Diversity of Life*, Edward O. Wilson states: "Humans dwell among the six-legged masses with a tenuous grip on the planet. Insects can thrive without us, but we would perish without them." Contemplate that possibility. Agree or disagree? Write a short essay in which you defend or refute Wilson's quote.
4. ***Sing the Praises*** Compose a poem or song entitled "Almighty Arthropod Armada" (or another suitable title of your choice) in which you touch on the great diversity of arthropods, their tremendous environmental success, and their importance to the rest of nature.