9–1 Invertebrate Evolution

Until recently, the origins of invertebrates were shrouded in mystery. This was because few fossils old enough to shed ;ht on this period in Earth's history had been found. But .going discoveries around the world are shedding new light on e origins of invertebrates. Treasure troves of beautifully eserved invertebrate fossils, dating between 575 and 543 illion years ago, have been discovered in the Ediacara Hills of ıstralia and in Chengjiang, China. These fossils join those ıown from the Burgess Shale deposits in the Canadian ɔckies to show a fascinating history of early multicellular life.

rigin of the Invertebrates

ıe Ediacaran fossils brought to light a strange group of ıcient invertebrates. These peculiar fossils puzzled paleontolo-sts for years because they seemed quite different from any .odern invertebrates. More recently, paleontologists have .entified beautifully preserved, microscopic fossils, between 10 and 570 million years old, that seem to be the developing nbryos of early multicellular animals. From the same time ɜriod, they also identified what are called trace fossils. Trace ıssils are tracks and burrows made by soft-bodied animals hose bodies were not fossilized.

Molecular biologists and paleontologists have also created a ew field called molecular paleontology. This research uses ıtting-edge studies in genetics to understand how different nimal body plans evolved. DNA comparisons among living ıvertebrates help determine which phyla are most closely ɜlated. In addition, geneticists are studying how small changes ı certain genes can cause major changes in body structures.

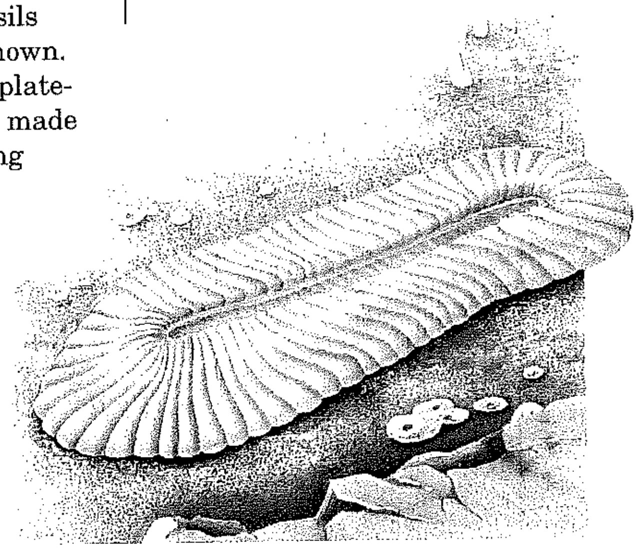
he First Multicellular Animals The Ediacaran fossils ıclude some of the earliest and most primitive animals known. Iost, like the animal shown in **Figure 29–1,** were flat and plate-haped and lived on the bottom of shallow seas. They were made f soft tissues that absorbed nutrients from the surrounding vater. Some may have had photosynthetic algae living vithin their tissues. These animals were segmented ınd had bilateral symmetry. However, they show little ɜvidence of cell specialization or organization into a ront and back end. Some of these early animals may ıave been related to soft-bodied invertebrates such as ellyfishes and worms. Their body plan, however, is listinct from anything alive today. Regardless of their relationships to other organisms, these animals were probably simple and had little internal specialization.

Guide for Reading

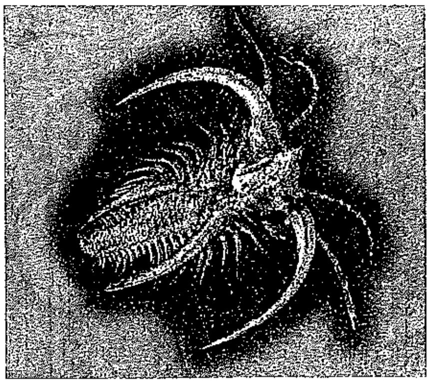
Key Concept
- What are the major trends in invertebrate evolution?

Vocabulary
radial symmetry
bilateral symmetry
cephalization
coelom

Reading Strategy: Using Visuals Before you read, preview **Figure 29–4.** As you read, notice how the evolutionary trends in the cladogram are discussed in the text.



▼ **Figure 29–1** The drawing is an artist's conception of what an early invertebrate might have looked like. **Applying Concepts** *In what environment did most early invertebrates live?*



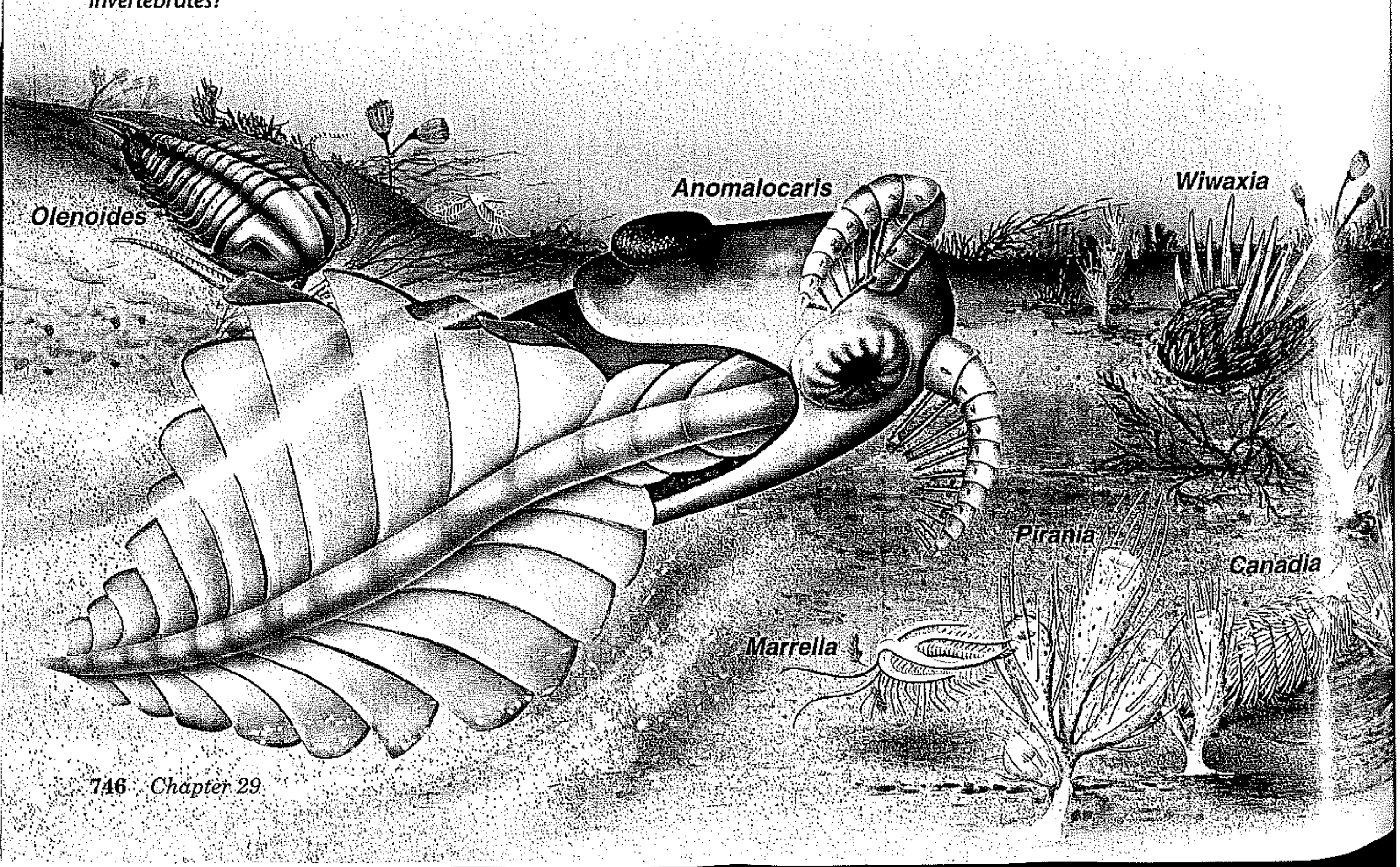
▲ **Figure 29–2** The fossilized arthropod *Marrella splendens,* like most Burgess Shale animals, had body symmetry, segmentation, a skeleton, a front and a back end, and appendages adapted for many functions. **Comparing and Contrasting** *How is this fossil similar to modern arthropods?*

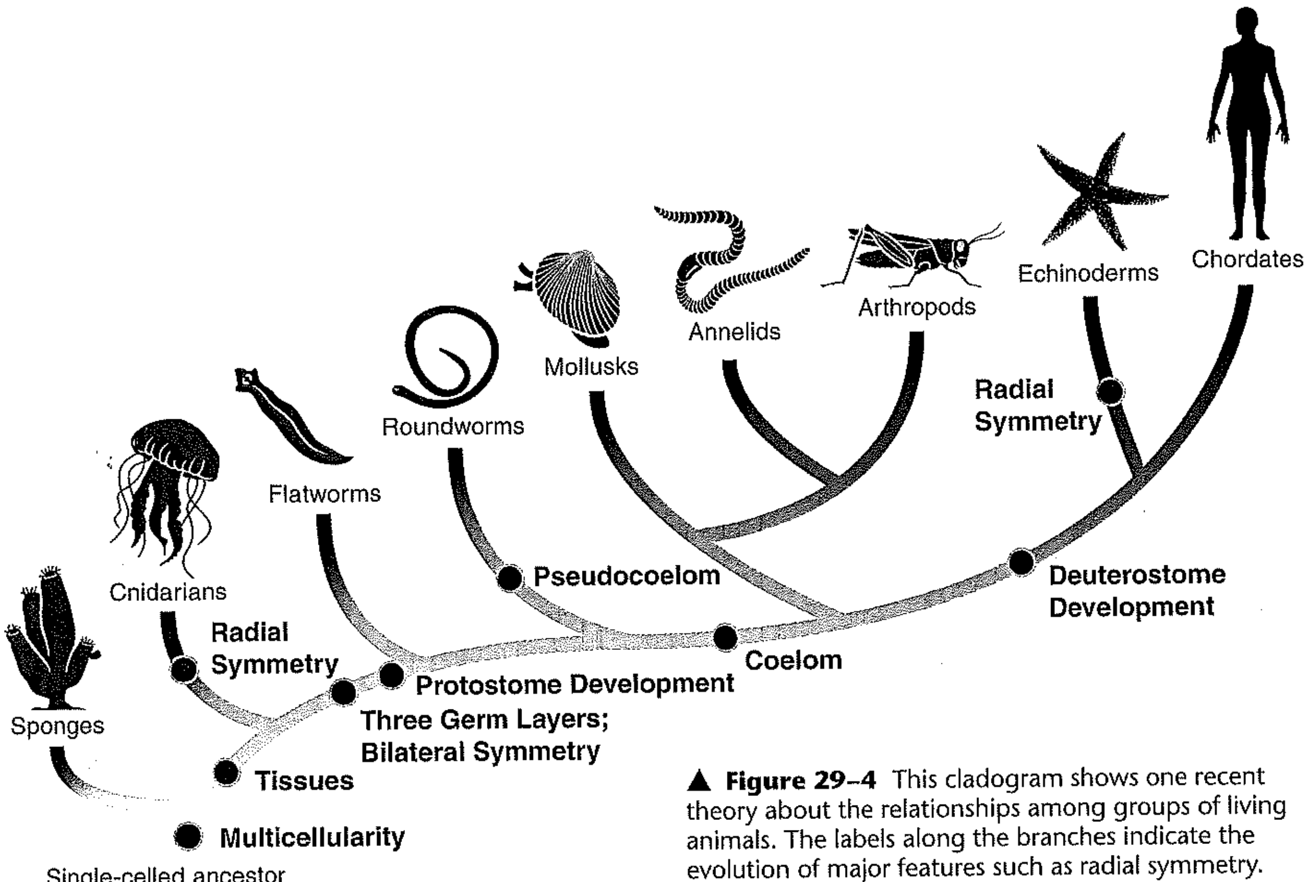
▼ **Figure 29–3** This illustration shows what some of the Cambrian organisms found in the Burgess Shale may have looked like. Note the wide variety of body shapes and appendages. **Observing** *What body features of these animals are similar to those of modern invertebrates?*

Beginnings of Invertebrate Diversity Fossils from a few million years later—a short period in geological time—paint a radically different picture of invertebrate life. The Cambrian Period, which began 544 million years ago, is marked by an abundance of different fossils. Why the difference from earlier periods? By the Cambrian period, some animals had evolved shells, skeletons, and other hard body parts—all of which are readily preserved in fossils. Suddenly, the fossil record provided a wealth of information about animal diversity, body plans, and adaptations to life. One of the best-known sites of Cambrian fossils is the Burgess Shale of Canada. A fossil from the Burgess Shale is shown in **Figure 29–2.**

You can see what some of the Burgess Shale animals may have looked like in **Figure 29–3.** Trilobites such as *Olenoides* moved along the ocean floor. *Wiwaxia* had two rows of long, pointed spikes. The annelid *Canadia,* like many annelids today, had prominent setae. *Anomalocaris,* the largest Burgess Shale fossil, had fearsome-looking forelimbs that were probably used to grasp prey. The animals of the Burgess Shale are far more numerous and diverse than anything that lived earlier.

In just a few million years, animals had evolved complex body plans. They acquired specialized cells, tissues, and organs. Because of the extraordinary growth in animal diversity, events of the early Cambrian Period are called the Cambrian Explosion. During that time, the ancestors of most modern animal phyla first appear in the fossil record.





▲ **Figure 29–4** This cladogram shows one recent theory about the relationships among groups of living animals. The labels along the branches indicate the evolution of major features such as radial symmetry. **Interpreting Graphics** *To which group of invertebrates are echinoderms least closely related?*

What features of the Cambrian animals made them so successful? One way of determining this is to find their common features—especially those that are present in animals today. Burgess Shale animals typically had body symmetry, segmentation, some type of skeleton, a front and a back end, and appendages adapted for a multitude of functions..These features are characteristic of most invertebrates living today.

Modern Evolutionary Relationships

The cladogram in **Figure 29–4** shows the evolutionary relationships among major groups of living invertebrates. It also indicates the sequence in which some important features evolved. These features include tissues and organs, patterns of early development, body symmetry, cephalization, segmentation, and the formation of three germ layers and a coelom. Many of these features, which have persisted up to modern times, evolved in animals of the Cambrian Period. As you review the major trends in invertebrate evolution, consider how each feature might have contributed to the evolutionary success of animals.

CHECKPOINT *What groups of animals are deuterostomes?*

Word Origins

The word *germ* in the term *germ layers* comes from the Latin word *germen,* which means "embryo" or "sprout." **If the suffix *-ate* means "to become," what happens to a seed when it germinates?**

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Evolutionary Trends

The appearance of each phylum in the fossil record represents the evolution of a successful and unique body plan. Features of this body plan typically change over time, leading to the formation of many new traits. The major trends of invertebrate evolution are summarized in **Figure 29–5.**

Specialized Cells, Tissues, and Organs Modern sponges and cnidarians have little internal specialization. They carry out essential functions using individual cells or simple tissues. As larger and more complex animals evolved, specialized cells joined together to form tissues, organs, and organ systems that work together to carry out complex functions. Flatworms have simple organs for digestion, excretion, response, and reproduction. More complex animals, such as mollusks and arthropods, have organ systems.

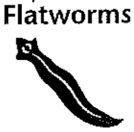
Body Symmetry Sponges lack body symmetry. **All invertebrates except sponges exhibit some type of body symmetry.** Cnidarians and echinoderms exhibit **radial symmetry**—body parts extend from the center of the body. Worms, mollusks, and arthropods exhibit **bilateral symmetry,** or have mirror-image left and right sides.

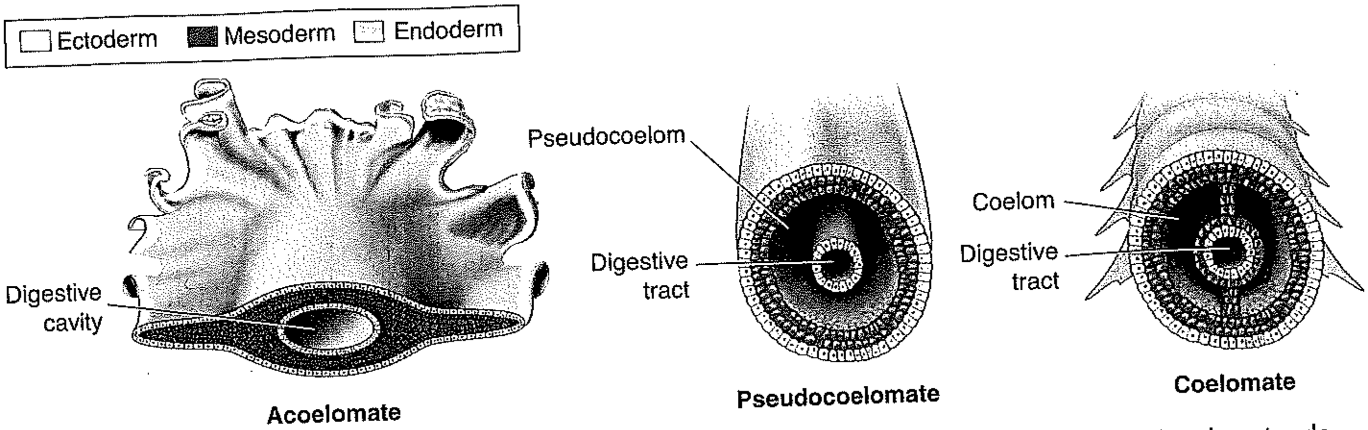
Cephalization Most invertebrates with bilateral symmetry rely on movement for feeding, defense, and other important functions. The evolution of this body plan and lifestyle was accompanied by the trend toward **cephalization,** which is the concentration of sense organs and nerve cells in the front of the body. **Invertebrates with cephalization can respond to the environment in more sophisticated ways than can simpler invertebrates.** In most worms and arthropods, nerve cells are arranged in structures called ganglia. In more complex invertebrates, such as certain mollusks, nerve cells form an organ called a brain.

CHECKPOINT *How does cephalization benefit an animal?*

▶ **Figure 29–5** This table shows the major characteristics of the main groups of invertebrates. **Germ layers, body symmetry, cephalization, and development of a coelom are more common in complex invertebrates than in simple ones.** Mollusks, for example, have all of these features, but sponges have none of them.

Comparing Invertebrates

	Sponges 	Cnidarians 	Flatworms 
Germ Layers	Absent	Two	Three
Body Symmetry	Absent	Radial	Bilateral
Cephalization	Absent	Absent	Present
Coelom	Absent	Absent	Absent
Early Development	———	———	Protostome

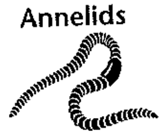


▲ **Figure 29–6** Acoelomates do not have a coelom, or body cavity, between their germ layers. Pseudocoelomates have body cavities that are partially lined with mesoderm. **Most complex animal phyla are coelomates, meaning that they have a true coelom that is lined completely with mesoderm.**

Segmentation Most invertebrates with bilateral symmetry also have segmented bodies. Over the course of evolution, different segments have often become specialized for specific functions. Because the same structures are repeated in each body segment, segmentation also allows an animal to increase in body size with a minimum of new genetic material.

Coelom Formation Jellyfishes have a simple construction in which a jellylike layer lies between ectoderm and endoderm tissues. Other invertebrates develop from three germ layers, the endoderm, mesoderm, and ectoderm, as shown in **Figure 29–6**. Invertebrate phyla differ in the arrangement of these layers. Flatworms are acoelomates, meaning that no **coelom,** or body cavity, forms between the germ layers. Pseudocoelomates, such as roundworms, have a body cavity lined partially with mesoderm. **Most complex animal phyla have a true coelom that is lined completely with mesoderm.**

Early Development In most invertebrates, the zygote divides repeatedly to form a blastula—a hollow ball of cells. In protostomes, the blastopore, or the opening of the blastula, develops into a mouth. In deuterostomes, the blastopore forms an anus. Worms, arthropods, and mollusks are protostomes, and echinoderms are deuterostomes.

Roundworms	Annelids	Mollusks	Arthropods	Echinoderms
				
Three	Three	Three	Three	Three
Bilateral	Bilateral	Bilateral	Bilateral	Radial (adults)
Present	Present	Present	Present	Absent (adults)
Pseudocoelom	True coelom	True coelom	True coelom	True coelom
Protostome	Protostome	Protostome	Protostome	Deuterostome

29–2 Form and Function in Invertebrates

To survive, all animals perform the same essential tasks: feeding and digestion, respiration, circulation, excretion, response, movement, and reproduction. In many ways, each animal phylum represents an "experiment" in the adaptation of body structures to carry out these tasks. The appearance of each phylum in the fossil record, therefore, represents the evolutionary development of a unique body plan. The continued history of each phylum is the story of further evolutionary changes to that plan.

Biologists can learn a great deal about the nature of life by comparing body systems among groups of living invertebrates. Body systems that perform the essential tasks of life have taken many different forms in different phyla. Each phylum has a particular type of breathing device, a certain type of body support system, and numerous variations on other body functions. More complicated systems are not necessarily better than simpler systems. The fact that any system is found in living animals testifies to its success in performing functions adequately. This section reviews the basic evolutionary trends in each body system, using examples from a variety of invertebrate groups.

Guide for Reading

Key Concept
- How do different invertebrate phyla carry out their essential life functions?

Vocabulary
intracellular digestion
extracellular digestion
open circulatory system
closed circulatory system
hydrostatic skeleton
exoskeleton
endoskeleton
external fertilization
internal fertilization

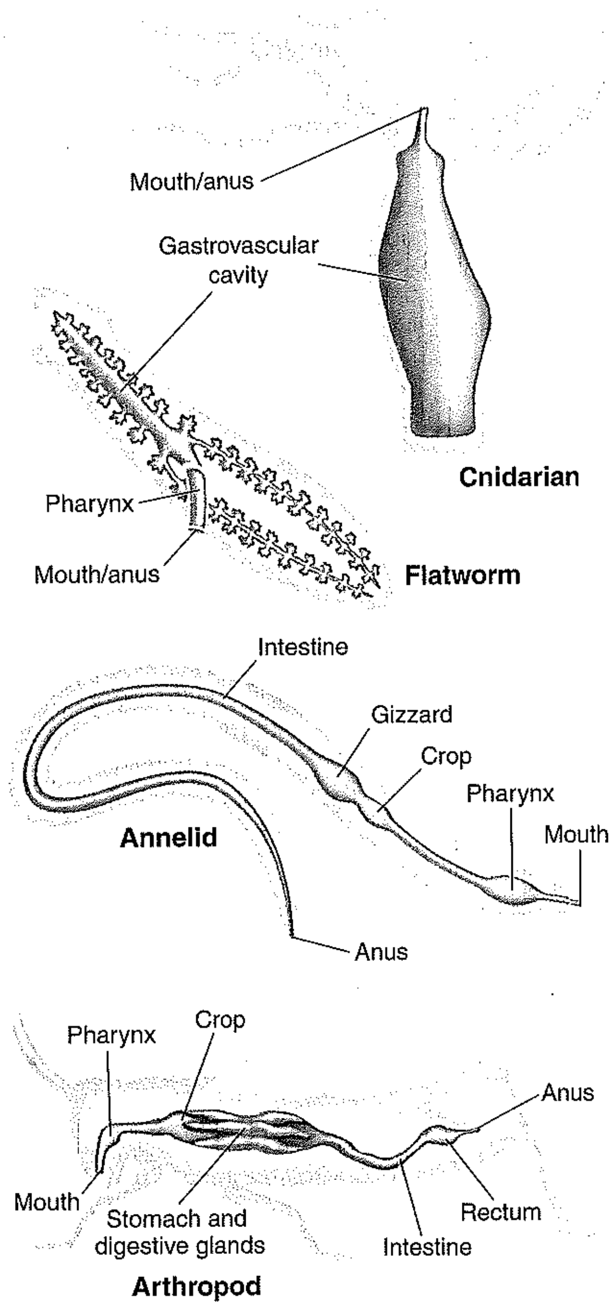
Reading Strategy: Finding Main Ideas Before you read, skim the section to identify the key ideas. Then, carefully read the section, making a list of supporting details for each main idea.

Feeding and Digestion

Invertebrates have evolved many different ways of obtaining food. The spider in **Figure 29–7**, for example, is feeding on a caterpillar after killing it with venom. Before food can be used for energy, the food must be broken down, or digested. The digested food must then be absorbed into the animal's body. Complex animals accomplish these processes in different ways than simpler ones.

Intracellular and Extracellular Digestion Invertebrates have evolved different ways of digesting food. **The simplest animals break down food primarily through intracellular digestion, but more complex animals use extracellular digestion.** Sponges digest their food inside archaeocytes, which pass nutrients to other cells by diffusion. Because food is digested inside cells, this process is known as **intracellular digestion.** In contrast, mollusks, annelids, arthropods, and echinoderms rely almost entirely on extracellular digestion. In **extracellular digestion,** food is broken down outside the cells in a digestive cavity or tract and then absorbed into the body. Flatworms and cnidarians use both intracellular and extracellular digestion.

▶ **Figure 29–7** **Complex animals break down food using extracellular digestion.** The spider's venom is breaking down the tissues of the caterpillar. Later, the broken-down food molecules will be absorbed into the spider's digestive tract.



▲ **Figure 29–8** Cnidarians and flatworms have a digestive system with only one opening. In more complex animals, the digestive system has two openings. In addition, the digestive organs have become more specialized. **Interpreting Graphics** *Which of these animals has the least specialized digestive system?*

Patterns of Extracellular Digestion

Invertebrates have a variety of digestive systems, as shown in **Figure 29–8.** Simple animals such as cnidarians and flatworms ingest food and expel wastes through a single opening. Food is digested in the gastrovascular cavity through both extracellular and intracellular means. Some cells of the gastrovascular cavity secrete enzymes and absorb the digested food. Other cells surround food particles and digest them in vacuoles. Digested food then diffuses throughout the body.

More-complex animals digest food in a tube called the digestive tract. Food enters the body through the mouth, and wastes leave through the anus. A one-way digestive tract (which is characteristic of roundworms, annelids, mollusks, arthropods, and echinoderms) often has specialized regions, such as a stomach and intestines. Specialization of the digestive tract allows food to be processed more efficiently, because each step in the process takes place in order, at a specific place along the digestive tract.

Respiration

All animals must exchange oxygen and carbon dioxide with the environment. The more surface area that is exposed to the environment, the greater the amount of gas exchange that can occur. In addition, gases diffuse most efficiently across a thin, moist membrane. Given these principles, all respiratory systems share two basic features. **Respiratory organs have large surface areas that are in contact with the air or water. Also, for diffusion to occur the respiratory surfaces must be moist.**

Aquatic Invertebrates Aquatic animals, such as cnidarians and some flatworms, naturally have moist respiratory surfaces. Many animals even respire through their skins. However, for most active animals larger than worms, skin respiration alone is not sufficient. Aquatic mollusks, arthropods, and many annelids exchange gases through gills. Gills are feathery structures that expose a large surface area to the water. Gills are rich in blood vessels that bring blood close to the surface for gas exchange.

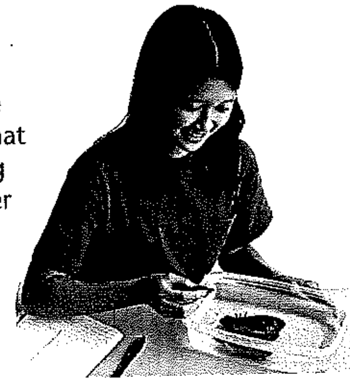
Quick Lab

How do clams and crayfishes breathe?

Materials live clam, food coloring, crayfish, small container of water

Procedure

1. Put a drop of food coloring in the water near a clam's siphons. Observe what happens to the coloring.
2. Put a drop of food coloring in the water near the middle of a crayfish's carapace. **CAUTION:** *Keep your fingers away from the crayfish's pincers.* Observe what happens to the coloring.



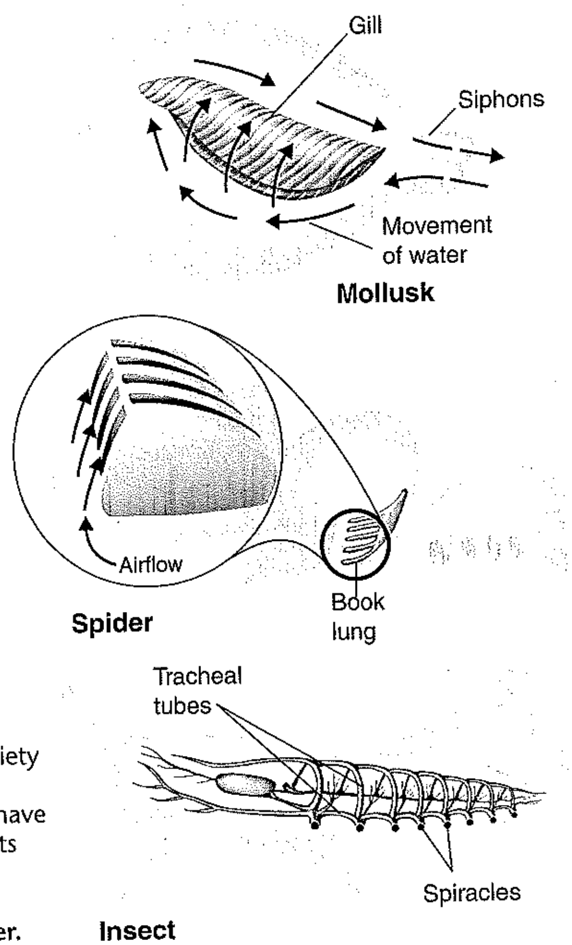
Analyze and Conclude

1. **Observing** Describe what happened to the coloring in step 1. How does water move past a clam's gills?
2. **Inferring** What is the clam's main defense? How is the location of the clam's siphons related to this defense?
3. **Comparing and Contrasting** What happened in step 2? Compare the flow of water past the gills of clams and crayfish.
4. **Inferring** Why do you think the crayfish has gills rather than spiracles, as some other arthropods do?

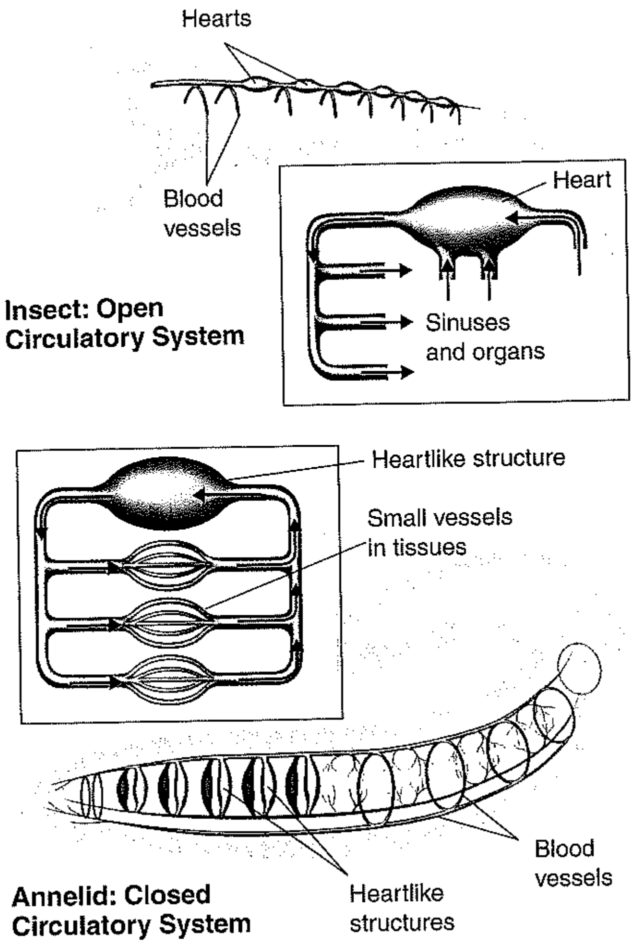
Terrestrial Invertebrates In terrestrial animals, respiratory surfaces are covered with water or mucus, thereby minimizing water loss. In addition, air is moistened as it travels through the body to the respiratory surface.

Terrestrial invertebrates have several types of respiratory surfaces. The mantle cavity of a land snail is a moist tissue that has an extensive surface area lined with blood vessels. Spiders respire using organs called book lungs, such as the one shown in **Figure 29–9.** Book lungs are made of parallel, sheetlike layers of thin tissues that contain blood vessels. In insects, air enters the body through openings called spiracles. It then enters a network of tracheal tubes, where gases diffuse in and out of surrounding body fluids.

✓CHECKPOINT *How does respiration in aquatic invertebrates differ from respiration in terrestrial invertebrates?*



▶ **Figure 29–9** Invertebrates have a variety of respiratory structures. Clams and other aquatic mollusks have gills. Many spiders have book lungs. Grasshoppers and other insects have spiracles and tracheal tubes. **All respiratory organs have large, moist surface areas in contact with air or water.**



▲ **Figure 29–10** **Most complex animals have one or more hearts to move fluid through their bodies in either an open or closed circulatory system.** An insect has an open circulatory system in which blood leaves blood vessels and then moves through sinuses, or body cavities. An annelid has a closed circulatory system in which blood stays in blood vessels as it moves through the body.

Circulation

All cells require a constant supply of oxygen and nutrients, and the cells must also remove metabolic wastes. The smallest and thinnest animals meet this requirement by simple diffusion between their body surface and the environment. But this system is usually insufficient for larger animals. **Most complex animals move blood through their bodies using one or more hearts and either an open or closed circulatory system.** Both types of circulatory systems are shown in **Figure 29–10.**

Open Circulatory Systems In an **open circulatory system,** blood is only partially contained within a system of blood vessels. Instead, one or more hearts or heartlike organs pump blood through blood vessels into a system of sinuses, or spongy cavities. The blood comes in direct contact with the tissues and eventually makes its way back to the heart. Open circulatory systems are characteristic of arthropods and most mollusks.

Closed Circulatory Systems In a **closed circulatory system,** a heart or heartlike organ forces blood through vessels that extend throughout the body. The blood stays within these blood vessels. Materials reach body tissues by diffusing across the walls of the blood vessels. Closed circulatory systems are characteristic of larger, more active animals. Because blood trapped within the blood vessels is kept at high pressure, it can be circulated more efficiently than in an open circulatory system. Among the invertebrates, closed circulatory systems are found in annelids and some mollusks.

✔ CHECKPOINT *Why are closed circulatory systems more efficient than open circulatory systems?*

Excretion

Multicellular animals, whether they are aquatic or terrestrial, must control the amount of water in their tissues. At the same time, all animals must get rid of ammonia, a toxic nitrogenous (nitrogen-containing) waste produced as a result of metabolism. Ammonia (NH_3) results from the breakdown of amino acids. **Most animals have an excretory system that rids the body of metabolic wastes while controlling the amount of water in the tissues.** The excretory systems of invertebrates carry out these functions in a variety of ways, as shown in **Figure 29–11.**

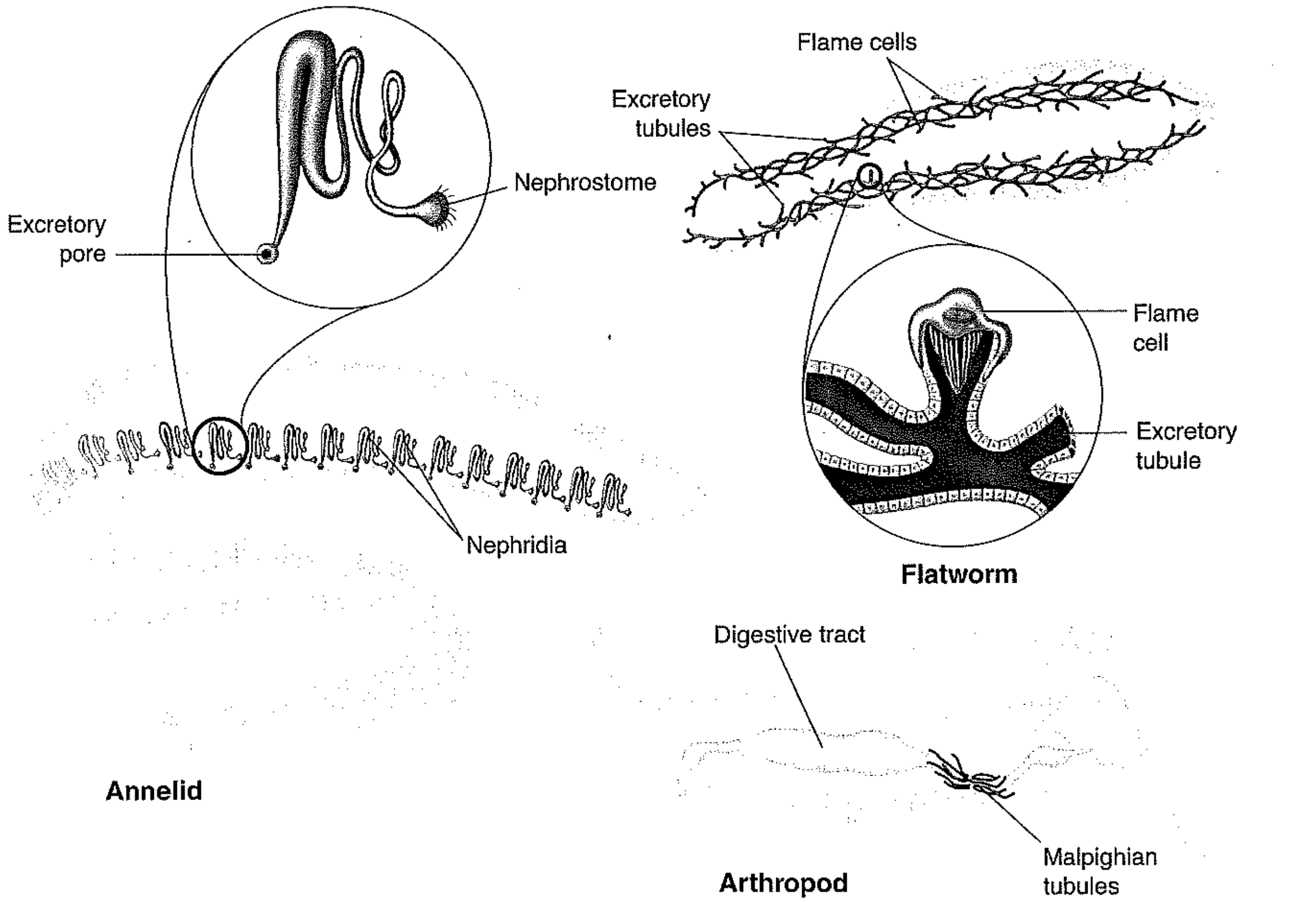
Aquatic Invertebrates In aquatic invertebrates such as sponges, cnidarians, and some roundworms, ammonia diffuses from their body tissues into the surrounding water. The water immediately dilutes the ammonia and carries it away.

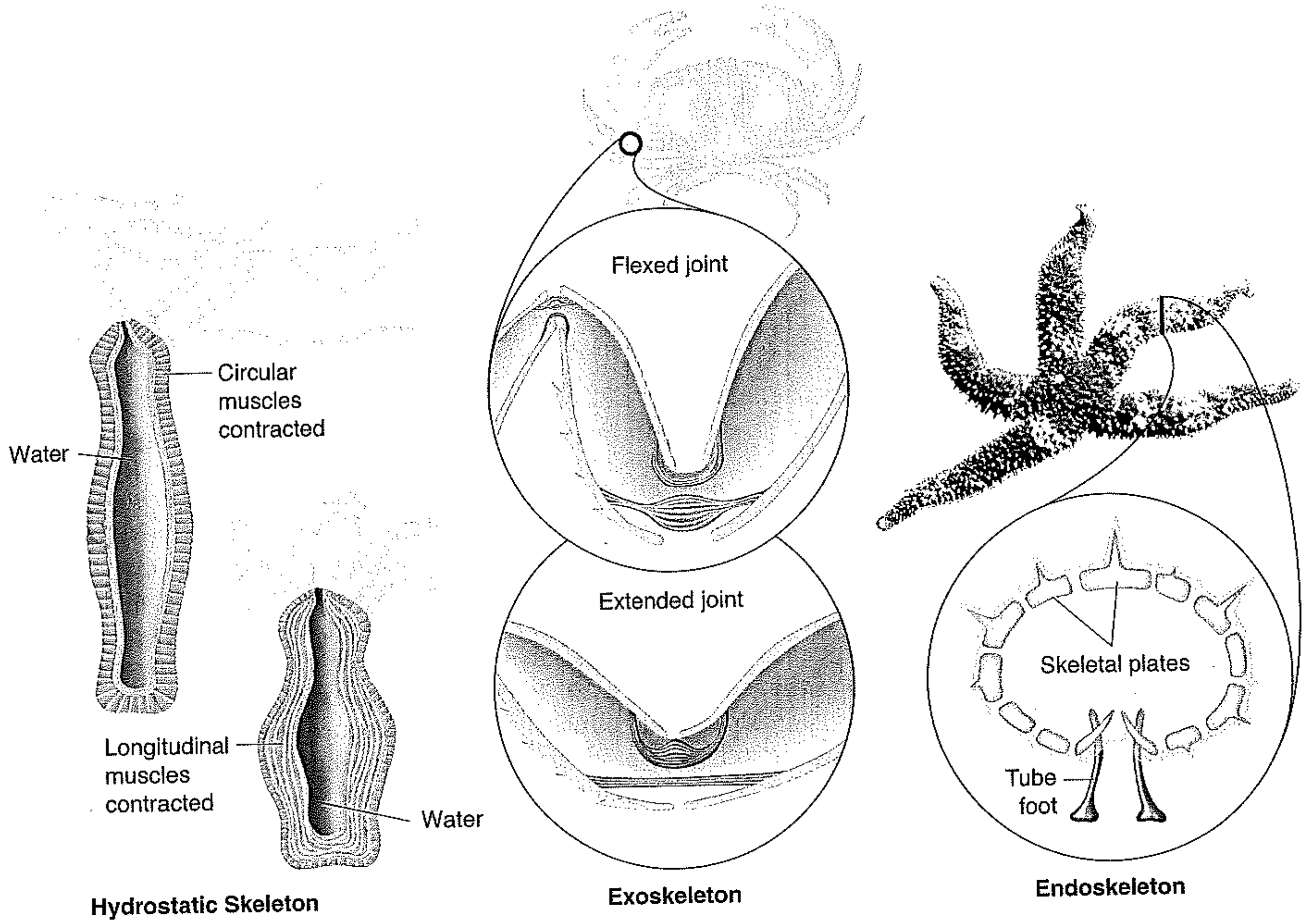
If freshwater invertebrates did not continually rid their bodies of excess water, they would swell up like water balloons. Flatworms use a network of flame cells to eliminate excess water. Fluid travels through execretory tubules and leaves the body through tiny pores in the animal's skin.

Terrestrial Invertebrates Terrestrial invertebrates must conserve body water while removing nitrogenous wastes from the body. To do this, many animals convert ammonia into a compound called urea, which is much less toxic than ammonia. Urea is eliminated from the body in urine. Urine is highly concentrated, so little water is lost. In annelids and mollusks, urine forms in tubelike structures called nephridia. Fluid enters the nephridia through openings called nephrostomes. Urine leaves the body through excretory pores.

Some insects and arachnids have Malpighian tubules, saclike organs that convert ammonia into uric acid. Uric acid is much less toxic than ammonia. Both uric acid and digestive wastes combine to form a thick paste that leaves the body through a structure called the rectum. Because the paste contains little water, this process also reduces water loss.

▼ Figure 29–11 Most animals dispose of wastes through excretory systems. Excretory systems also control an organism's water levels. Flatworms excrete ammonia directly into the water and use flame cells to remove excess water. Annelids use nephridia to convert ammonia into urea and to concentrate it in urine. Some arthropods have Malpighian tubules, which convert ammonia into uric acid. Uric acid is eliminated from the body in a paste.





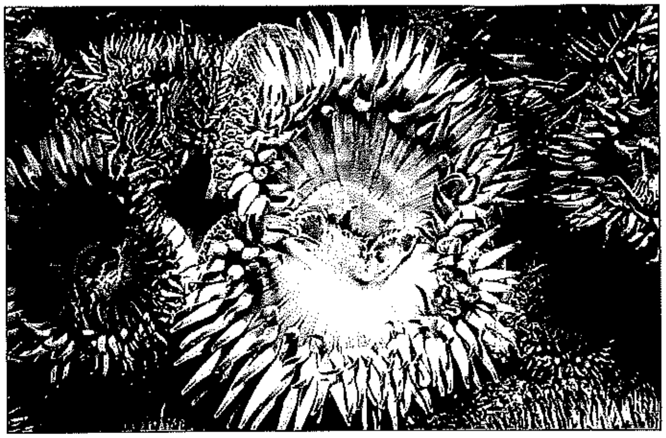
▲ **Figure 29–13 The three main types of invertebrate skeletons are hydrostatic skeletons, exoskeletons, and endoskeletons.** In animals with hydrostatic skeletons, muscles contract against a fluid-filled body cavity. In animals with exoskeletons, the muscles pull against the insides of the exoskeleton. Echinoderms and some sponges have endoskeletons.

Exoskeletons In arthropods, the **exoskeleton,** or external skeleton, is a hard body covering made of chitin. Arthropods move by using muscles that are attached to the inside of the exoskeleton. These muscles bend and straighten different joints. The shells of some mollusks can also be considered exoskeletons. Muscles attached to the shell make it possible for snails to withdraw into their shells and for bivalves to close.

Endoskeletons An **endoskeleton** is a structural support located inside the body. Sea stars and other echinoderms have an endoskeleton made of calcified plates. These plates function in support and protection, and also give these animals a bumpy and irregular texture. Vertebrates' bones are also endoskeletons.

Reproduction

Most invertebrates reproduce sexually during at least part of their life cycle. Depending on environmental conditions, however, many invertebrates may also reproduce asexually. Each form of reproduction has advantages and disadvantages. Asexual reproduction allows animals to reproduce rapidly and take advantage of favorable conditions in the environment. Sexual reproduction, however, maintains genetic diversity in a population by creating individuals with new combinations of genes.



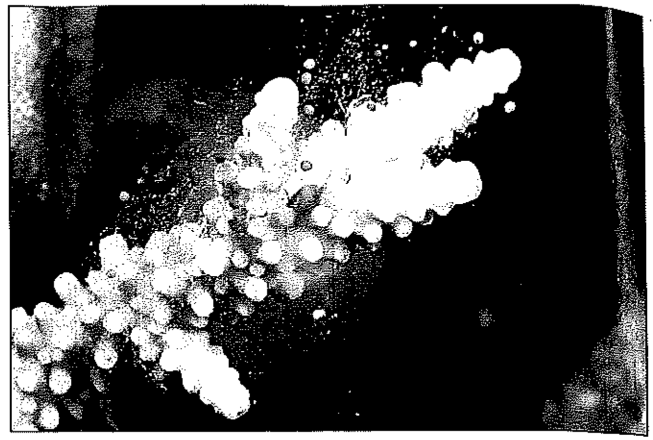


Figure 29–14 Invertebrates may reproduce asexually or sexually. Note that the largest sea anemone in this group is undergoing asexual reproduction by splitting into two parts (left). The *Acorpora* coral (right) is releasing brown eggs into the water. The eggs will be fertilized externally. This is an example of sexual reproduction.

In asexual reproduction, all offspring produced are genetically identical to the parent. Asexual reproduction may occur by fragmentation, in which an organism breaks into pieces that grow into new individuals. It may also occur by budding, in which new individuals are produced from outgrowths of the parent's body wall. Some animals, such as the sea anemone on the left in **Figure 29–14,** reproduce asexually by dividing in two.

Most multicellular animals reproduce sexually. Sexual reproduction is the production of offspring from the fusion of male and female gametes. Most animals have separate sexes, meaning that an individual produces either sperm or eggs. But some animals, including certain mollusks and annelids, are hermaphrodites, or individual animals that can produce both sperm and eggs.

Sperm and eggs may meet in two different ways. In **external fertilization,** eggs are fertilized outside the female's body. Adults may release sperm and eggs into the surrounding water, and the sperm swim to the eggs and fertilize them. In **internal fertilization,** eggs are fertilized inside the female's body. Males typically use specialized organs to deposit sperm inside the female's reproductive tract.

29–2 Section Assessment

1. **Key Concept** In your own words, describe the evolution of three different body systems of invertebrates.
2. Compare circulation in annelids and arthropods.
3. What are the three main kinds of skeleton systems in invertebrates?
4. Compare asexual and sexual reproduction. What are the advantages and disadvantages of each?
5. **Critical Thinking Applying Concepts** List the three forms of nitrogenous wastes excreted by animals. How are the ways in which animals dispose of these wastes related to each animal's environment?

iTEXT Assessment Use iText to review the important concepts in Section 29–2.

Take It to the NET

Many invertebrates live in marine ecosystems. Choose one species of marine invertebrate to research. Then present your findings. Include a description and photograph of the animal, its species and common name, phylum, and habitat. Use the links provided in the Biology area at the Prentice Hall Web site for help in completing this activity: **www.phschool.com**