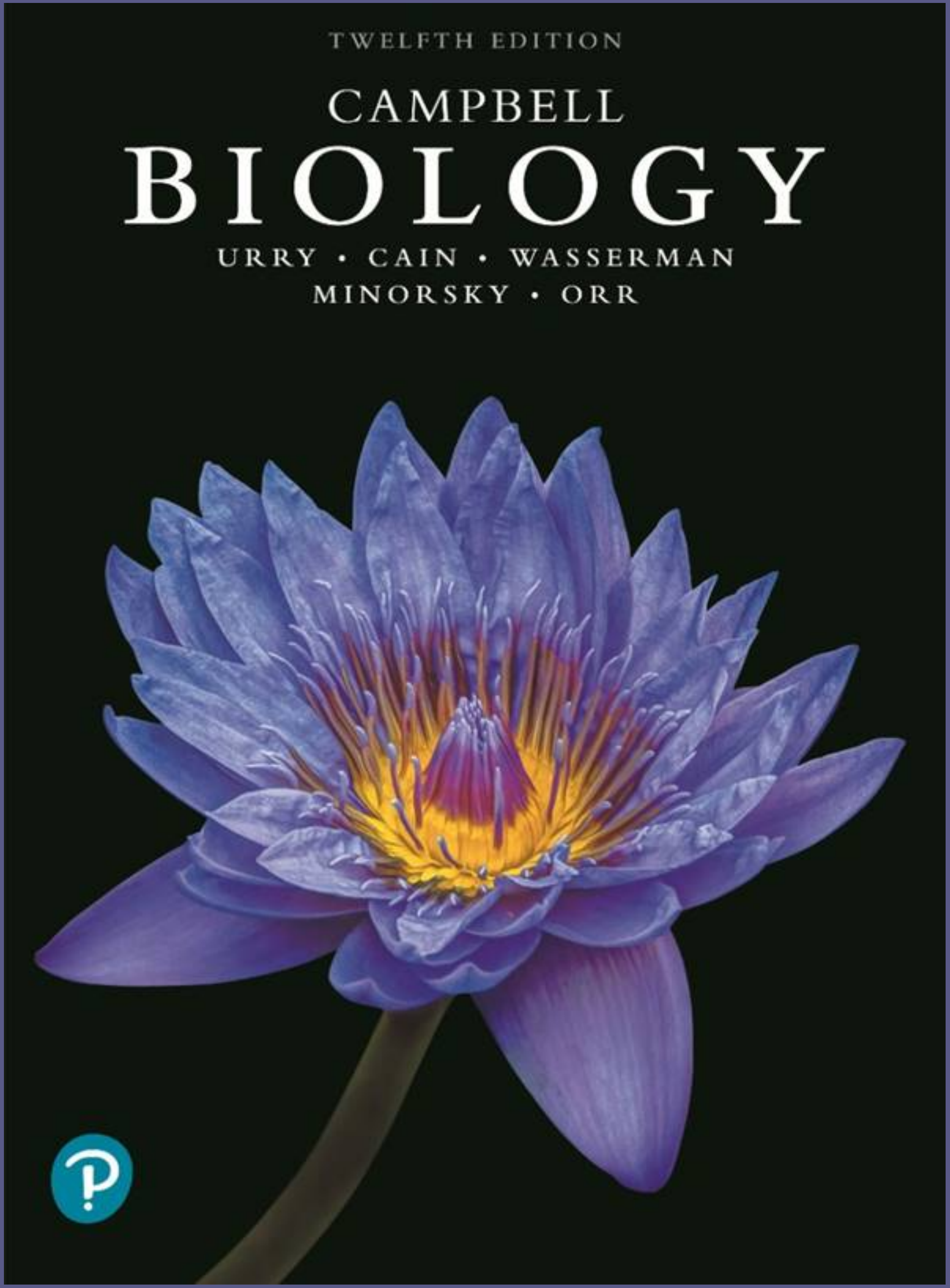


Chapter 33

An Introduction to Invertebrates

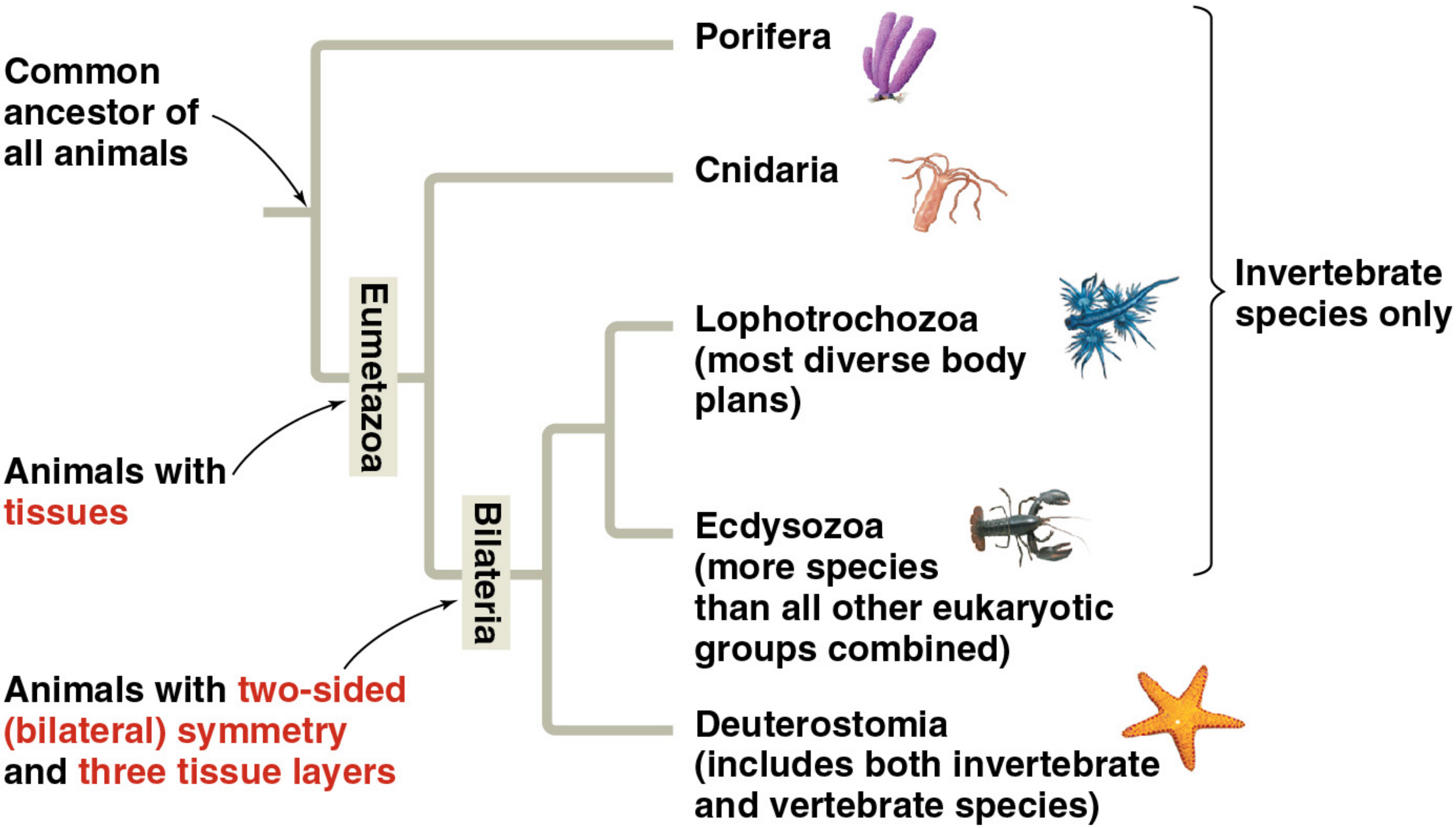
Lecture Presentations by
Nicole Tunbridge and
Kathleen Fitzpatrick

Figure 33.1a

Figure 33.1b

How can we make sense of the great number and morphological diversity of invertebrates?

Classifying invertebrate species into groups based on evolutionary relationships helps us to understand their great diversity.



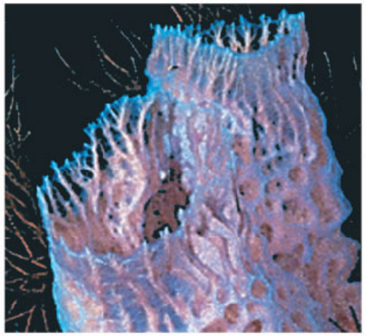
How can we make sense of the great number and morphological diversity of invertebrates?

- **Invertebrates**, animals that lack a backbone, account for over 95% of known animal species
- They occupy almost every habitat on Earth
- They are morphologically diverse, including species that are microscopic and those that are 18 m long

Figure 33.2 Exploring invertebrate diversity

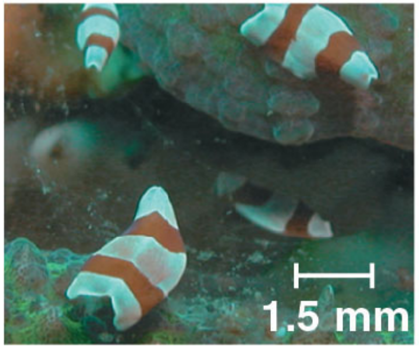
- Kingdom Animalia has 1.3 million known species; estimates of all species range high as 10–20 million

Porifera (5,500 species)



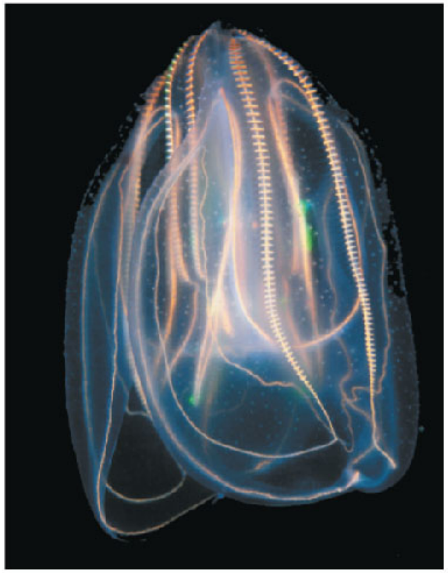
A sponge

Acoela (400 species)



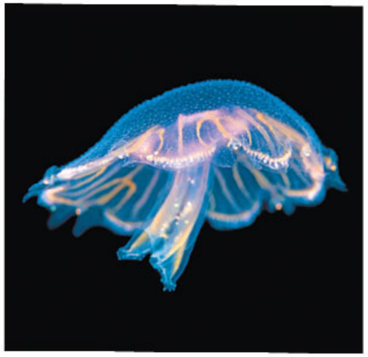
Acoela

Ctenophora (100 species)



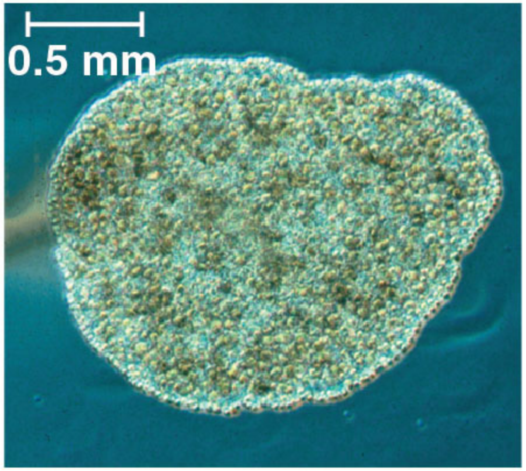
A ctenophore, or comb jelly

Cnidaria (10,000 species)



A jelly

Placozoa (1 species)



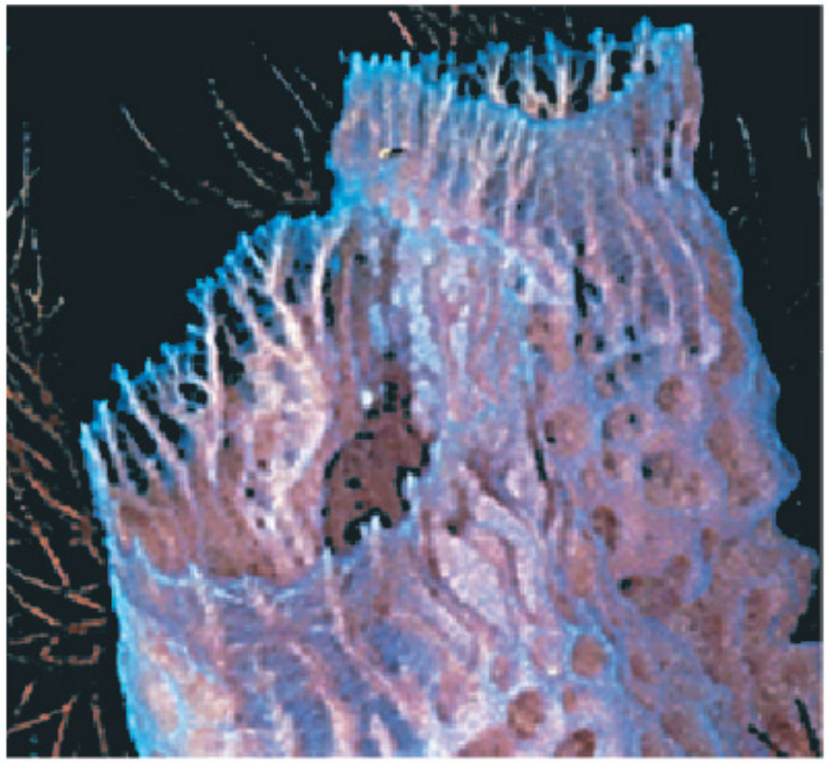
A placozoan (LM)

Figure 33.2 Exploring invertebrate diversity (Part 1a: Porifera)

Porifera (5,500 species)

- Porifera (sponges) are sessile, filter feeders that lack true tissues

Porifera
(5,500 species)



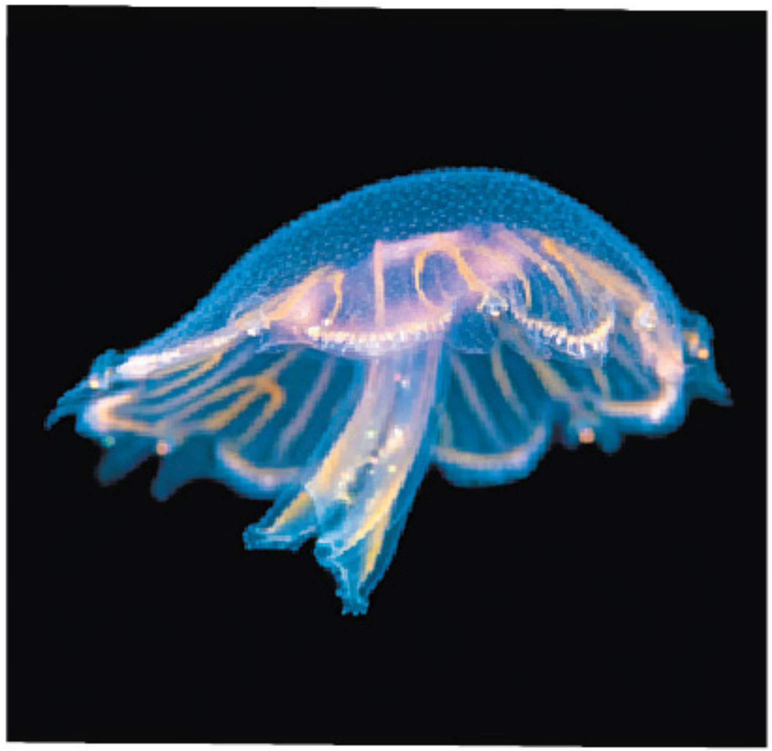
A sponge

Figure 33.2 Exploring invertebrate diversity (Part 1b: Cnidaria)

Cnidaria (10,000 species)

- Cnidarians are radially symmetrical, diploblastic animals with a gastrovascular cavity
- Corals, jellies, and hydras belong to this phylum

Cnidaria (10,000 species)



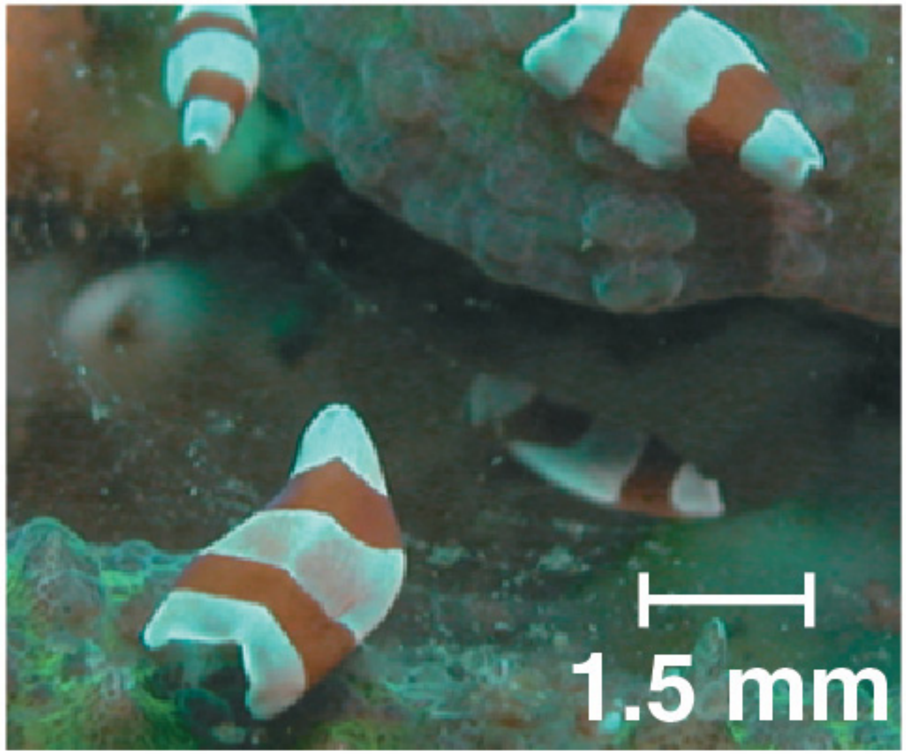
A jelly

Figure 33.2 Exploring invertebrate diversity (Part 1c: Acoela)

Acoela (400 species)

- Phylum Acoela includes flatworms with a simple nervous system and saclike gut

Acoela
(400 species)



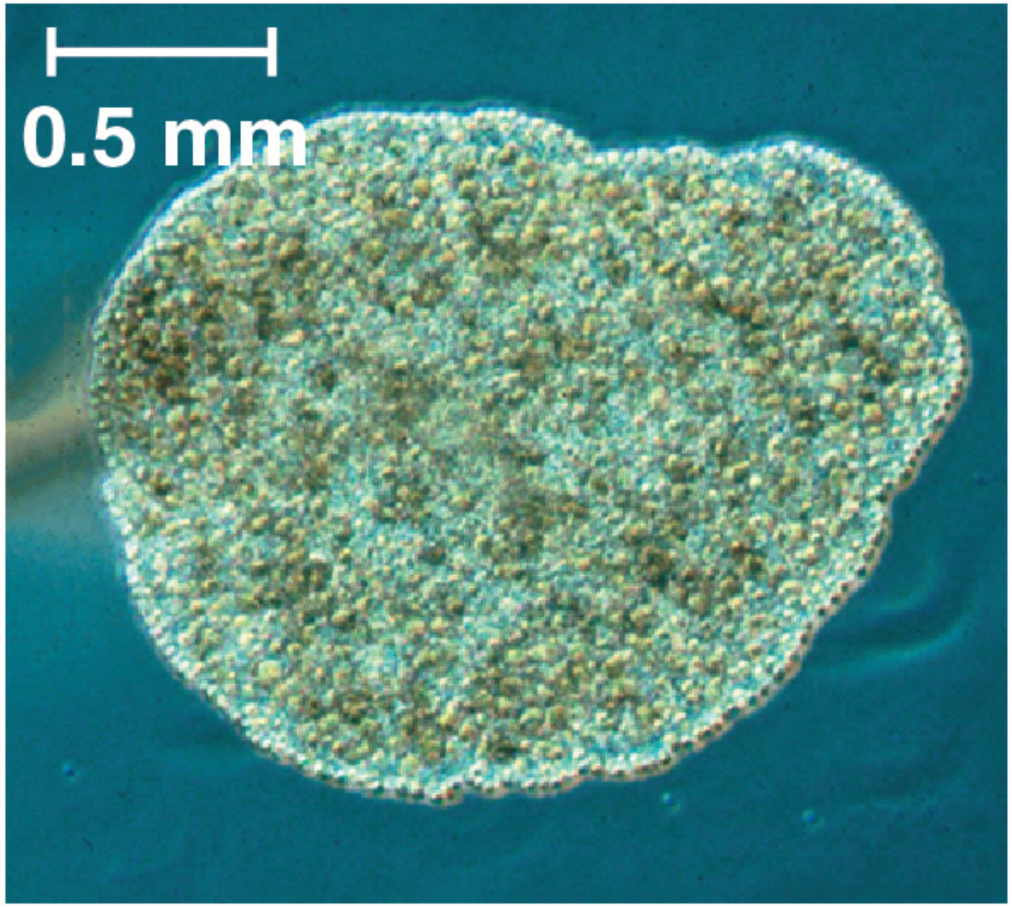
Acoela

Figure 33.2 Exploring invertebrate diversity (Part 1d: Placozoa)

Placozoa (1 species)

- *Trichoplax adhaerens*, the only placozoan species, is composed of a bilayer of a few thousand cells
- They reproduce by dividing into two or budding off many multicellular individuals

Placozoa (1 species)



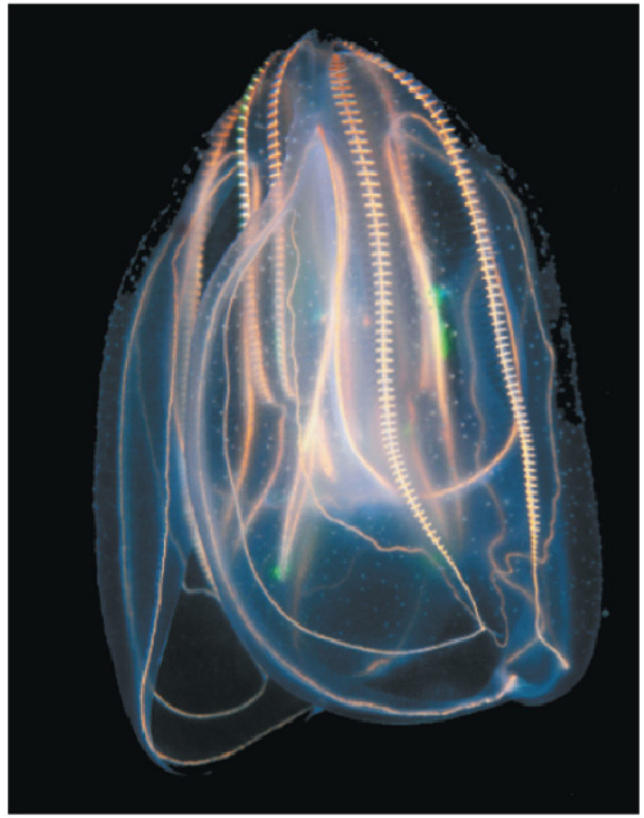
A placozoan (LM)

Figure 33.2 Exploring invertebrate diversity (Part 1e: Ctenophora)

Ctenophora (100 species)

- Ctenophores (comb jellies) are diploblastic, radially symmetrical animals
- They have eight “combs” of cilia that propel them through the water
- Comb jellies compose much of the ocean’s plankton

Ctenophora
(100 species)



A ctenophore, or comb jelly

Figure 33.2 Exploring invertebrate diversity (Part 2: Lophotrochozoa)

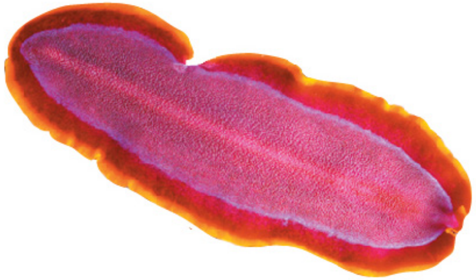
Lophotrochozoa

- This group includes phyla with diverse body plans such as flatworms, molluscs, and segmented worms

Figure 33.2_2a

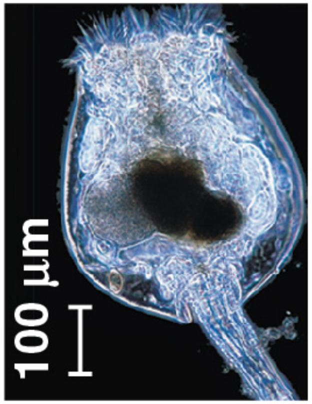
Lophotrochozoa

Platyhelminthes (20,000 species)



A marine flatworm

Syndermata (2,900 species)



A rotifer (LM)

Ectoprocta (4,500 species)

Ectoprocts

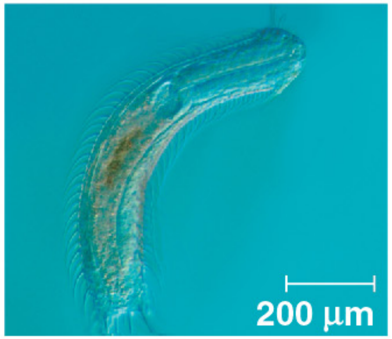
Brachiopoda (335 species)

A brachiopod

Figure 33.2_2b

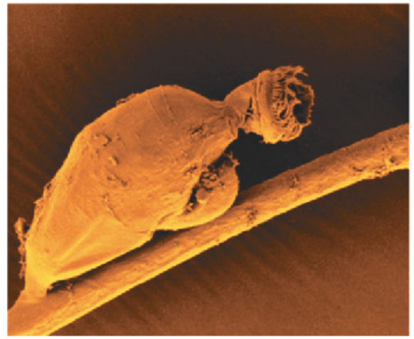
Lophotrochozoa

Gastrotricha
(800 species)



A gastrotrich (differential interference contrast LM)

Cycliophora
(1 species)



A cycliophoran (colorized SEM)

Nemertea
(900 species)

A ribbon worm

Annelida
(16,500 species)

A marine annelid

Mollusca
(100,000 species)

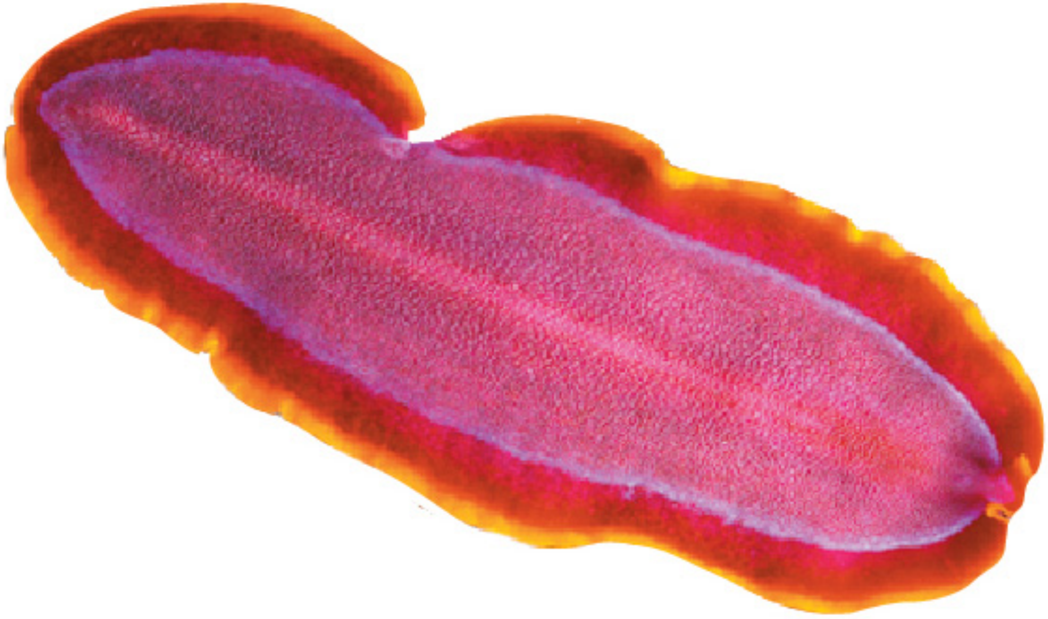
An octopus

Figure 33.2 Exploring invertebrate diversity (Part 2aa: Platyhelminthes)

Platyhelminthes (20,000 species)

- Platyhelminthes are flatworms that have bilateral symmetry and a central nervous system
- They do not have a body cavity or circulatory organs
- Tapeworms, planarians, and flukes belong to platyhelminthes

Platyhelminthes (20,000 species)



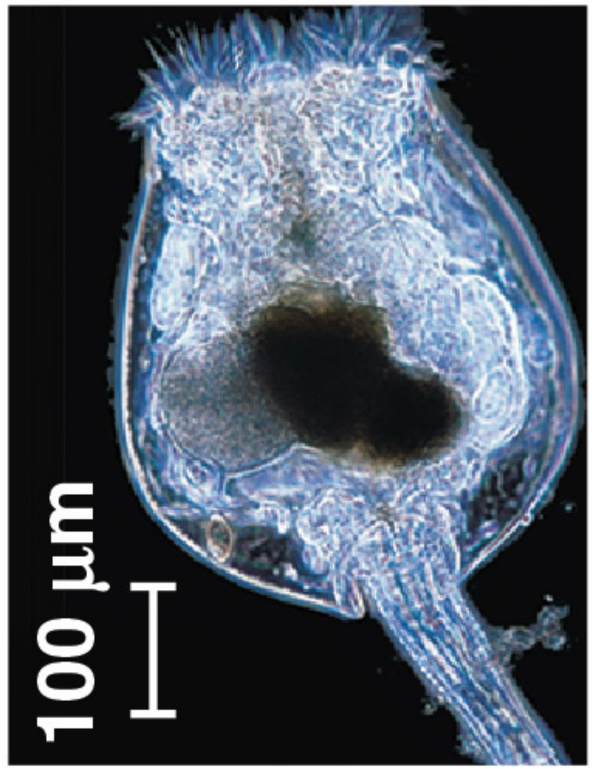
A marine flatworm

Figure 33.2 Exploring invertebrate diversity (Part 2ab: Syndermata)

Syndermata (2,900 species)

- Syndermata includes two former phyla
  - Rotifers are microscopic and have complex organ systems
  - Acanthocephalans are highly modified parasites of vertebrates

**Syndermata
(2,900 species)**



A rotifer (LM)

Figure 33.2 Exploring invertebrate diversity (Part 2ac: Ectoprocta)

Ectoprocta (4,500 species)

- Ectoprocts (bryozoans) live as sessile colonies covered by a tough exoskeleton

Ectoprocta
(4,500 species)

Ectoprocts

Figure 33.2 Exploring invertebrate diversity (Part 2ad: Brachiopoda)

Brachiopoda (355 species)

- Brachiopods (lamp shells) superficially resemble clams and other molluscs
- Most have a unique stalk anchoring them to the substrate, and a crown of cilia called a lophophore

Brachiopoda (335 species)

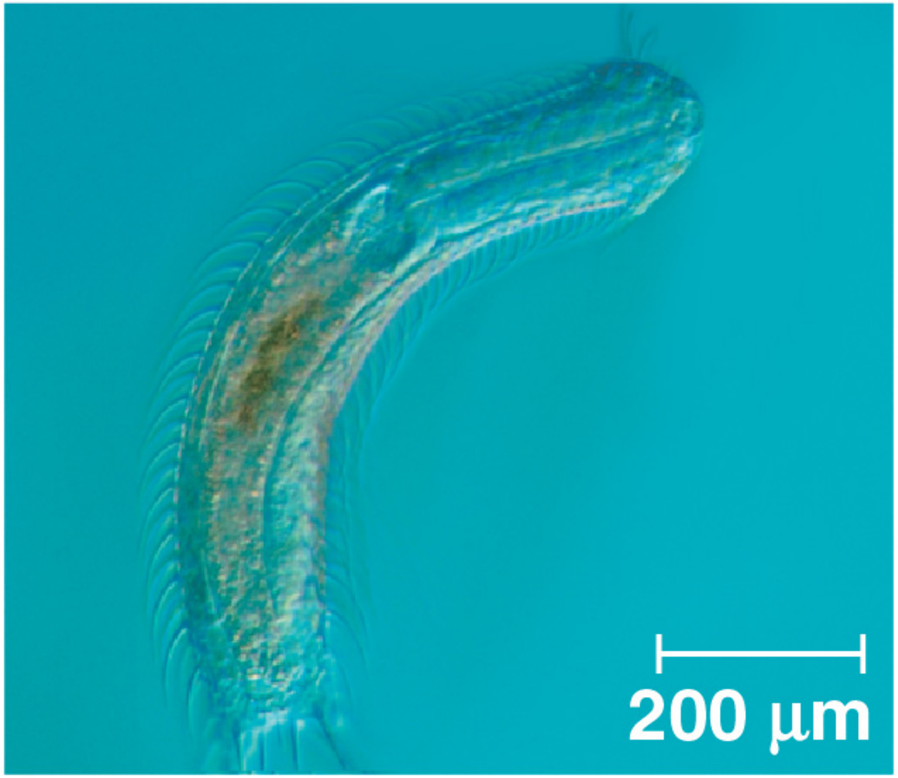
A brachiopod

Figure 33.2 Exploring invertebrate diversity (Part 2ba: Gastrotricha)

Gastrotricha (800 species)

- Gastrotrichs (hairy bellies) are tiny worms that have cilia covering their ventral surface
- Most species live at the bottoms of lakes or oceans

Gastrotricha (800 species)



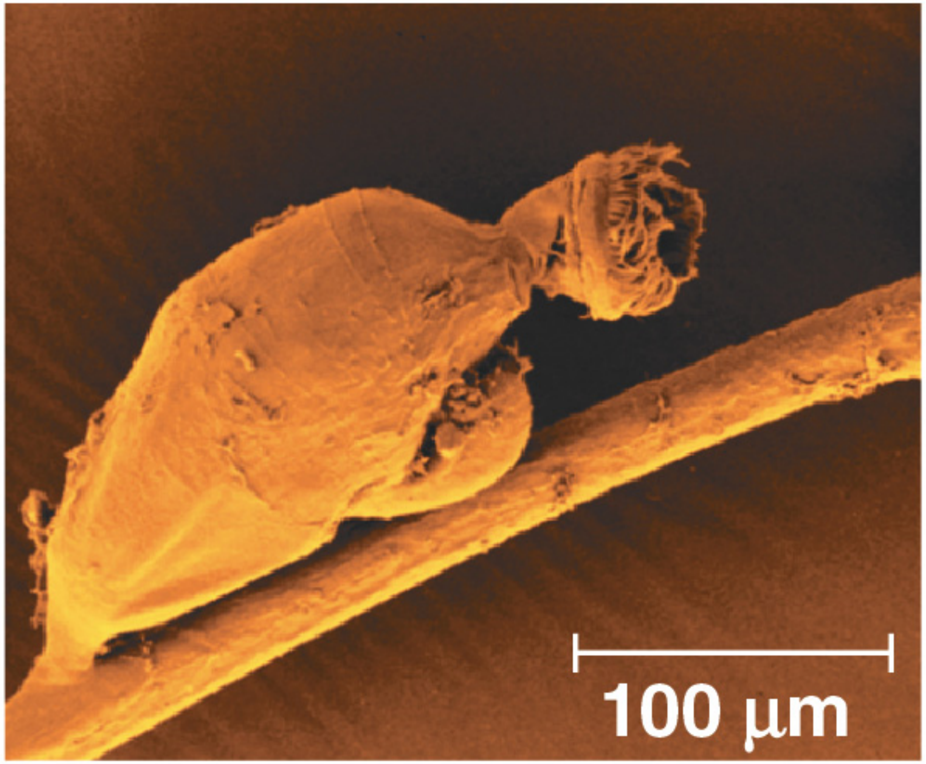
A gastrotrich (differential interference contrast LM)

Figure 33.2 Exploring invertebrate diversity (Part 2bb: Cycliophora)

Cycliophora (1 species)

- *Symbion pandora,* the only known species in this phylum, lives on the bodies of lobsters
- Males impregnate females that are still developing within their mother's bodies

Cycliophora (1 species)



A cycliophoran
(colorized SEM)

Figure 33.2 Exploring invertebrate diversity (Part 2bc: Nemertea)

Nemertea (900 species)

- Nemerteans (ribbon worms) swim or burrow in sand
- They have a unique proboscis for capturing prey, an alimentary canal, and a closed circulatory system
- The coelom is reduced and the body is solid

Nemertea
(900 species)

A ribbon worm

Figure 33.2 Exploring invertebrate diversity (Part 2bd: Annelida)

Annelida (16,500 species)

- Most of these segmented worms live in marine or freshwater habitats
- The most familiar group, earthworms, live in soil

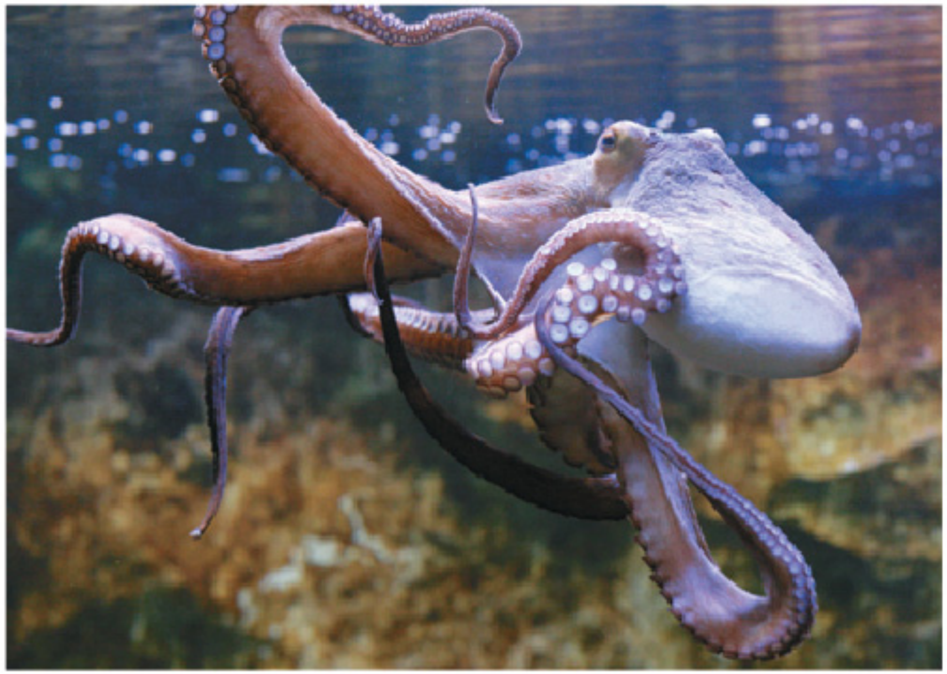
Annelida
(16,500 species)

Figure 33.2 Exploring invertebrate diversity (Part 2be: Mollusca)

Mollusca (100,000 species)

- Molluscs have a soft body, protected by a hard shell in many species
- This phylum includes snails, clams, squids, and octopuses

Mollusca
(100,000 species)



An octopus

Figure 33.2 Exploring invertebrate diversity (Part 3: Ecdysozoa)

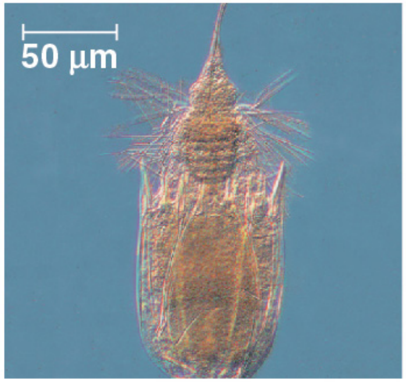
Ecdysozoa

- The phyla in this group include more species than all other eukaryotic groups combined

Figure 33.2_3

Ecdysozoa

Loricifera (10 species)

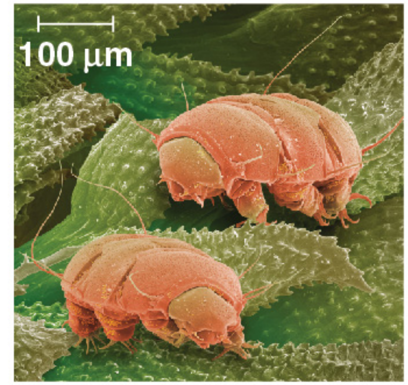


A loriciferan (LM)

Priapula (16 species)

A priapulan

Tardigrada (800 species)



Tardigrades (colorized SEM)

Onychophora (110 species)

An onychophoran

Nematoda (25,000 species)

A roundworm

Arthropoda (1,000,000 species)

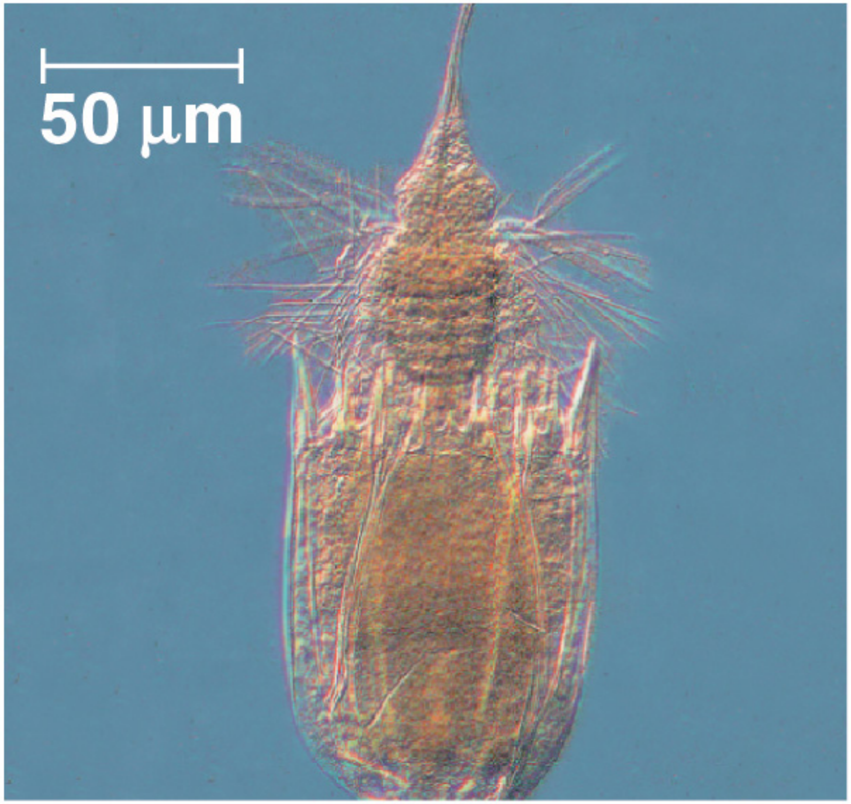
A spider (an arachnid)

Figure 33.2 Exploring invertebrate diversity (Part 3a: Loricifera)

Loricifera (10 species)

- Loriciferans are tiny and live in marine sediments
- The lorica, a pocket formed by six plates, surrounds the abdomen
- The head, neck, and thorax telescope in and out of the lorica

Loricifera (10 species)



A loriciferan (LM)

Figure 33.2 Exploring invertebrate diversity (Part 3b: Priapula)

Priapula (16 species)

- These worms have a large, rounded proboscis at their anterior end
- They range from 0.5 mm to 20 cm in length
- Most species burrow in seafloor sediments
- Priapulans were major predators during the Cambrian period

Priapula (16 species)

A priapulan

Figure 33.2 Exploring invertebrate diversity (Part 3c: Onychophora)

Onychophora (110 species)

- Onychophorans (velvet worms) originated during the Cambrian explosion
- Originally marine, today they live in humid forests
- They have fleshy antennae and several dozen pairs of saclike legs

Onychophora
(110 species)

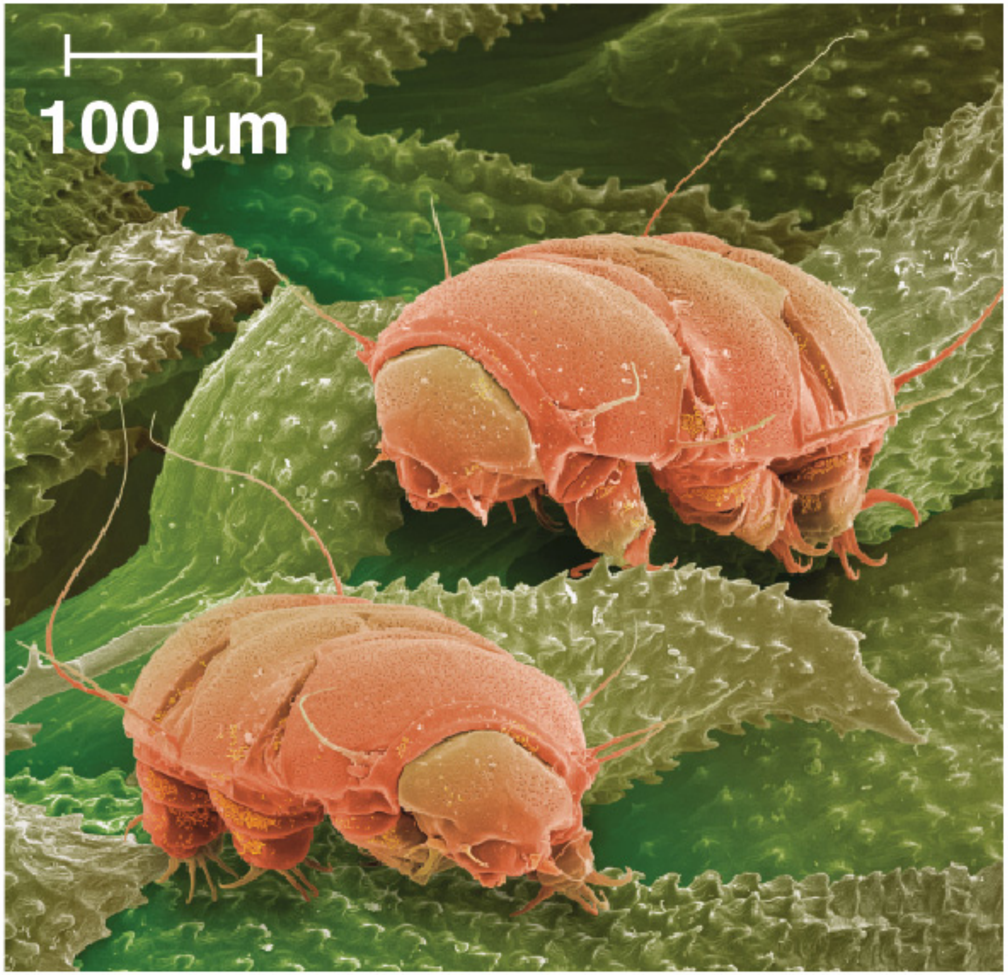
An onychophoran

Figure 33.2 Exploring invertebrate diversity (Part 3d: Tardigrada)

Tardigrada (800 species)

- Tardigrades (water bears) have a bearlike shape and gait, though most are less than 0.5 mm long
- They live in aquatic habitats, or on plants or animals
- In the dormant state, they can survive for days at temperatures as low as −200°C

Tardigrada (800 species)



Tardigrades (colorized SEM)

Figure 33.2 Exploring invertebrate diversity (Part 3e: Nematoda)

Nematoda (25,000 species)

- Nematodes (roundworms) are abundant in soil and aquatic habitats
- Many species parasitize plants and animals
- A tough cuticle coats their body

Nematoda
(25,000 species)

A roundworm

Figure 33.2 Exploring invertebrate diversity (Part 3f: Arthropoda)

Arthropoda (1,000,000 species)

- The majority of known animal species, including insects, crustaceans, and arachnids, are arthropods
- All arthropods have a segmented exoskeleton with jointed appendages

Figure 33.2_3f

Arthropoda
(1,000,000 species)

A spider (an arachnid)

Figure 33.2 Exploring invertebrate diversity (Part 4: Deuterostoma)

Deuterostomia

- This group includes both invertebrate and vertebrate species

Deuterostomia

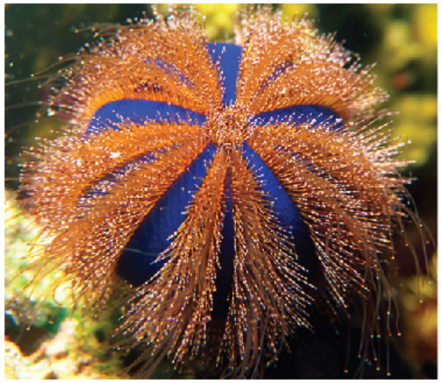
Hemichordata (85 species)

An acorn worm

Chordata (60,000 species)

A tunicate

Echinodermata (7,000 species)



A sea urchin

Figure 33.2 Exploring invertebrate diversity (Part 4a: Hemichordata)

Hemichordata (85 species)

- Hemichordates share some traits with chordates, such as gill slits and a dorsal nerve cord
- The largest group is the acorn worms, marine animals that live in mud or under rocks
- They can grow to more than 2 m in length

Hemichordata (85 species)

An acorn worm

Figure 33.2 Exploring invertebrate diversity (Part 4b: Chordata)

Chordata (60,000 species)

- More than 90% of all chordates are vertebrates
- There are also two groups of invertebrates: lancelets and tunicates

Chordata (60,000 species)

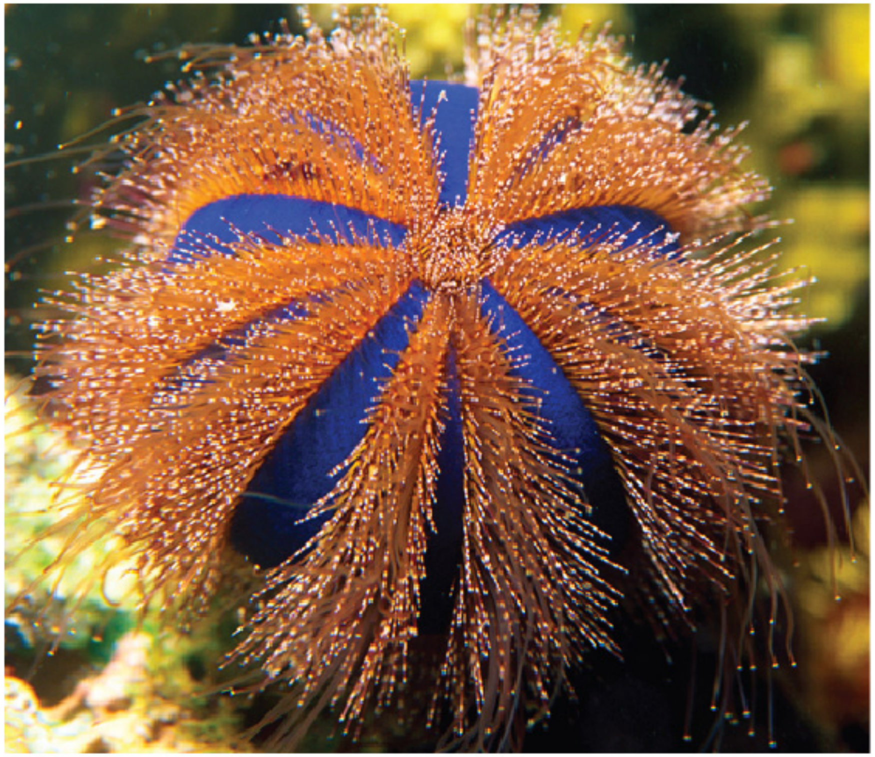
A tunicate

Figure 33.2 Exploring invertebrate diversity (Part 4c: Echiodermata)

Echinodermata (7,000 species)

- Echinoderms are marine animals that are bilaterally symmetrical as larvae, but not as adults
- They move and feed by pumping water through a network of internal canals
- Sand dollars, sea stars, and sea urchins are echinoderms

Echinodermata (7,000 species)



A sea urchin

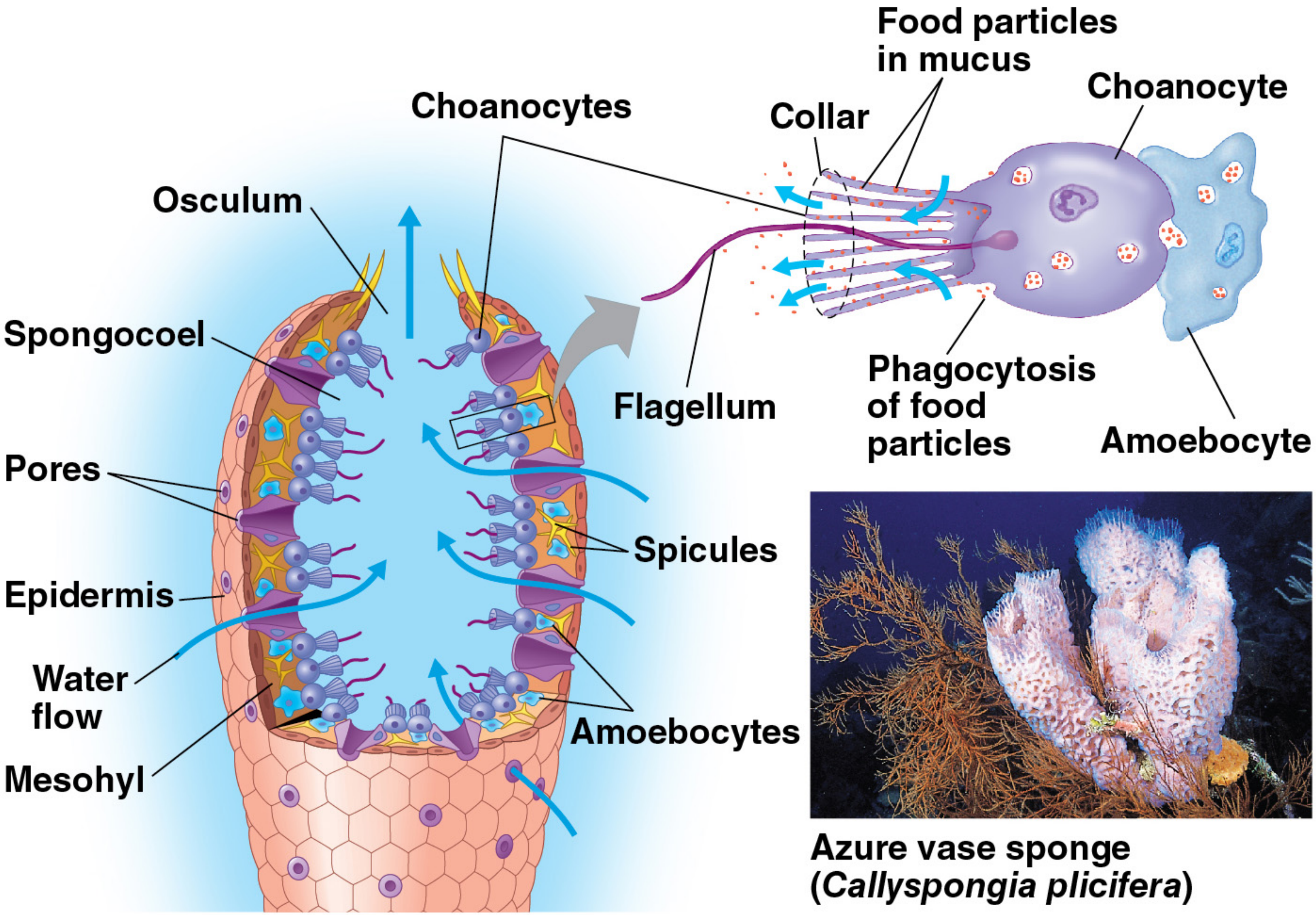
CONCEPT 33.1: Sponges are basal animals that lack tissues

- Porifera (sponges) are among the simplest animals
- They are sedentary, mostly marine animals that range in size from millimeters to meters

Figure 33.UN01

- A sponge’s body is like a sac perforated with pores
- As a **filter feeder**, it captures particles suspended in the water that passes through its body
- Water is drawn into a central cavity, the **spongocoel**, and flows out through the **osculum**

Figure 33.3



Azure vase sponge (*Callyspongia plicifera*)

- The Porifera lineage split from other animals early in the history of the group
- Unlike most other animals, their cells are not organized into tissues

- Sponges have several different cell types
  - **Choanocytes**, flagellated collar cells, engulf bacteria and food particles by phagocytosis
  - The body consists of two layers of cells separated by a gelatinous region called the **mesohyl**
  - **Amoebocytes** are totipotent cells within the mesohyl that digest food, transport nutrients, and make skeletal fibers

- Most sponges are **hermaphrodites**: Each individual functions as both male and female
- Most exhibit sequential hermaphroditism: They function first as one sex and then as the other
- Zygotes develop into flagellated, swimming larvae
- Larvae eventually settle on substrate and develop into sessile adults

CONCEPT 33.2: Cnidarians are an ancient phylum of eumetazoans

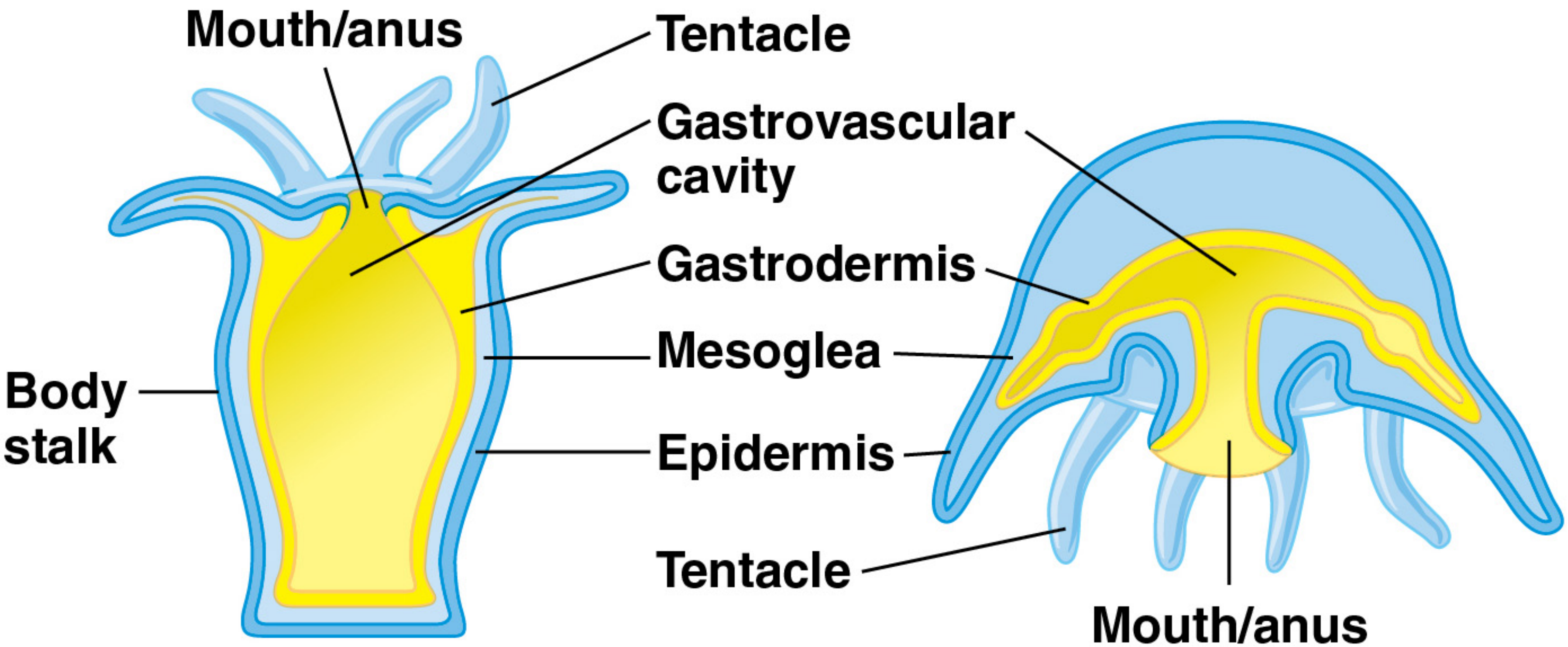
- All animals except sponges and a few other groups are eumetazoans, animals with true tissues
- The oldest phylum in this clade is Cnidaria

Figure 33.UN02

- Cnidaria includes diverse sessile and motile forms including corals, hydras, and jellies (“jellyfish”)
- They are diploblastic with radially symmetrical bodies
- The basic body plan is a sac with a central digestive compartment, the **gastrovascular cavity**
- A single opening functions as both mouth and anus

- There are two variations on the body plan: the sessile polyp and motile medusa
  - **Polyps** adhere to the substrate by the aboral end of the body (the end opposite the mouth)
  - A **medusa** is a free-swimming form that has a bell-shaped body with the mouth on the underside

Figure 33.4

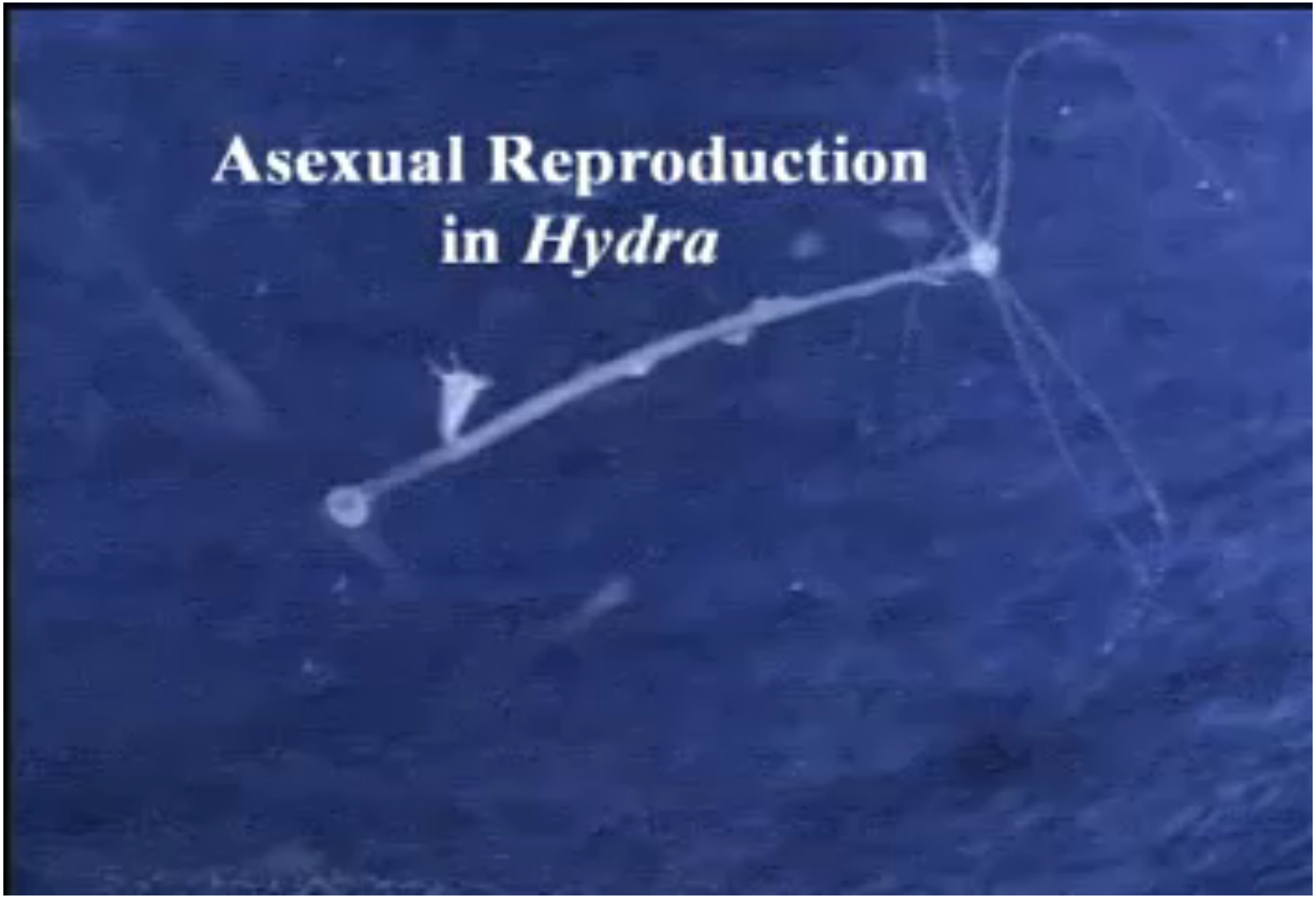


Polyp (cross section)

Medusa (cross section)

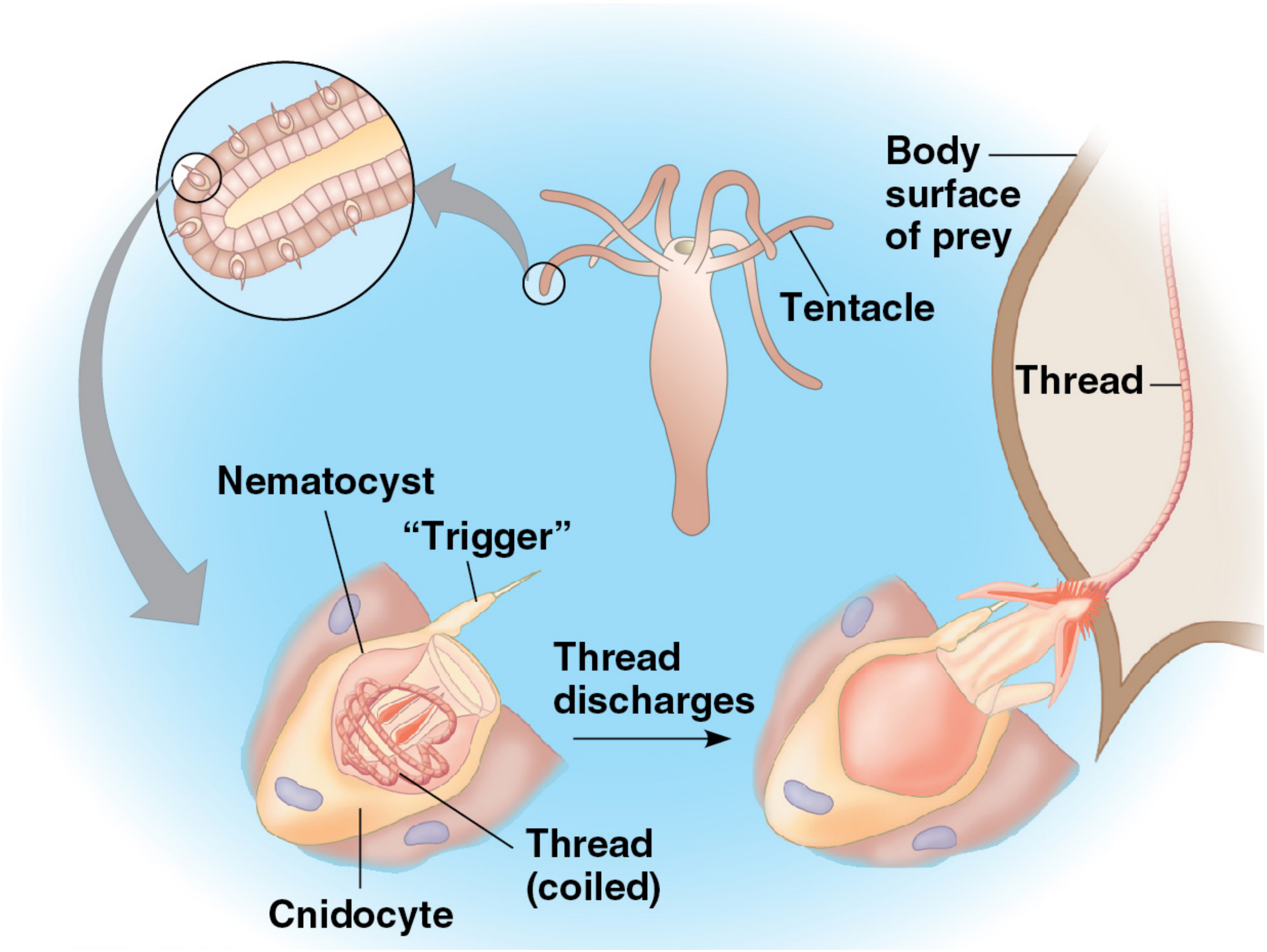
Video: Hydra Eating *Daphnia*

Video: Hydra Budding



- Cnidarians are predators that use tentacles to capture and consume prey
- Tentacles are armed with **cnidocytes**, unique cells used in defense and prey capture
- **Nematocysts** are specialized organelles within cnidocytes that eject a stinging thread

Figure 33.5



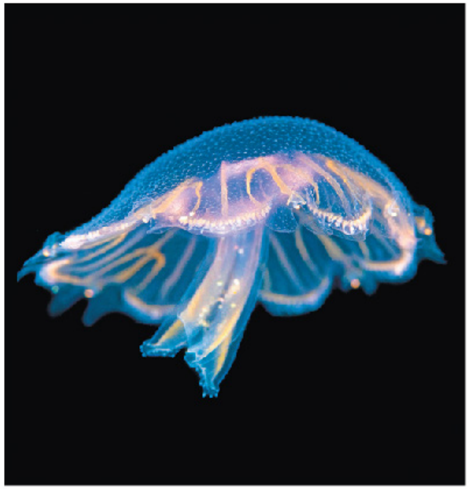
Body surface of prey
Tentacle
Thread
Nematocyst
"Trigger"
Thread discharges
Thread (coiled)
Cnidocyte

- The gastrovascular cavity acts as a hydrostatic skeleton against which contractile cells can work
- A noncentralized nerve net coordinates movement
- Sensory structures throughout the body allow cnidarians to detect and respond to stimuli

- Phylum Cnidaria include two major clades, Medusozoa and Anthozoa

Figure 33.6

(a) Medusozoans



Jellies

Sea wasp

(b) Anthozoans

Sea anemones

Star corals

Video: Jelly Swimming

Video: Thimble Jellies

Video: Clownfish and Anemone

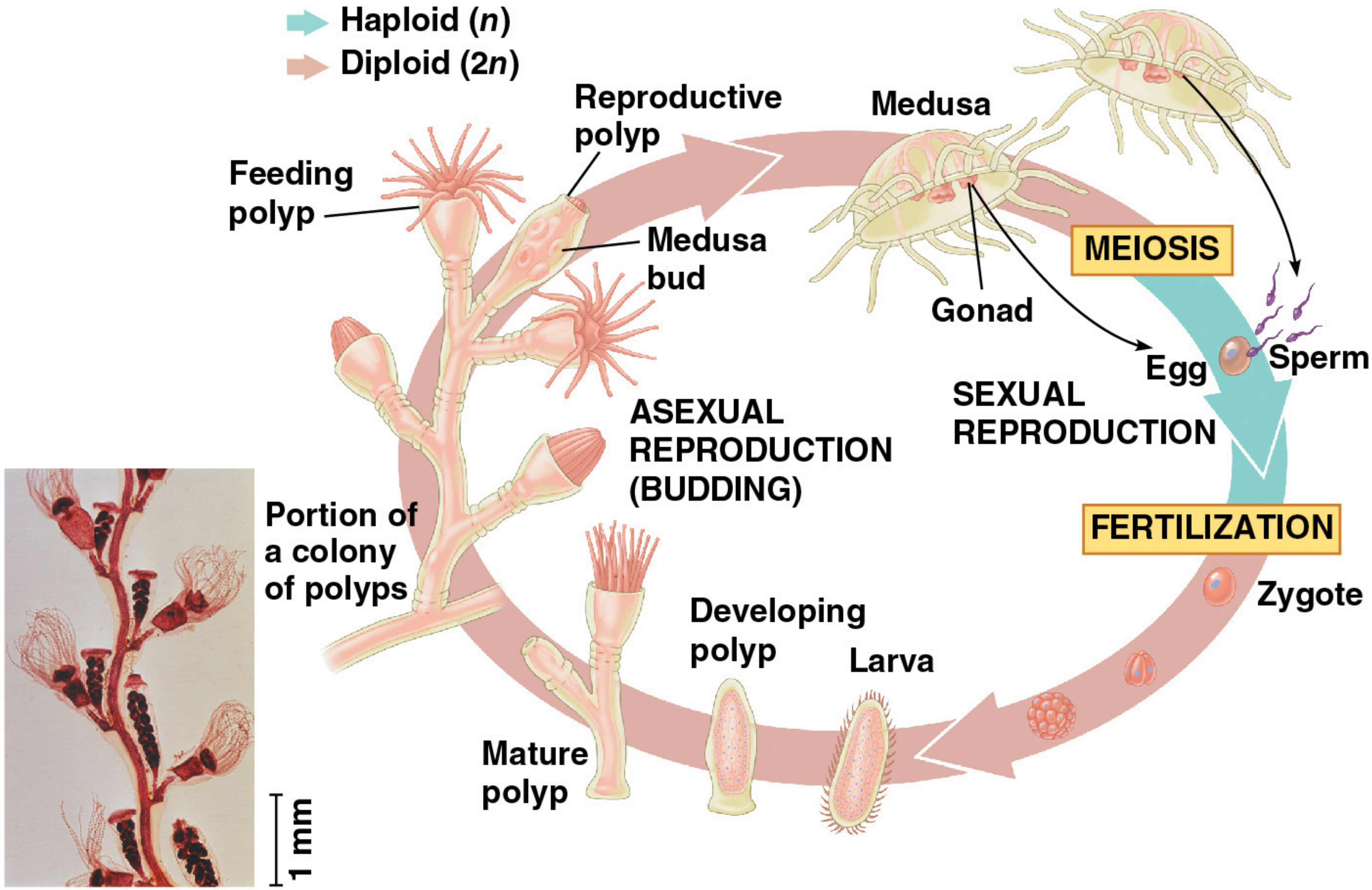
Video: Coral Reef

Medusozoans

- Medusozoans include all cnidarians that produce a medusa
  - Scyphozoans (jellies)
  - Cubozoans (box jellies)
  - Hydrozoans

- Most hydrozoans, such as *Obelia*, alternate between polyp and medusa forms
- Hydra, a rare freshwater cnidarian, exists only in polyp form

Figure 33.7



Haploid (*n*)
Diploid (2*n*)
Feeding polyp
Reproductive polyp
Medusa bud
Medusa
Gonad
MEIOSIS
Egg
Sperm
SEXUAL REPRODUCTION
ASEXUAL REPRODUCTION (BUDDING)
Portion of a colony of polyps
1 mm
FERTILIZATION
Zygote
Developing polyp
Larva
Mature polyp

- The medusa is the predominant stage in the life cycle of most scyphozoans and cubozoans
  - For example, coastal scyphozoans have a brief polyp stage, whereas open ocean species generally have no polyp stage

- In cubozoans, the medusa stage is box-shaped
- Most cubozoans live in tropical oceans and have highly toxic cnidocytes
  - For example, the sting of a sea wasp can cause respiratory failure, cardiac arrest, and sudden death

Anthozoans

- Anthozoans, which occur only as polyps, include sea anemones and corals
- Corals can be solitary or colonial, form symbioses with algae, and secrete a hard **exoskeleton** (external skeleton) of calcium carbonate

- Coral polyps form rocklike reefs that provide habitat for many other species
- Coral reefs are being destroyed rapidly by pollution, overharvesting, and ocean acidification
- Climate change is also raising water temperatures above their optimal range

CONCEPT 33.3: Lophotrochozoans, a clade identified by molecular data, have the widest range of animal body forms

- Most animal species are bilaterians, which have bilateral symmetry and triploblastic development
- Most bilaterians have a coelom and a digestive tract with two openings (mouth and anus)
- The clade Bilateria contains Lophotrochozoa, Ecdysozoa, and Deuterostomia

Figure 33.UN03

- The clade Lophotrochozoa was identified by molecular data, but is named for its morphology
- Some have a lophophore for feeding, others have a trochophore larval stage, and a few have neither

- Lophotrochozoans are a diverse group composed of 18 phyla including
  - Flatworms
  - Rotifers and acanthocephalans
  - Ectoprocts
  - Brachiopods
  - Molluscs
  - Annelids

Flatworms

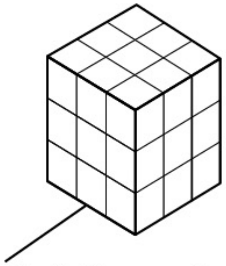
- Phylum Platyhelminthes includes flatworms that live in marine, freshwater, and damp terrestrial habitats
- Many are parasites, such as flukes and tapeworms
- They are dorsoventrally flattened acoelomates
- The gastrovascular cavity branches throughout the body

- The flat body increases surface area, placing all cells close to water, either in the surroundings or the gut
- This enables elimination of nitrogenous waste and gas exchange by diffusion across the body surface

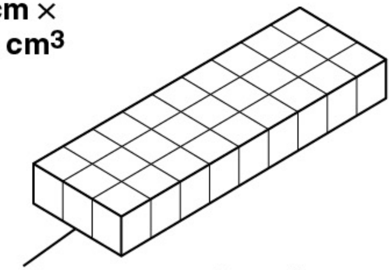
- When an organism grows without changing shape, volume increases more rapidly than surface area
- Larger organisms have proportionally less surface area over which exchange processes can occur
- The surface area of structures is maximized by branching, flattening, folding, and projections

Figure 33.8

MAKE CONNECTIONS: Maximizing Surface Area



SA: 6 (3 cm × 3 cm) = 54 cm^2
V: 3 cm × 3 cm × 3 cm = 27 cm^3

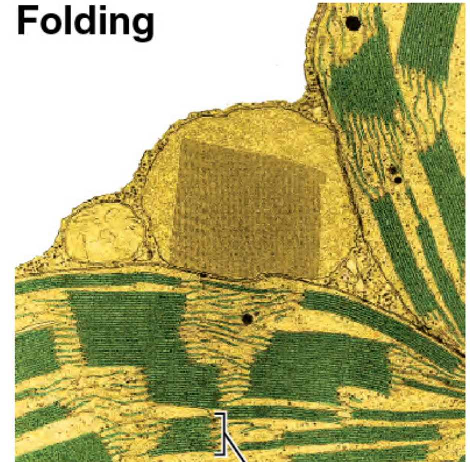


SA: 2 (3 cm × 1 cm) + 2 (9 cm × 1 cm) + 2 (3 cm × 9 cm) = 78 cm^2
V: 1 cm × 3 cm × 9 cm = 27 cm^3

Diagrams comparing surface area (SA) for two different shapes with the same volume (V)

Flattening

Folding



1 µm

Thylakoid

Branching

Projections

- The excretory apparatus of flatworms maintains osmotic balance with the surroundings
- It consists of **protonephridia**, networks of tubules with ciliated structures called flame bulbs
- Flame bulbs pull fluid through branched ducts open to the external environment

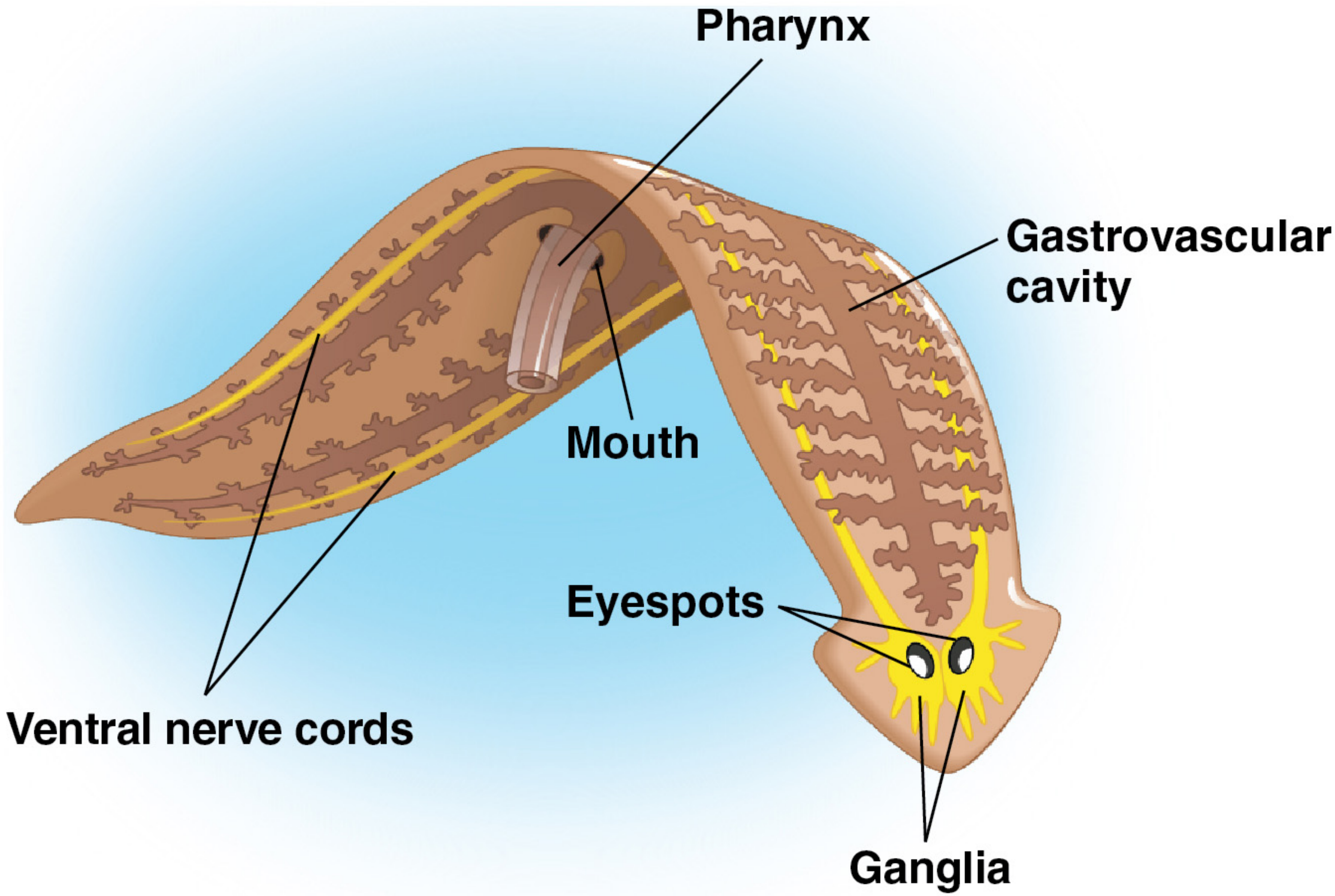
- Flatworms are divided into two lineages
  - Catenulida, (“chain worms”), live in freshwater, and reproduce asexually by budding into chains of individuals
  - Rhabditophora are more diverse, can be found in both marine and freshwater habitats, and have free-living and parasitic species

Free-Living Species

- **Planarians** are rhabditophorans that live in fresh water and prey on smaller or feed on dead animals
- On their head, they have light-sensitive eyespots as well as lateral flaps for the detection of chemicals
- The nervous system is centralized and more complex than that of cnidarians

- Some planarians reproduce asexually by fission
- Planarians are hermaphrodites; copulating mates cross-fertilize each other during sexual reproduction

Figure 33.9


Pharynx
Gastrovascular cavity
Mouth
Eyespots
Ventral nerve cords
Ganglia

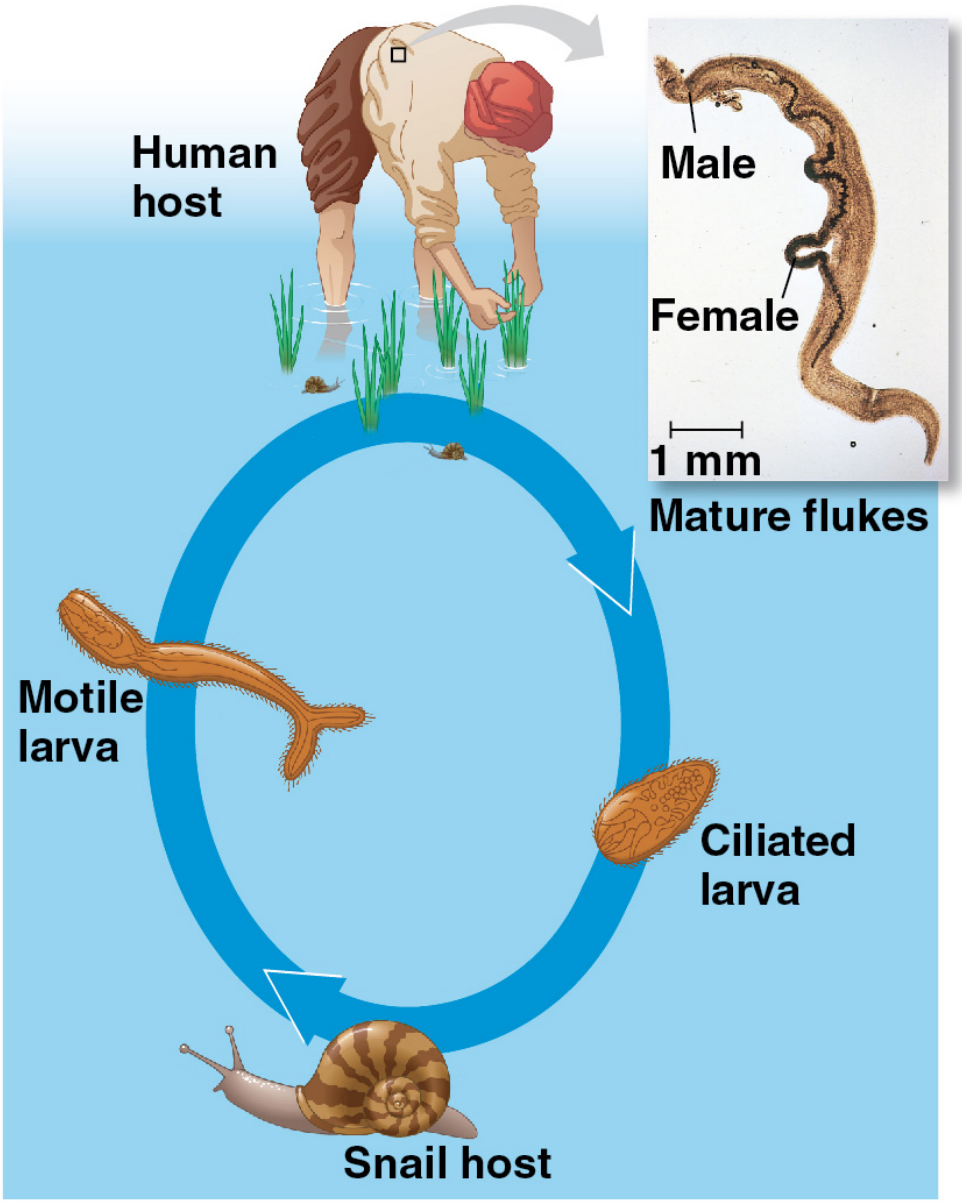
Parasitic Species

- More than half of rhabditophorans are parasites living in or on other animals
- Two important groups of parasitic rhabditophorans are the trematodes and the tapeworms

Trematodes

- Trematodes have diverse hosts, and complex life cycles with alternating sexual and asexual stages
- Many require an intermediate host in which larvae develop before infecting the final host
  - For example, blood flukes, trematodes that cause schistosomiasis in humans, spend part of their lives inside snails

Figure 33.10


Human host
Male
Female
1 mm
Mature flukes
Motile larva
Ciliated larva
Snail host

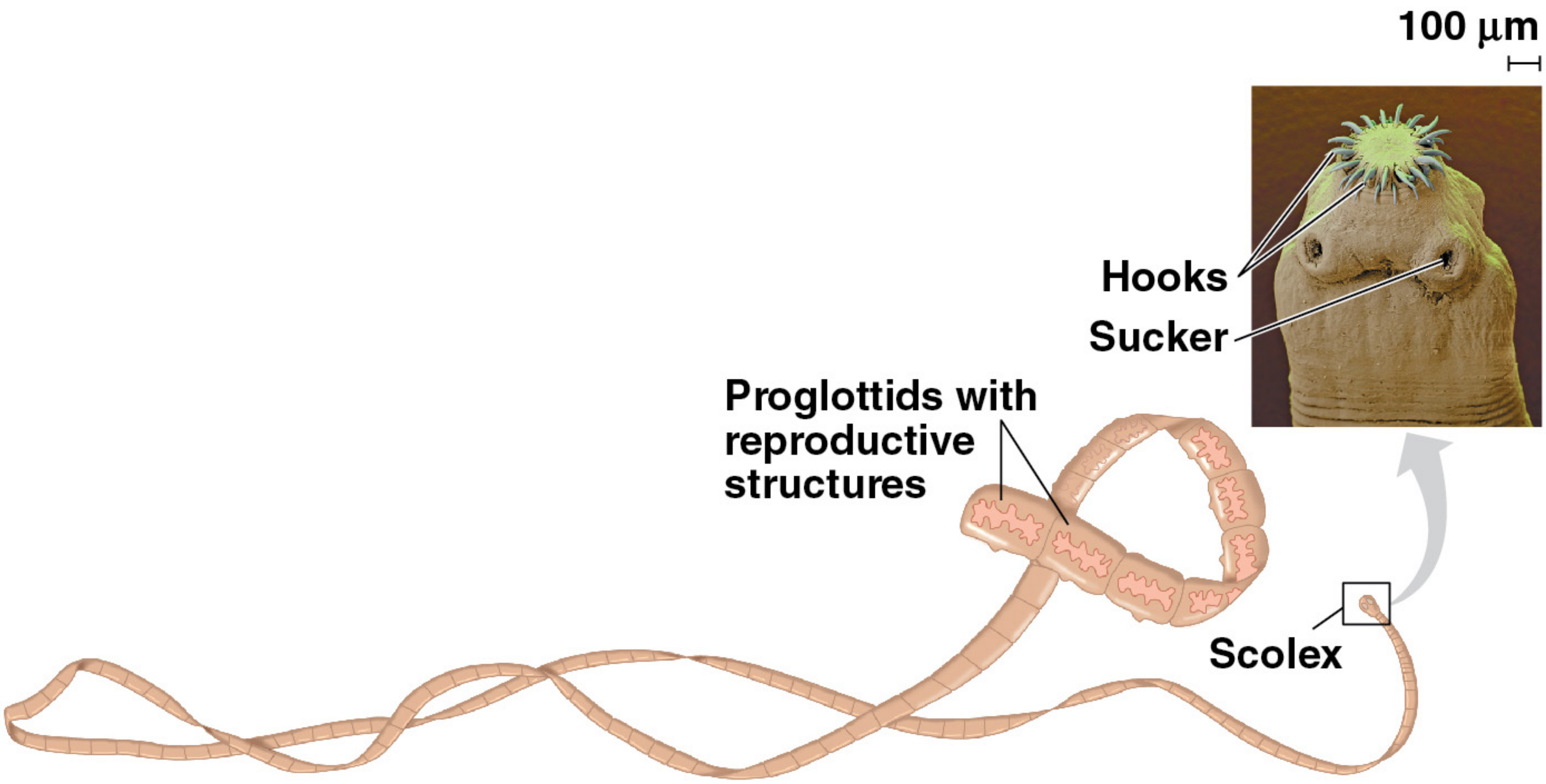
Tapeworms

- Tapeworms are parasites of mostly vertebrates, including humans
- They do not have a mouth or gastrovascular cavity; they absorb nutrients directly from the host intestine

Tapeworms

- A scolex at the anterior end contains suckers and hooks for attaching to the host
- Proglottids are units that contain sex organs and form a ribbon behind the scolex
- After sexual reproduction, proglottids carrying thousands of eggs leave the host's body in feces

Figure 33.11


100 µm
Hooks
Sucker
Proglottids with reproductive structures
Scolex

Tapeworms

- Feces containing eggs are consumed in the food or water of intermediate hosts, such as pigs or cattle
- Humans acquire larvae encysted in the muscle of intermediate hosts by eating undercooked meat
- Tapeworms mature in human intestines, robbing them of nutrients and potentially causing blockages

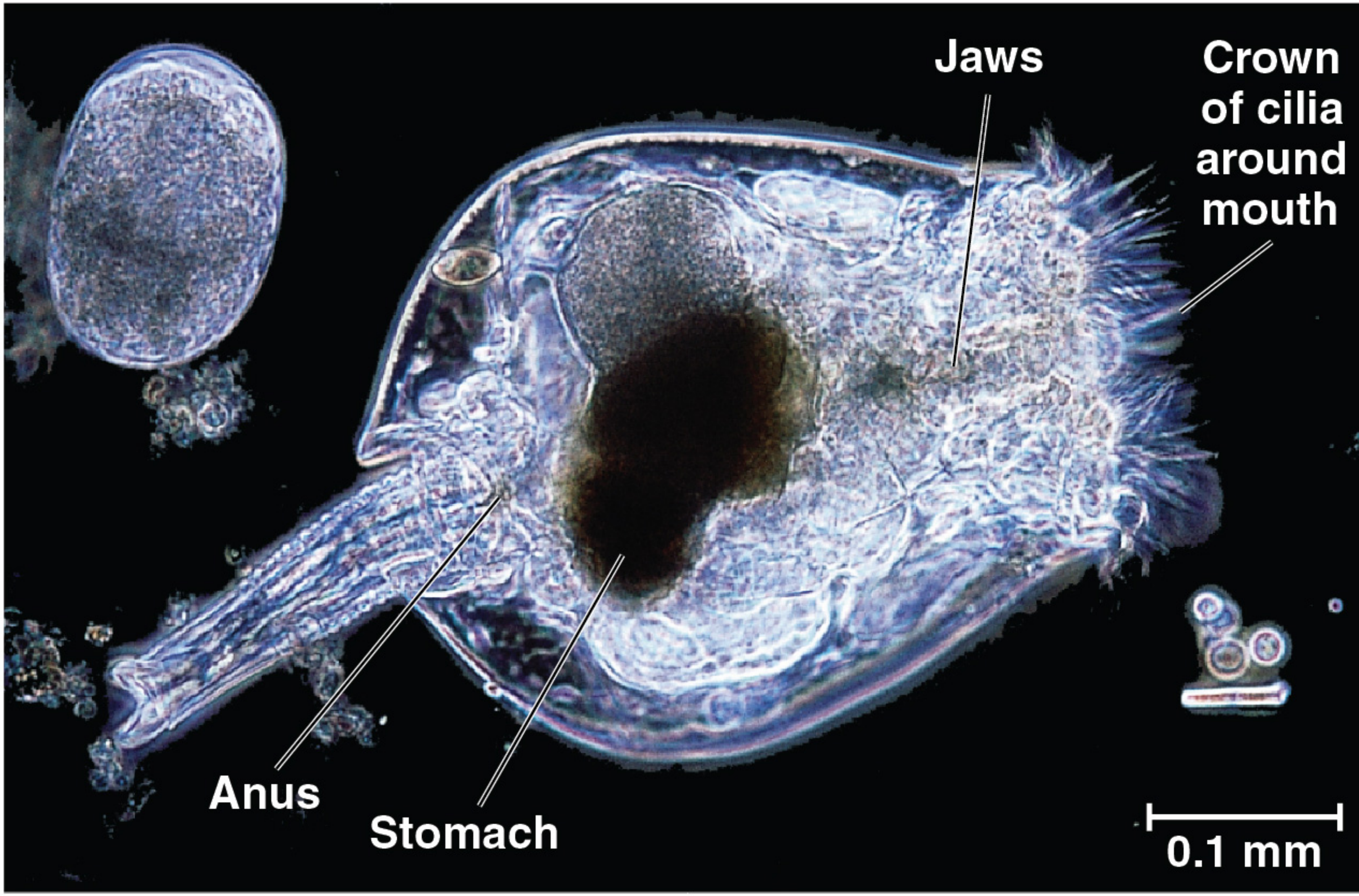
Rotifers and Acanthocephalans

- Phylogenetic analyses have shown that rotifers and acanthocephalans should be combined into a single phylum, Syndermata

Rotifers

- There are roughly 1,800 species of rotifers
- Rotifers are tiny animals that inhabit freshwater, marine, and damp soil habitats
- They are smaller than many protists but are truly multicellular and have specialized organ systems

Figure 33.12



Video: Rotifer

- A crown of cilia draw water and food particles into the mouth; food is ground up in jaws called trophi
- Food is further digested in the **alimentary canal**, a digestive tube with a separate mouth and anus
- Fluid in the hemocoel functions as a hydrostatic skeleton
- Body movements distribute nutrients in the fluid to internal organs suspended within the hemocoel

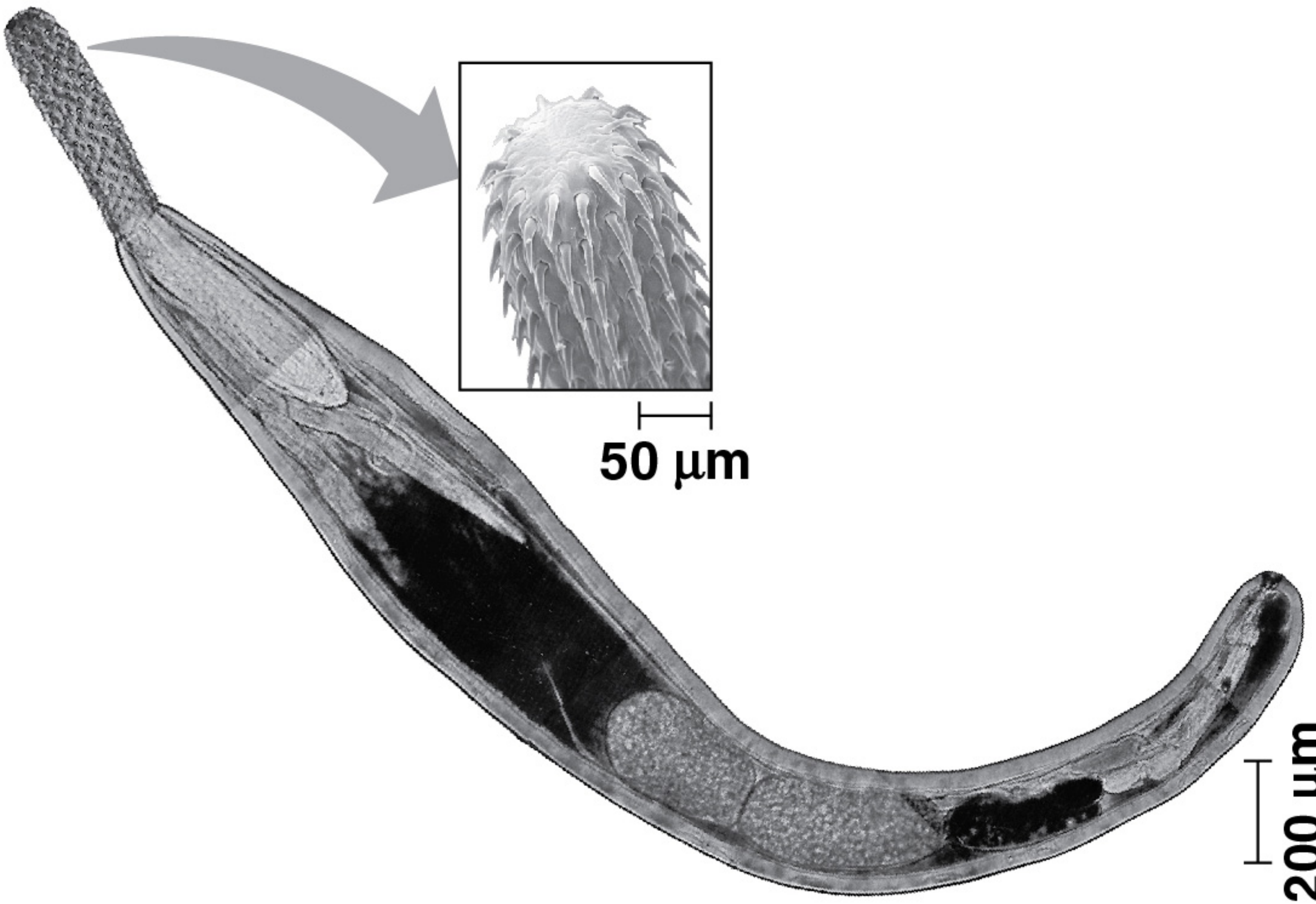
- Some rotifer species reproduce entirely by **parthenogenesis**, where females produce female offspring from unfertilized eggs
- Other species also reproduce sexually under certain conditions, such as crowding

- Bdelloidea rotifers have been asexual for over 50 million years
- They tolerate high levels of desiccation and rehydrate when conditions improve
- Genetic diversity is introduced when they rehydrate
- DNA from other species enters through cracks in the cell membrane and is incorporated into their genome

Acanthocephalans

- Acanthocephalans are sexually reproducing parasites of vertebrates
- They lack a complete digestive tract and are less than 20 cm long
- They are commonly called spiny-headed worms after the curved hooks on the proboscis

Figure 33.13



- All acanthocephalans are parasites that have complex life cycles with multiple hosts
- Some species manipulate the intermediate host's behavior to increase transmission to the final host
  – For example, infected New Zealand mud crabs move to areas more visible to birds, the final host

Ectoprocts and Brachiopods

- Ectoprocts and brachiopods share several traits
  - A lophophore, a crown of ciliated tentacles around their mouth used for feeding
  - A U-shaped alimentary canal
  - The absence of a distinct head
  - A coelom

- **Ectoprocts** (bryozoans) are sessile colonial animals that superficially resemble clumps of moss
- In some species, the colony is encased in a hard exoskeleton; the lophophores extend through pores
- Most live in the sea; several are reef builders

Figure 33.14a

(a) Creeping bryozoan, an ectoproct

- **Brachiopods** (lamp shells) superficially resemble clams and other hinge-shelled molluscs
- The two halves of the shell are dorsal and ventral rather than lateral as in clams
- All brachiopods are marine; most attach to the seafloor by a stalk

Figure 33.14b

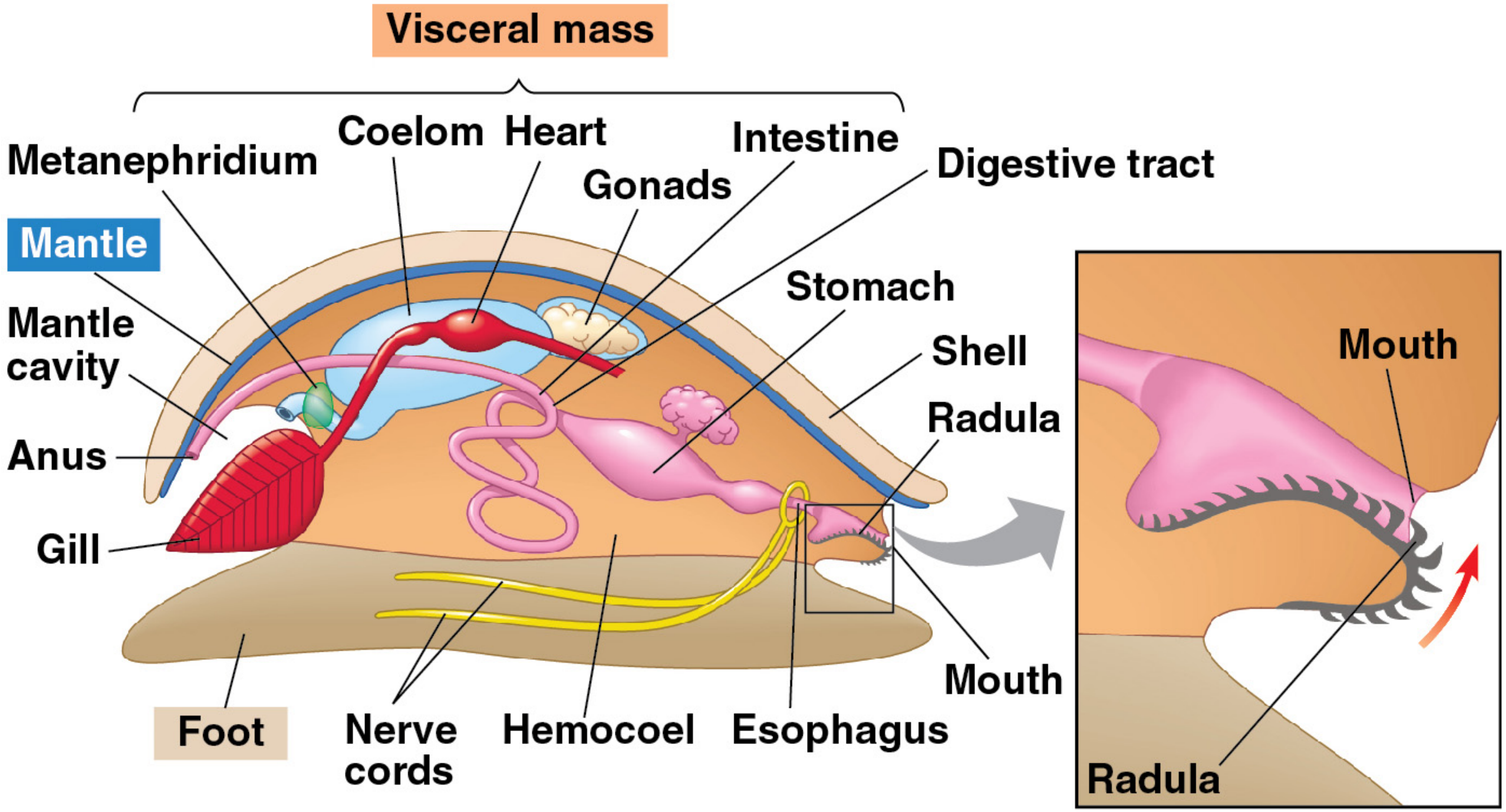
(b) Lampshell, a brachiopod

Molluscs

- Phylum Mollusca includes snails and slugs, oysters and clams, and octopuses and squids
- Most molluscs are marine, some inhabit fresh water, and some snails and slugs are terrestrial
- The soft bodies of many species are surrounded by a protective calcium carbonate shell
- Slugs, squids, and octopuses have a reduced internal shell

- All molluscs have a similar body plan with three parts
  - Muscular **foot**, usually used for movement
  - **Visceral mass**, containing most of the internal organs
  - **Mantle**, a fold of tissue draping over the visceral mass that secretes the shell
- Many also have a water-filled **mantle cavity** housing the gills, anus and excretory pores
- Many feed using a straplike **radula** to scrape up food

Figure 33.15



Visceral mass
Coelom
Heart
Intestine
Metanephridium
Gonads
Digestive tract
Mantle
Stomach
Mantle cavity
Shell
Radula
Anus
Gill
Foot
Nerve cords
Hemocoel
Esophagus
Mouth
Mouth
Radula

- Most molluscs have separate sexes, but many snails are hermaphrodites
- Many molluscs have a ciliated larval stage called the trochophore

- Four of the eight major clades of molluscs are
  - Polyplacophora (chitons)
  - Gastropoda (snails and slugs)
  - Bivalvia (clams, oysters, and other bivalves)
  - Cephalopoda (squids, octopuses, cuttlefish, and chambered nautiluses)

Chitons

- Chitons are marine animals with oval-shaped bodies and a shell made of eight dorsal plates
- The foot is used to grip and creep slowly along rock
- The radula is used to scrape algae off the surface

Figure 33.16

Gastropods

- About three-quarters of molluscs are gastropods
- Most are marine, but there are also freshwater and terrestrial species
- Gastropods move slowly using cilia or by a rippling motion of the foot

- Most gastropods have a single, spiraled shell that protects them from injury, dehydration, and predation
- Most are herbivores, but some species use modified radula to feed on prey
- Many have a head with eyes at the tips of tentacles
- Terrestrial snails lack gills; they use the lining of the mantle cavity for gas exchange with the air

Figure 33.17

(a) A land snail

(b) A sea slug

Video: Nudibranchs

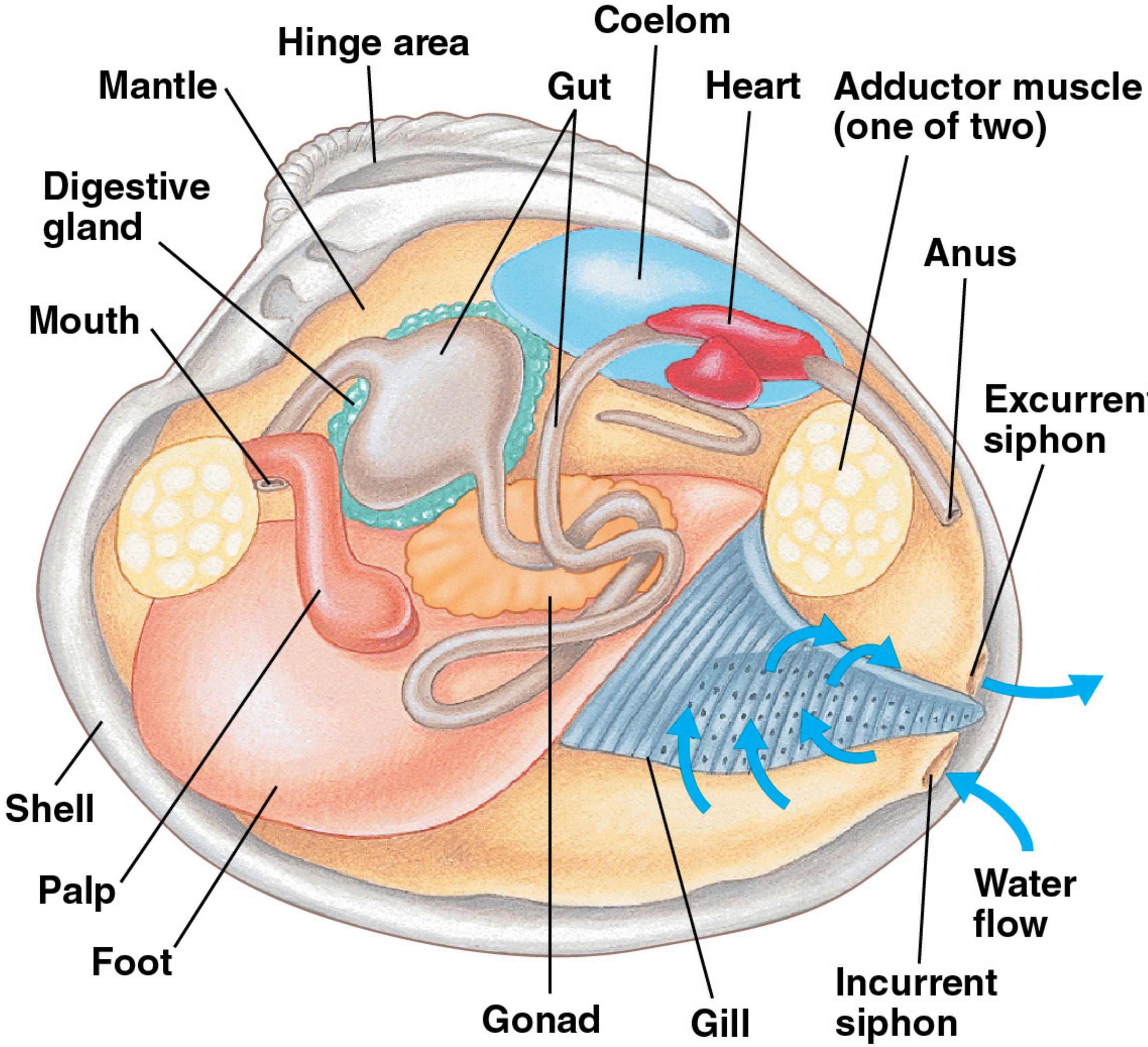
Bivalves

- Bivalves are all aquatic and include many species of clams, oysters, mussels, and scallops
- They have a shell divided into two hinged halves drawn together by adductor muscles
- They have no distinct head or radula
- Some have eyes and sensory tentacles along the edge of their mantle

Figure 33.18

- Bivalve gills are housed inside the mantle cavity and are used for suspension feeding and gas exchange
- Water enters the mantle cavity through an incurrent siphon and leaves through an excurrent siphon

Figure 33.19



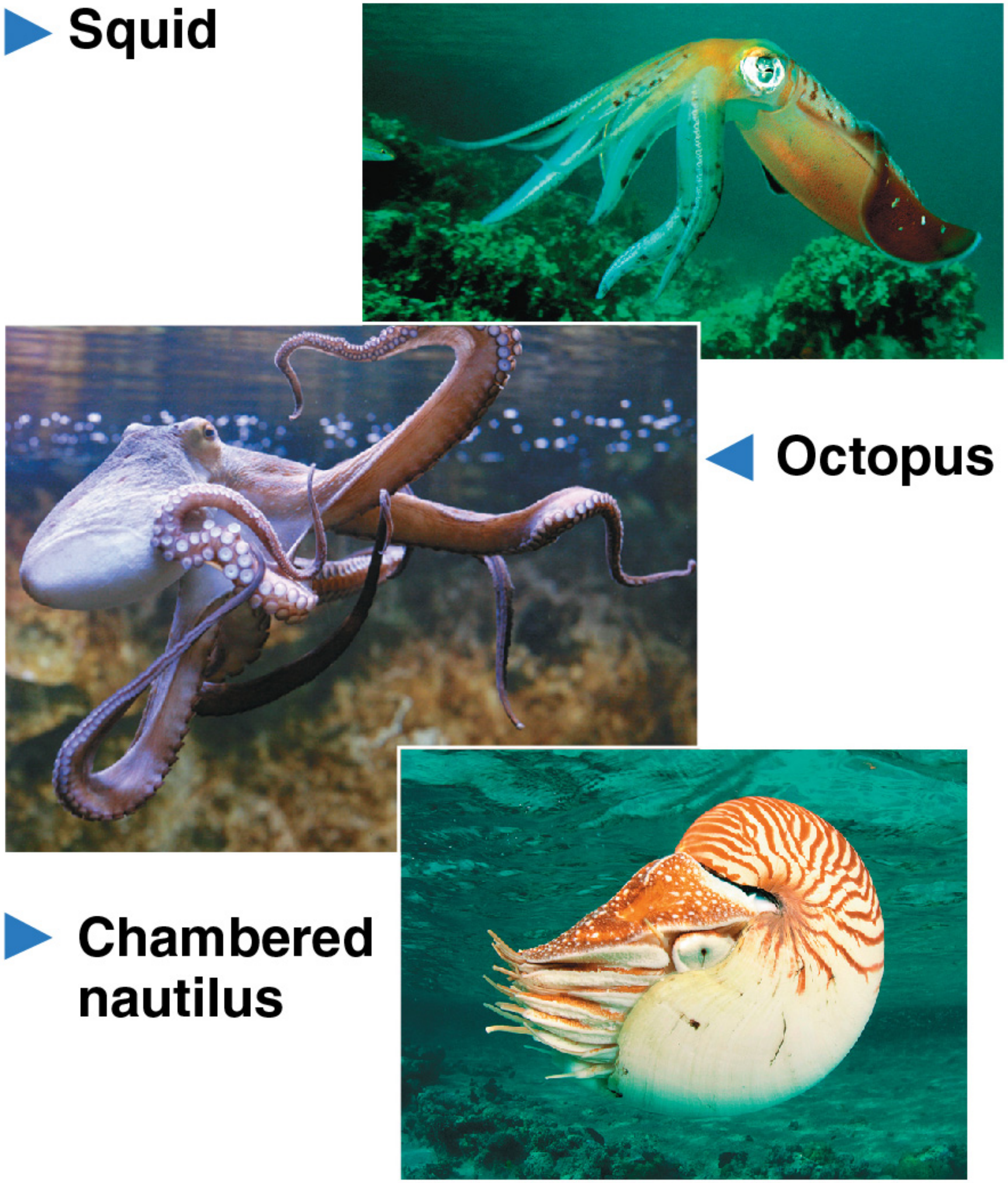
Hinge area
Coelom
Mantle
Gut
Heart
Adductor muscle (one of two)
Digestive gland
Anus
Mouth
Excurrent siphon
Shell
Water flow
Palp
Foot
Incurrent siphon
Gonad
Gill

- Most species are sedentary and anchored to the substrate, but some have limited mobility
  - Clams can use their foot to dig into sand or mud
  - Scallops flap their shells to skitter across the sea floor

Cephalopods

- Cephalopods are active marine predators with beak-like jaws surrounded by tentacles
- They immobilize prey using a poison in their saliva
- The foot is modified into a muscular excurrent siphon and part of the tentacles
- Water is drawn into the mantle cavity and shot out through the excurrent siphon for rapid movement

Figure 33.20



Squid

Octopus

Chambered nautilus

- The shell is reduced and internal or missing in most cephalopods, except the chambered nautiluses
- Cephalopods are the only molluscs with a closed circulatory system
- They also have well-developed sense organs, and a complex brain

- Shelled cephalopods called **ammonites** were once the dominant invertebrate predators of the seas
- They went extinct at the end of the Cretaceous period, 66 million years ago

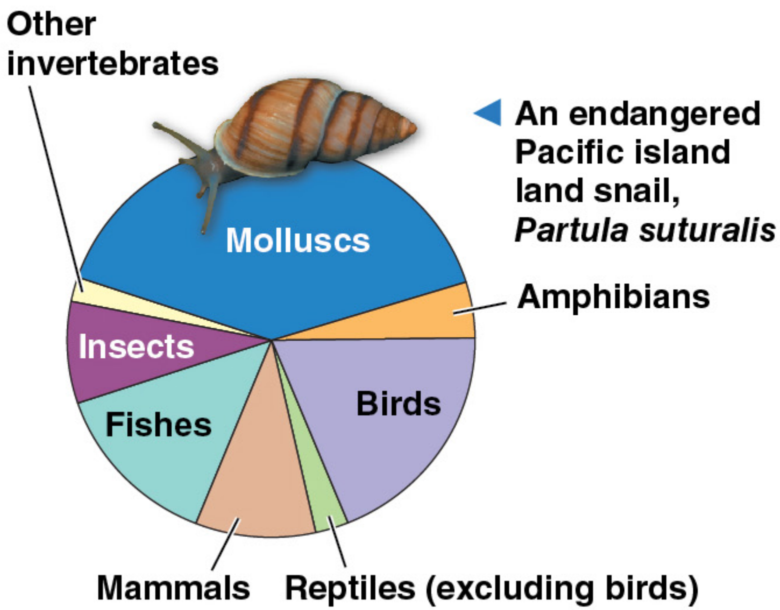
- Most squid species are less than 75 cm long, but some are much larger
  - For example, the giant squid (*Architeuthis dux*) grows up to 13 m in length
  - The colossal squid (*Mesonychoteuthis hamiltoni*) grows up to 14 m

Protecting Freshwater and Terrestrial Molluscs

- Molluscs have the largest number of documented extinctions among animals
- Freshwater bivalves and terrestrial gastropods are the most severely threatened
  - About 10% of freshwater pearl mussels in North America have become extinct in the past 100 years
  - Two-thirds of remaining species are threatened
  - Over 50% of the Pacific island land snails are extinct or threatened

- Threats to freshwater and terrestrial molluscs include
  - Habitat loss
  - Pollution
  - Competition or predation by non-native species
  - Overharvesting by humans

Figure 33.21



◀ An endangered Pacific island land snail, *Partula suturalis*

▲ Recorded extinctions of animal species

▲ Workers on a mound of pearl mussels killed to make buttons (ca. 1919)

Annelids

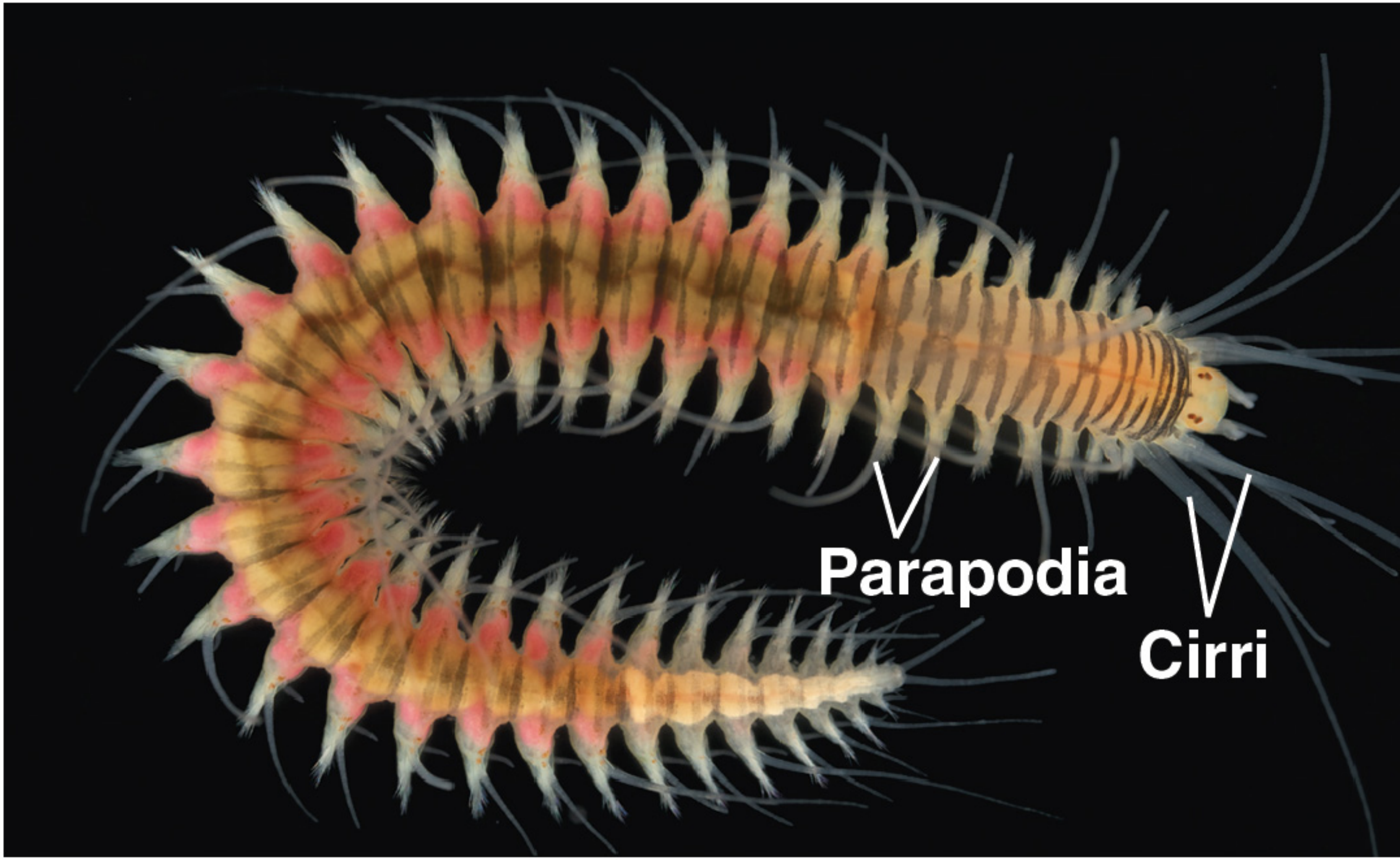
- Annelids are segmented worms that live in marine, freshwater, and damp soil habitats
- They have a coelom (no hemocoel) and range from less than 1 mm to more than 3 m in length

- Traditionally, phylum Annelida was divided into three clades: Polychaeta, Oligochaeta, and Hirudinea
- Based on phylogenomic analysis, annelids are now divided into two clades, Errantia and Sedentaria

Errantians

- Errantia is a large and diverse, mostly marine, clade
- Many are mobile swimmers, crawlers, or burrowers; others are relatively immobile tube-dwellers
- Many have well-developed jaws used for predation or grazing on multicellular algae

Figure 33.22



- Many errantians have a pair of paddle- or ridge-like parapodia on each body segment
- Parapodia are used for locomotion, and as gills in many species
- Each parapodium has numerous chaetae, bristles made of chitin

Sedentarians

- Sedentarians tend to be less mobile than errantians
- Some species burrow slowly in the substrate, others live in protective tubes
- Tube-dwellers often filter feed using gills or tentacles
- Earthworms and leeches are included in this clade

Figure 33.23

Leeches

- Leeches range in length from 1 to 30 cm
- Most species inhabit fresh water; some are marine
- Terrestrial species live in moist vegetation

Leeches

- Most leeches are predators of invertebrates; some are blood sucking parasites of vertebrates
- Some parasitic leeches slit the skin of their host and secrete an anesthetic to prevent detection
- Secretion of hirudin prevents coagulation, enabling them to gorge on the host’s blood

Figure 33.24

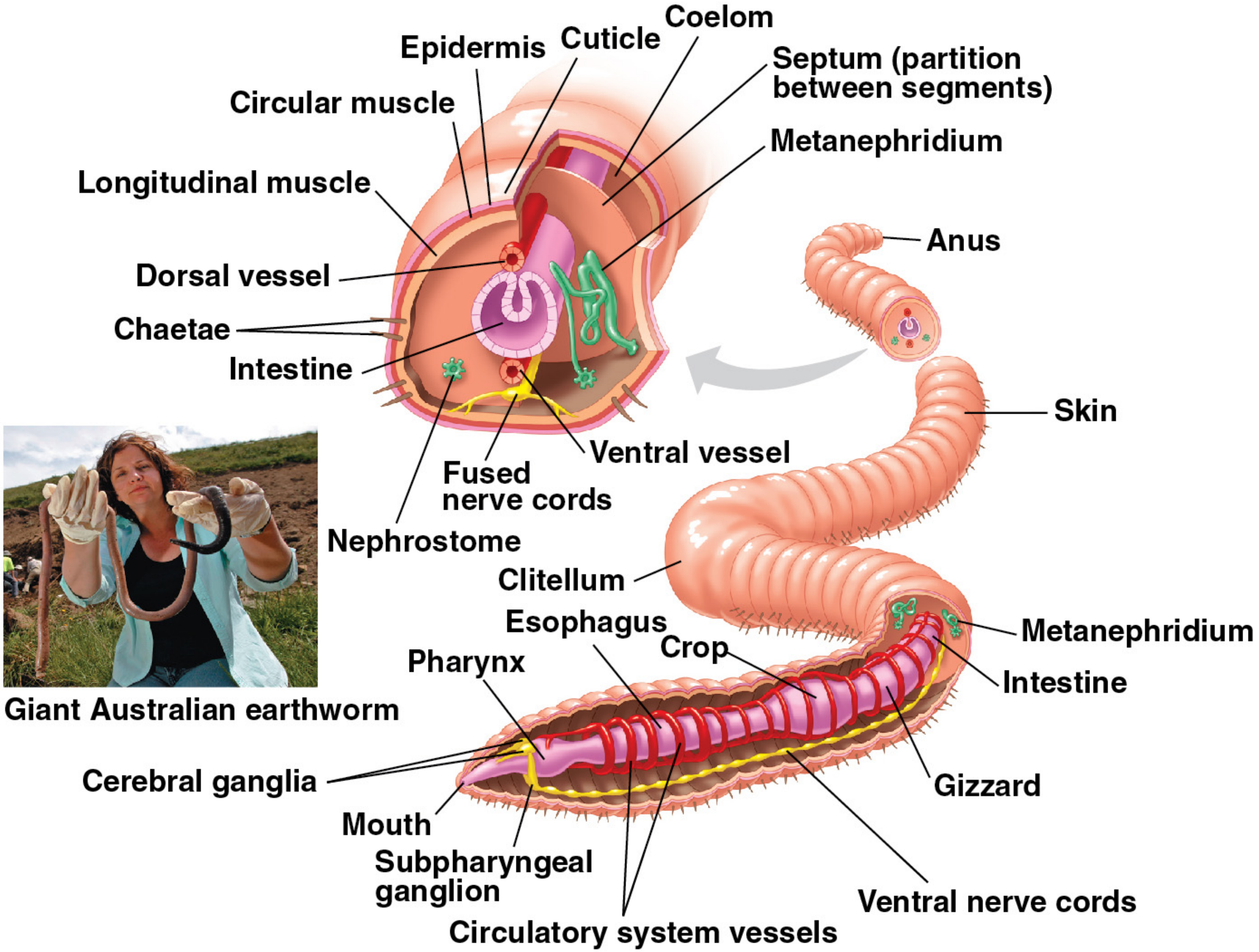
Earthworms

- Earthworms eat through soil, extracting nutrients and eliminating undigested material as fecal castings
- They are valued for their role in tilling, aerating, and improving the texture of agricultural soils

Earthworms

- Earthworms are hermaphrodites that cross-fertilize by joining in opposite directions to exchange sperm
- Some reproduce asexually by fragmentation and regeneration

Figure 33.25



Giant Australian earthworm

Video: Earthworm Locomotion

CONCEPT 33.4: Ecdysozoans are the most species-rich animal group

- Ecdysozoans are animals with a **cuticle**, a tough external coat
- The cuticle is shed during ecdysis, or **molting**
- Nematodes and arthropods are the largest of about eight ecdysozoan phyla

Figure 33.UN04

Nematodes

- Nematodes (roundworms) have cylindrical bodies tapered at the ends and covered by a cuticle
- They range in length from less than 1 mm to more than 1 m

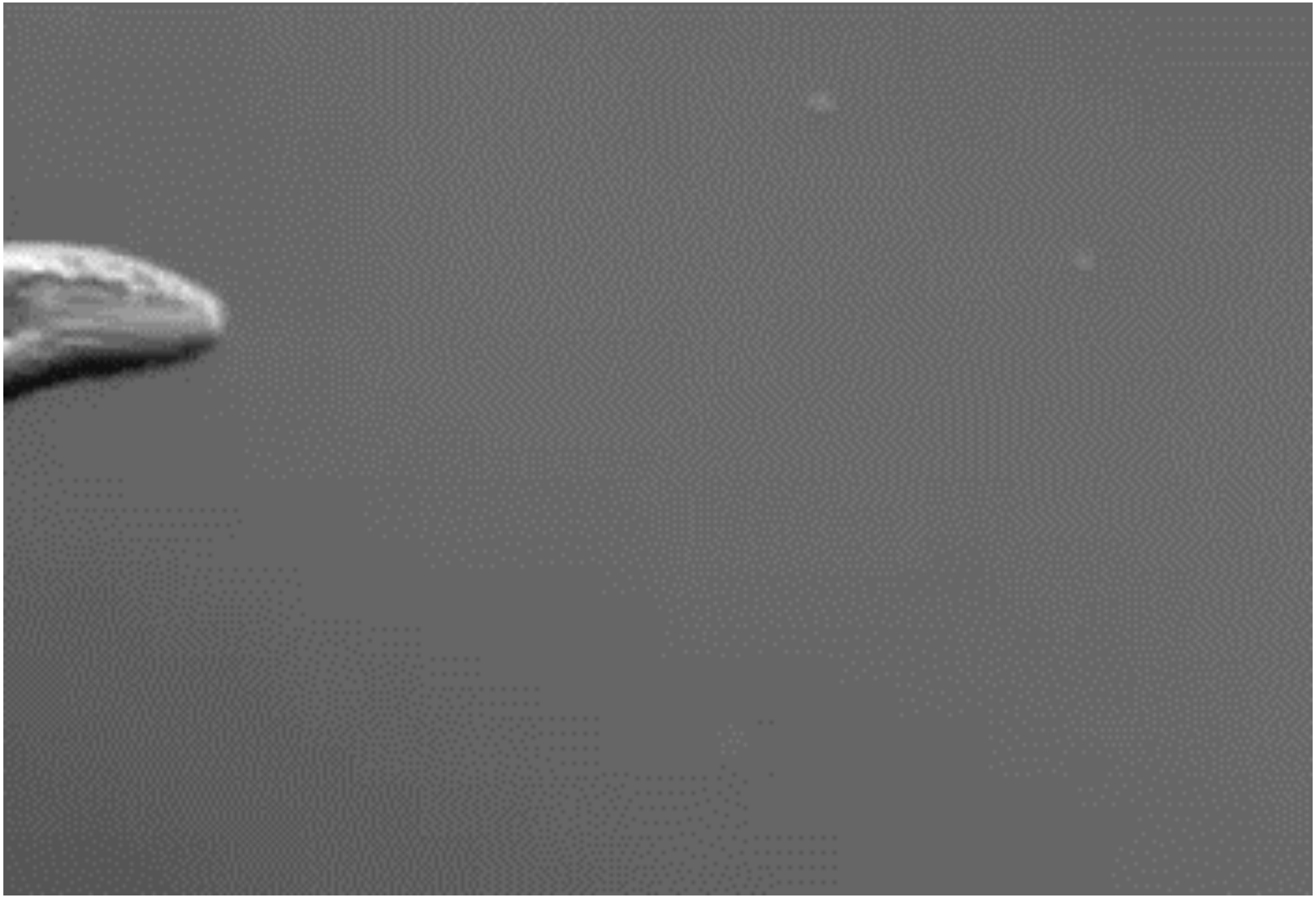
Figure 33.26

- Nematodes have an alimentary canal, but lack a circulatory system
- Nutrients are transported by fluid in the hemocoel
- The body wall muscles are all longitudinal, and their contraction produces a thrashing motion

- Many nematodes live freely in moist soils and at the bottoms of lakes and oceans
  - For example, *Caenorhabditis elegans* is a soil nematode that has become a model organism for research including aging in humans

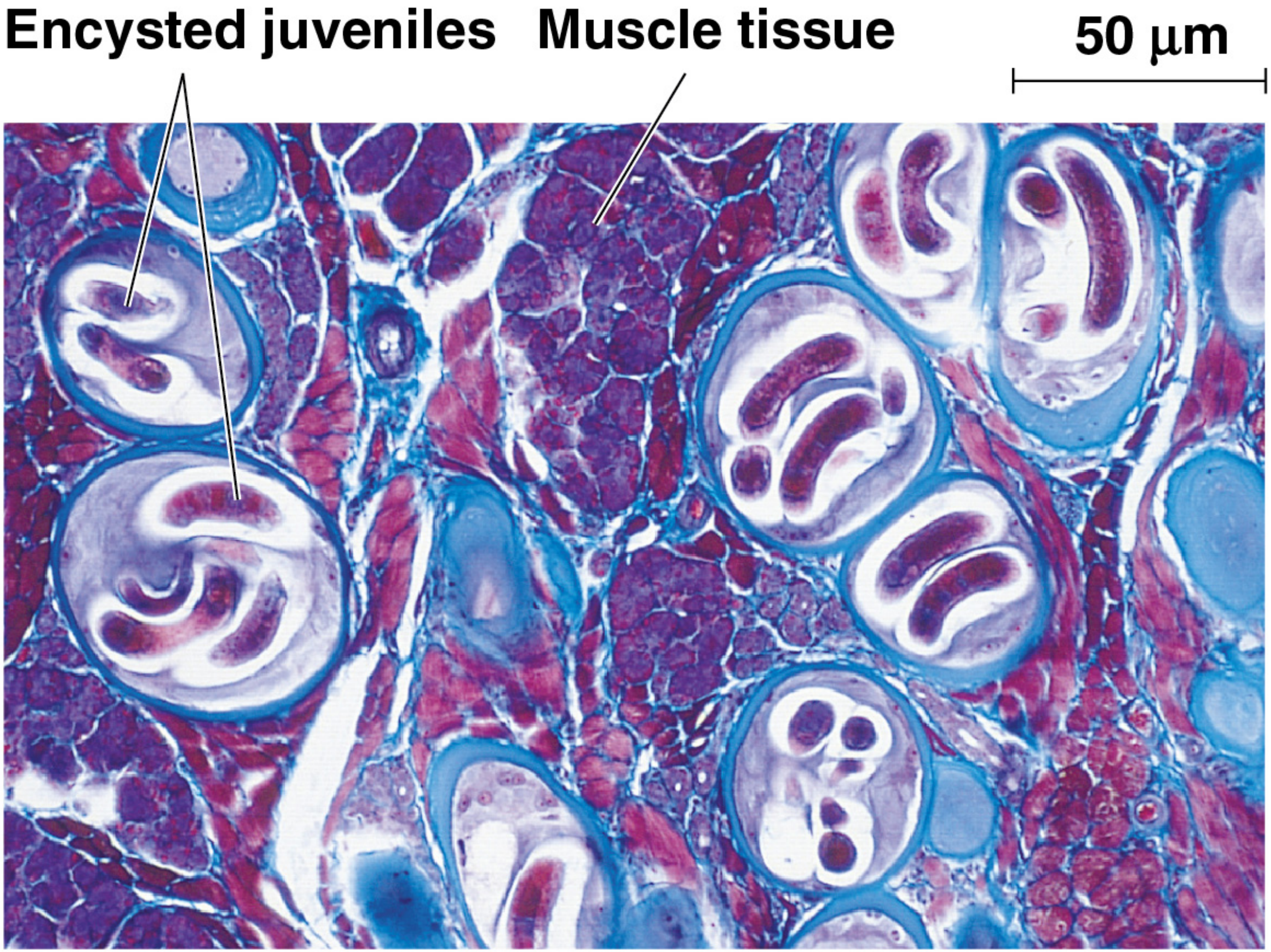
Video: *C. elegans* Embryo Development

Video: *C. elegans* Crawling



- Phylum Nematoda includes many parasites of plants and animals, including humans
  - For example, *Trichinella spiralis* is a parasite that can be acquired by humans by eating undercooked pork
  - The worms ultimately become encysted in human muscle tissue and other organs, causing trichinosis

Figure 33.27



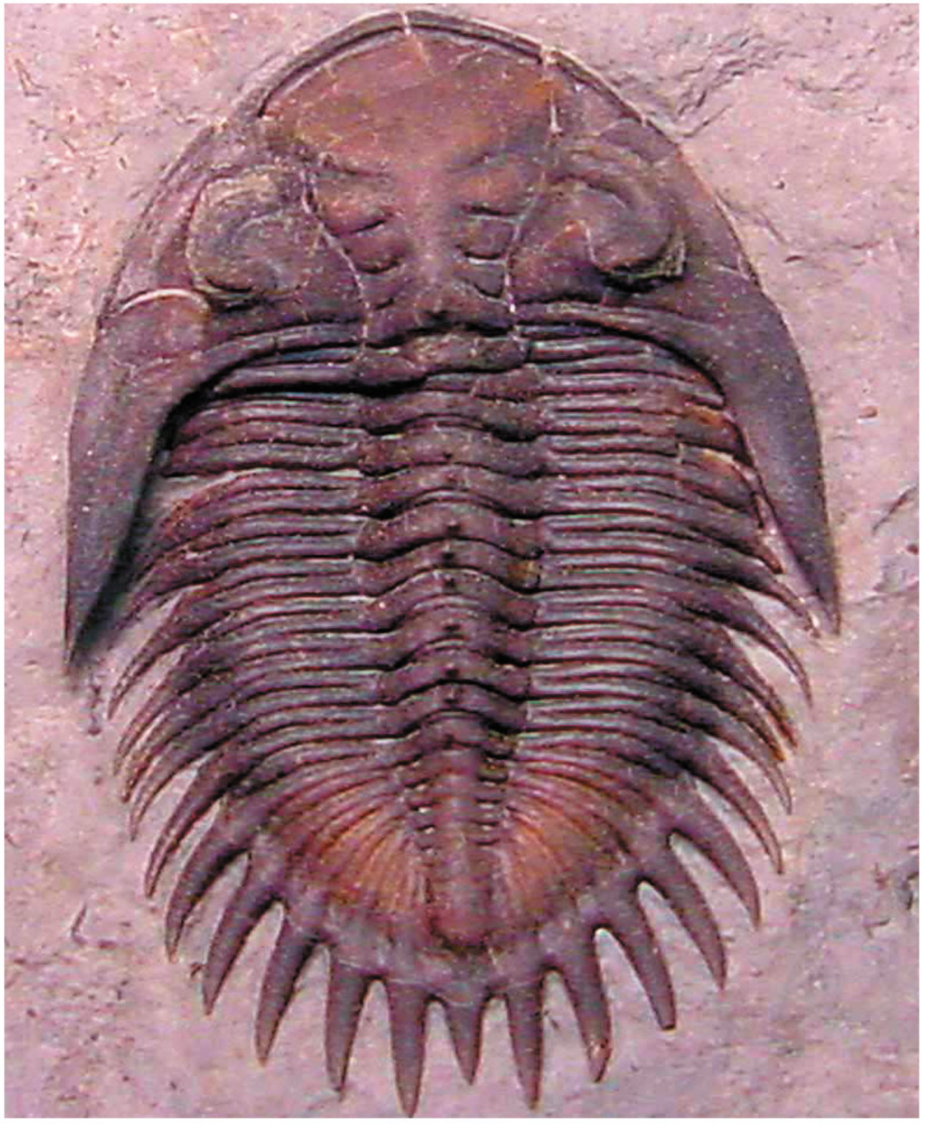
Arthropods

- Zoologists estimate that there are about a billion billion (10^{18}) arthropods living on Earth
- More than 1 million species have been described
- Two of every three known species are arthropods
- Arthropods are found in nearly all habitats on Earth

Arthropod Origins

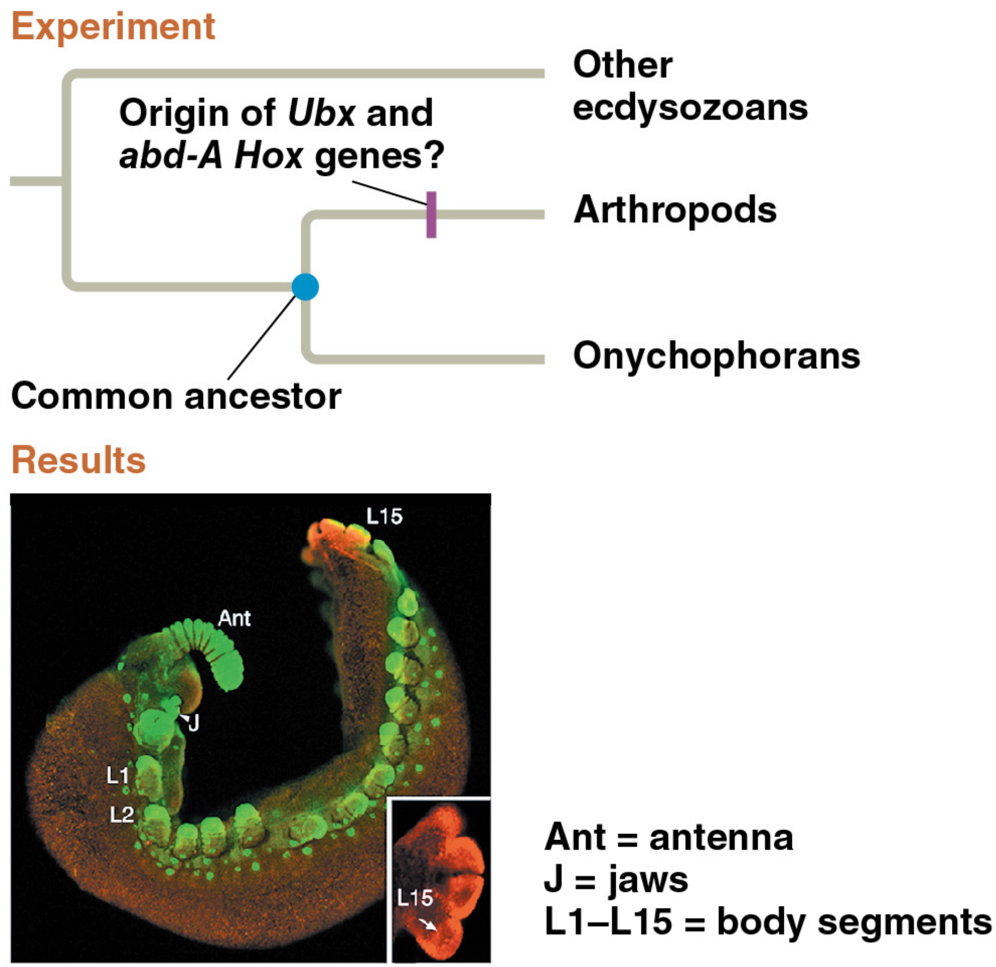
- The **arthropod** body plan consists of a segmented body, hard exoskeleton, and jointed appendages
- Arthropods date back to the Cambrian explosion (535–525 million years ago)
- Early arthropods, such as trilobites, showed little variation from segment to segment

Figure 33.28



- Over time, segments united to form “body regions” specialized for feeding, walking, or swimming
- Diverse body plans likely arose due to changes in the sequence or regulation of existing *Hox* genes, rather than the acquisition of new ones

Figure 33.29

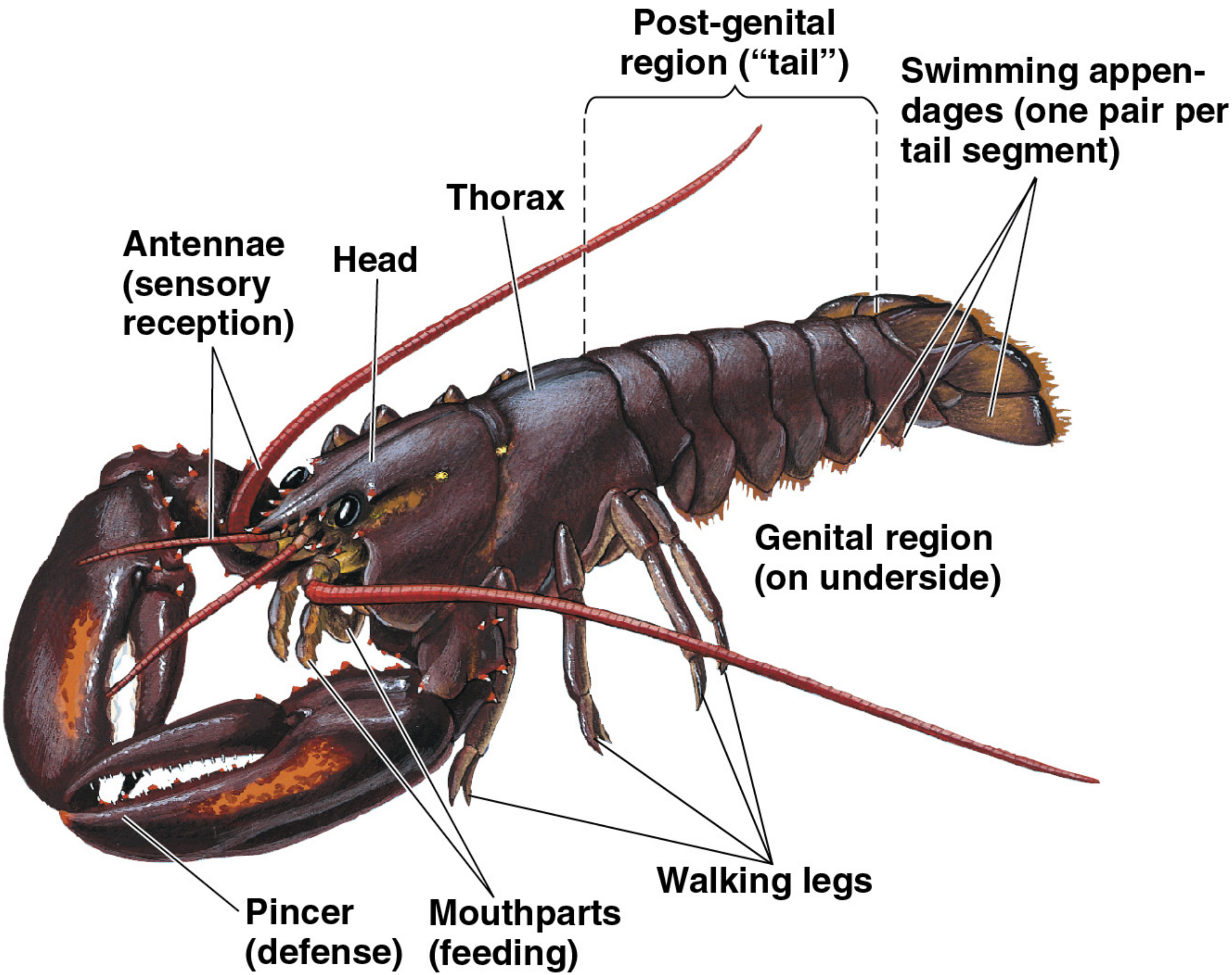


Data from J. K. Grenier et al., Evolution of the entire arthropod Hox gene set predated the origin and radiation of the onychophoran/arthropod clade, *Current Biology* 7:547–553 (1997).

General Characteristics of Arthropods

- Arthropod appendages have become modified for walking, feeding, sensory reception, reproduction, and defense
- Modified appendages are jointed and come in pairs

Figure 33.30


Post-genital region ("tail")
Swimming appen-dages (one pair per tail segment)
Thorax
Antennae (sensory reception)
Head
Genital region (on underside)
Walking legs
Pincer (defense)
Mouthparts (feeding)

Video: Lobster Mouth Parts

- The cuticle, an exoskeleton made of layers of protein and the polysaccharide chitin, covers the entire body
- The rigid exoskeleton provides protection and points of attachment for muscles
- The exoskeleton must be shed for growth to occur

- Evolution of the exoskeleton enabled arthropods to be among the first animals to colonize land because
  - It reduces water loss and prevents desiccation
  - It provides structural support without the buoyancy of water

- Arthropods have eyes, olfactory receptors, and antennae that function in both touch and smell
- The **open circulatory system** uses a heart to pump hemolymph into the cavity surrounding the tissues and organs (the hemocoel)

- A variety of specialized gas exchange organs have evolved to circumvent the exoskeleton
  - Most aquatic species have gills with feathery extensions to maximize surface exposed to the water
  - Terrestrial species have internal surfaces specialized for gas exchange, such as the insect tracheal system

- Living arthropods consist of three major lineages that diverged early in the phylum’s evolution
  - **Chelicerates** (sea spiders, horseshoe crabs, scorpions, ticks, mites, and spiders)
  - **Myriapods** (centipedes and millipedes)
  - **Pancrustaceans** (insects, lobsters, shrimp, barnacles, and other crustaceans)

Chelicerates

- Chelicerates are named for clawlike feeding appendages called **chelicerae**
- **Eurypterids** (water scorpions), the earliest members of the clade, were predators that grew up to 3 m long
- Most marine chelicerates are extinct; sea spiders and horseshoe crabs are the only surviving groups

Figure 33.31

- Most modern chelicerates are **arachnids**, which include spiders, scorpions, ticks, and mites

Figure 33.32

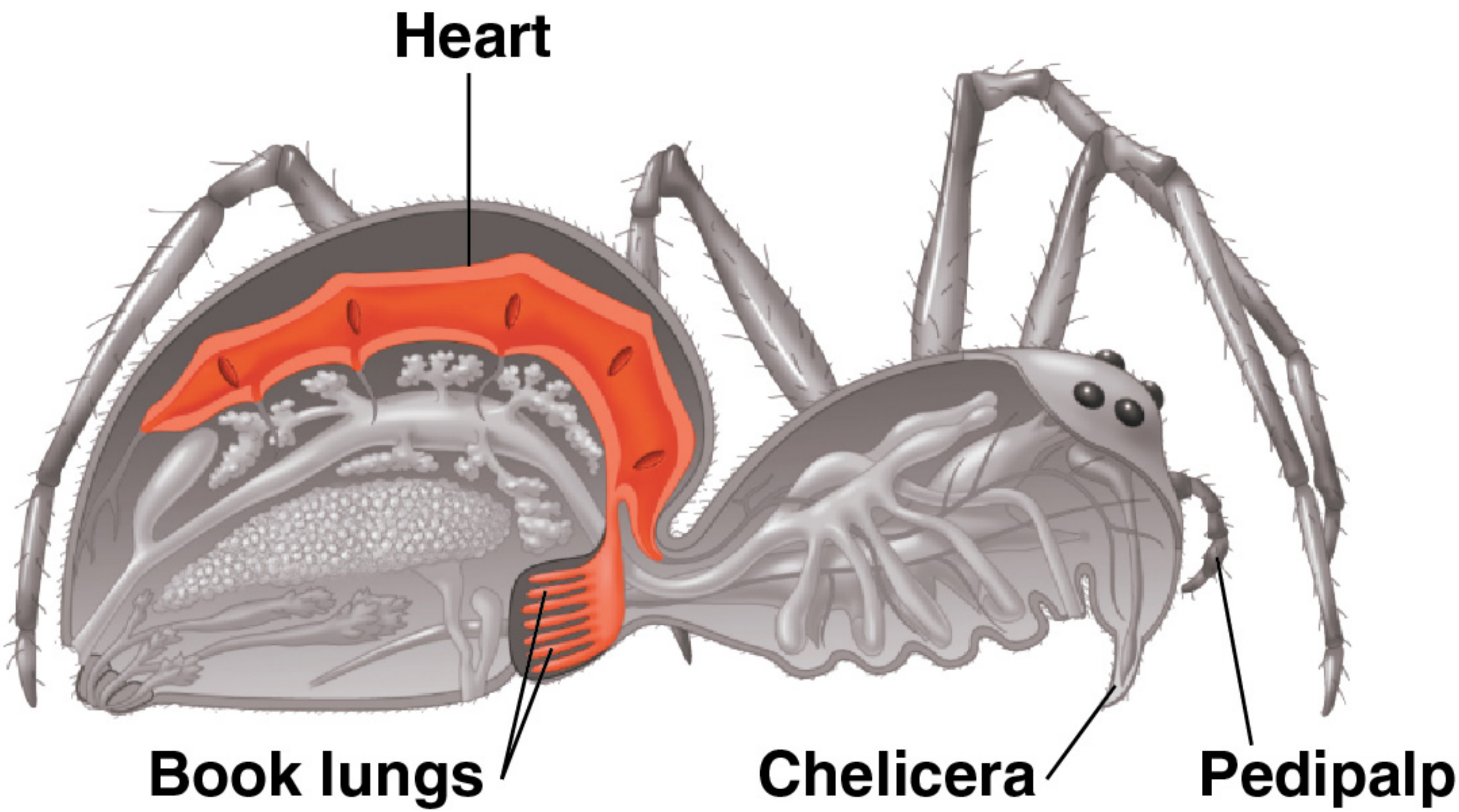
▲ **Scorpion**

▲ **Dust mite**

◀ **Web-building spider**

- Arachnids have six paired appendages: chelicerae, pedipalps, and four pairs of walking legs
- Pedipalps function in sensing, feeding, defense, or reproduction
- In most spiders, gas exchange is carried out by **book lungs**, stacked platelike structures

Figure 33.33



- Many spiders produce silk from specialized abdominal glands for a variety of uses
  - Construction of a web for capturing prey
  - Dropline for rapid escape
  - Cover for eggs
  - “Gift wrap” for male courtship offerings
  - Transport (“ballooning”)

Myriapods

- Myriapoda includes millipedes and centipedes
- All living myriapods are terrestrial
- They have a pair of antennae and three pairs of appendages modified as mouthparts

(a) Millipede

(b) Centipede

- Millipedes have many legs, but fewer than a thousand
- They have two pairs of legs per trunk segment
- They eat decaying leaves and other plant matter

(a) Millipede

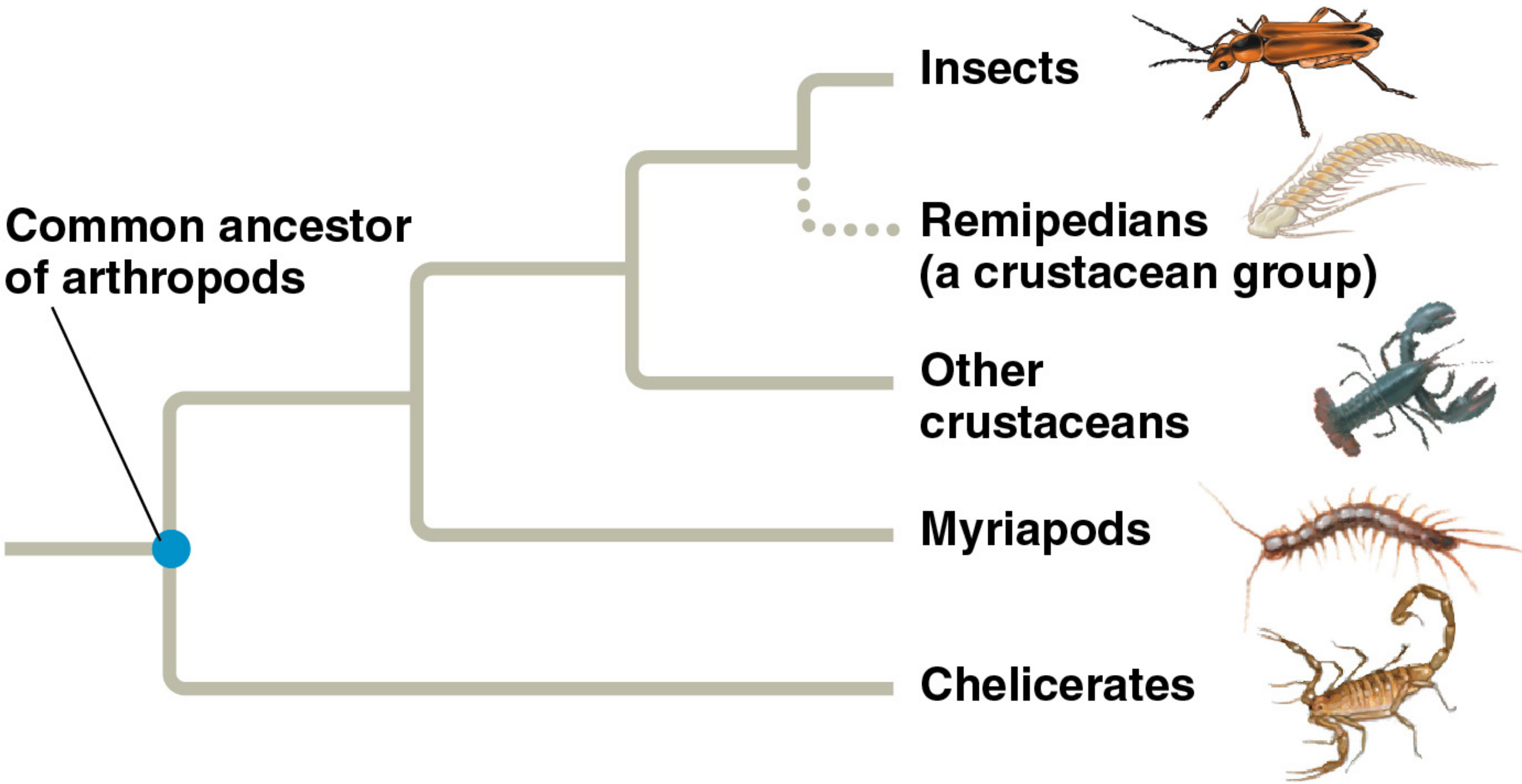
- Centipedes are carnivores
- They have one pair of legs per trunk segment
- Poison claws on the foremost trunk segment paralyze prey and aid in defense

(b) Centipede

Pancrustaceans

- Recent evidence indicates that terrestrial insects are more closely related to crustaceans than myriapods
- Some lineages of crustaceans are more closely related to insects than they are to other crustaceans
- Together, insects and crustaceans form the clade Pancrustacea

Figure 33.35



Common ancestor of arthropods
Insects
Remipedians (a crustacean group)
Other crustaceans
Myriapods
Chelicerates

Crustaceans

- Crustaceans (crabs, lobsters, shrimps, and others) live in marine, freshwater, and terrestrial habitats
- Small crustaceans exchange gases through the cuticle; larger crustaceans have gills
- Nitrogenous wastes diffuse through the cuticle; a pair of glands regulates salt balance

Crustaceans

- Many crustaceans have highly specialized appendages
  - The anterior-most form two pairs of antennae
  - Three or more pairs are modified as mouthparts
  - Walking legs are located on the thorax
  - Swimming appendages are located on the tail

Crustaceans

- Most crustaceans have separate sexes
- Most aquatic species have one or more swimming larval stages

Crustaceans

- Isopods, one of the largest groups of crustaceans, live in terrestrial, freshwater, and marine habitats
- Pill bugs are common terrestrial isopods that live under moist logs and leaves

Crustaceans

- Decapods are all relatively large crustaceans including lobsters, crabs, crayfish, and shrimp
- The cuticle is hardened by calcium carbonate
- Most are marine, but crayfishes live in fresh water, and some tropical crabs live on land

Figure 33.36

Crustaceans

- Planktonic crustaceans are small and numerous
  - Copepods are among the most abundant animals
  - Shrimplike krill are a food source for baleen whales
  - Larval stages of many larger crustaceans are planktonic

Figure 33.37

Crustaceans

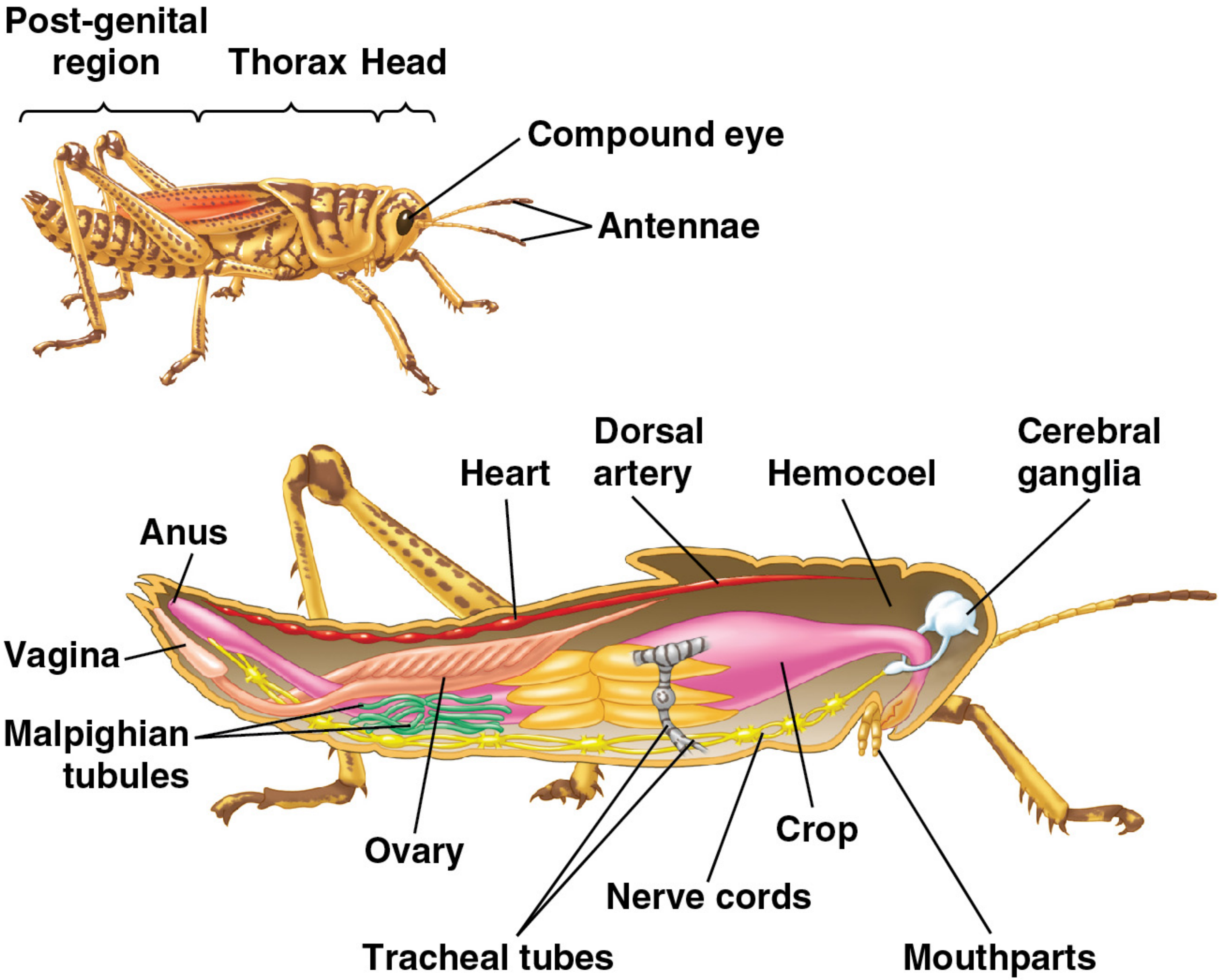
- Barnacles are mostly sessile crustaceans with a cuticle hardened into a calcium carbonate shell
- Most anchor to submerged surfaces such as rocks, boat hulls, or pilings
- Feeding appendages extend from the shell to strain food from water

Figure 33.38

Insects

- Clade Hexapoda includes insects and their relatives
- Insects live in most terrestrial habitats and in fresh water, but are rare in marine habitats
- They have several complex internal organ systems

Figure 33.39



Post-genital region
Thorax
Head
Compound eye
Antennae
Dorsal artery
Cerebral ganglia
Heart
Hemocoel
Anus
Vagina
Malpighian tubules
Ovary
Crop
Nerve cords
Tracheal tubes
Mouthparts

Insects

- The oldest insect fossils are 415 million years old
- Rapid insect diversification followed the evolution of flight 359–252 million years ago
- Flight improved the ability to evade predators, locate food and mates, and disperse to new habitats
- Insect wings are an extension of the cuticle, enabling flight without sacrificing a pair of walking legs

Figure 33.40

Insects

- Insect radiations followed periods of diversification in their food plants
  - For example, following the rise of the gymnosperms during the Carboniferous period and
  - Following the expansion of flowering plants during the mid-Cretaceous period

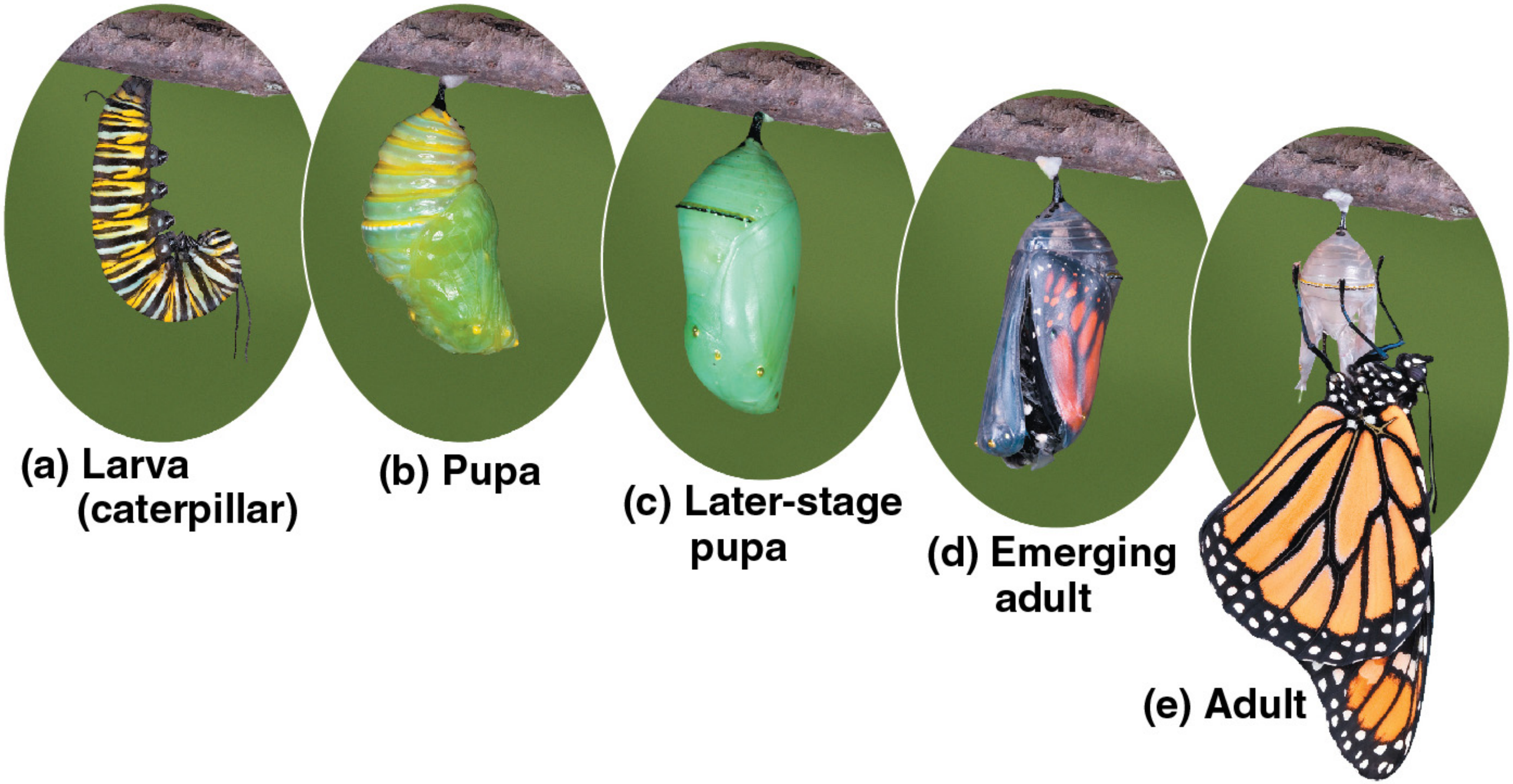
Insects

- Some insects undergo **incomplete metamorphosis** during their development
- The young (nymphs) resemble small, wingless adults
- They undergo a series of molts as they grow
- They reach full size, acquire wings, and become sexually mature with the final molt

Insects

- Other insects undergo **complete metamorphosis**
- They have larval stages (called maggots, grubs, or caterpillars) specialized for eating and growing
- Larval stages look very different from the adult stage
- Metamorphosis from larva to adult occurs during a pupal stage

Figure 33.41



(a) Larva (caterpillar)
(b) Pupa
(c) Later-stage pupa
(d) Emerging adult
(e) Adult

Video: Butterfly Emerging

Insects

- Most insects reproduce sexually, and have separate males and females
- Individuals find and identify members of their own species using bright colors, sounds, or odors
- Fertilization is generally internal
- Some species copulate; in others, females pick up a sperm packet deposited by the male
- Eggs are generally laid on a food source

Insects

- Insects are classified into more than 30 orders
- Two orders of wingless insects, Archaeognatha and Zygentoma, diverged from other insects early

Figure 33.42

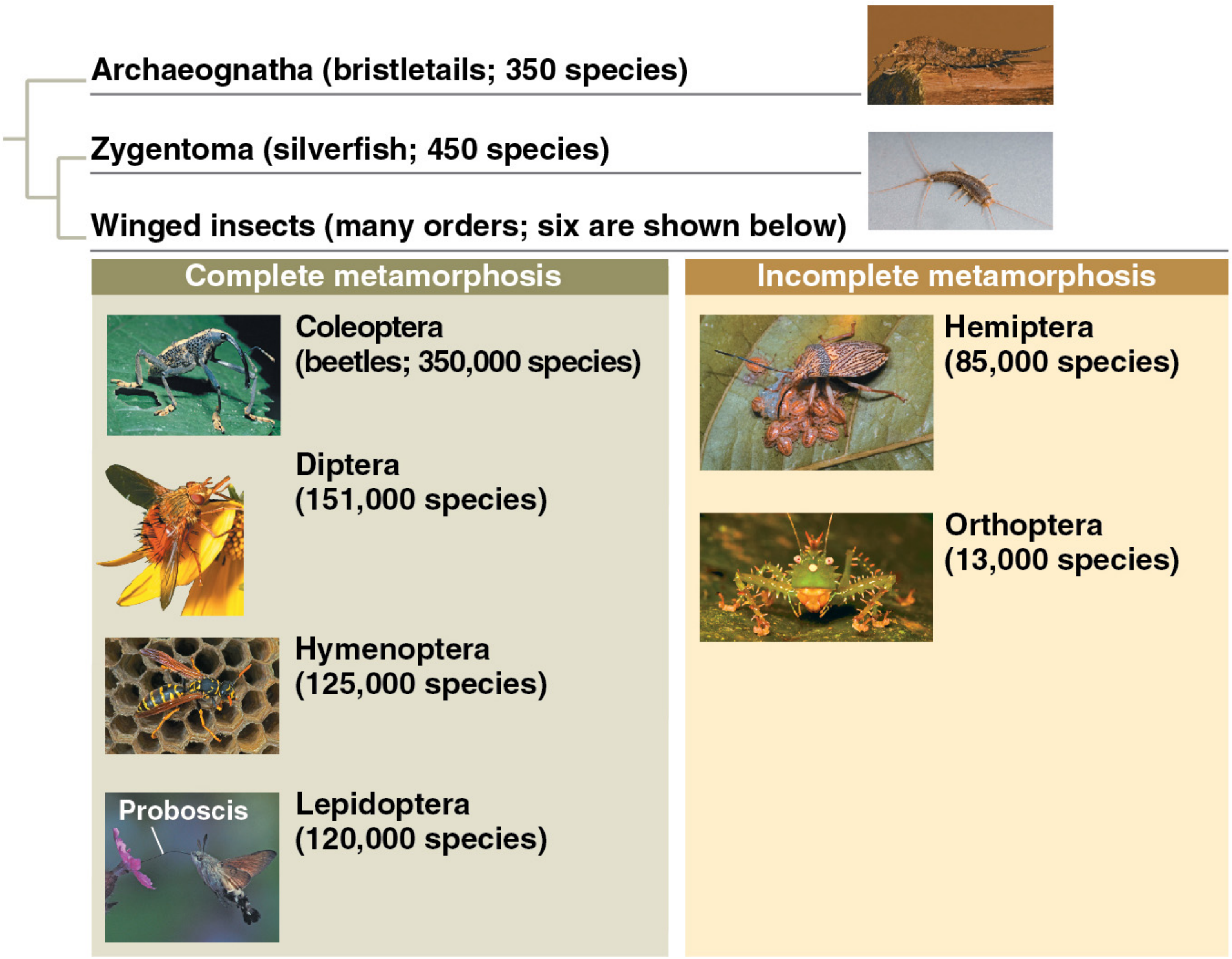

Archaeognatha (bristletails; 350 species)
Zygentoma (silverfish; 450 species)
Winged insects (many orders; six are shown below)
Complete metamorphosis
Coleoptera
(beetles; 350,000 species)
Diptera
(151,000 species)
Hymenoptera
(125,000 species)
Proboscis
Lepidoptera
(120,000 species)
Incomplete metamorphosis
Hemiptera
(85,000 species)
Orthoptera
(13,000 species)

Figure 33.42 Exploring insect diversity: Archaeognatha

Archaeognatha (bristletails; 350 species)

- Bristletails are wingless insects found in moist, dark terrestrial habitats, such as leaf litter or under bark
- They feed on algae, plant debris, and lichens

Archaeognatha (bristletails; 350 species)

Figure 33.42 Exploring insect diversity: Zygentoma

Zygentoma (silverfish; 450 species)

- Small, wingless insects with a flattened body and reduced eyes
- They live in leaf litter, under bark, or infest buildings

Zygentoma (silverfish; 450 species)

Figure 33.42 Exploring insect diversity: Winged insects

Winged insects

- There are many orders of winged insects with complete or incomplete metamorphosis
  - For example, coleopterans, dipterans, lepidopterans, and hymenopterans have complete metamorphosis
  - Hemipterans and orthopterans have incomplete metamorphosis

Figure 33.42 Exploring insect diversity: Winged insects, Coleoptera

Coleoptera (beetles; 350,000 species)

- Beetles are the most species-rich order of insects
- They have two pairs of wings, one thick and stiff, the other membranous
- They have an armored exoskeleton and mouthparts adapted for biting and chewing

Figure 33.42c

Coleoptera (beetles; 350,000 species)

Figure 33.42 Exploring insect diversity: Winged insects, Diptera

Diptera (151,000 species)

- Dipterans have one pair of wings; the second pair forms balancing organs called halteres
- Mouthparts are adapted for sucking, piercing, or lapping
- Flies and mosquitoes are common dipterans

Diptera
(151,000 species)

Figure 33.42 Exploring insect diversity: Winged insects, Hymenoptera

Hymenoptera (125,000 species)

- Hymenopterans are highly social insects including ants, bees, and wasps
- They have two pairs of membranous wings, a mobile head, and chewing or sucking mouthparts
- Females of many species have a posterior stinger
- Many build elaborate nests

Hymenoptera (125,000 species)

Figure 33.42 Exploring insect diversity: Winged insects, Lepidoptera

Lepidoptera (120,000 species)

- Butterflies and moths have two pairs of wings covered with tiny scales
- A long proboscis is uncoiled to feed on nectar, or animal blood or tears

Figure 33.42f

Lepidoptera (120,000 species)

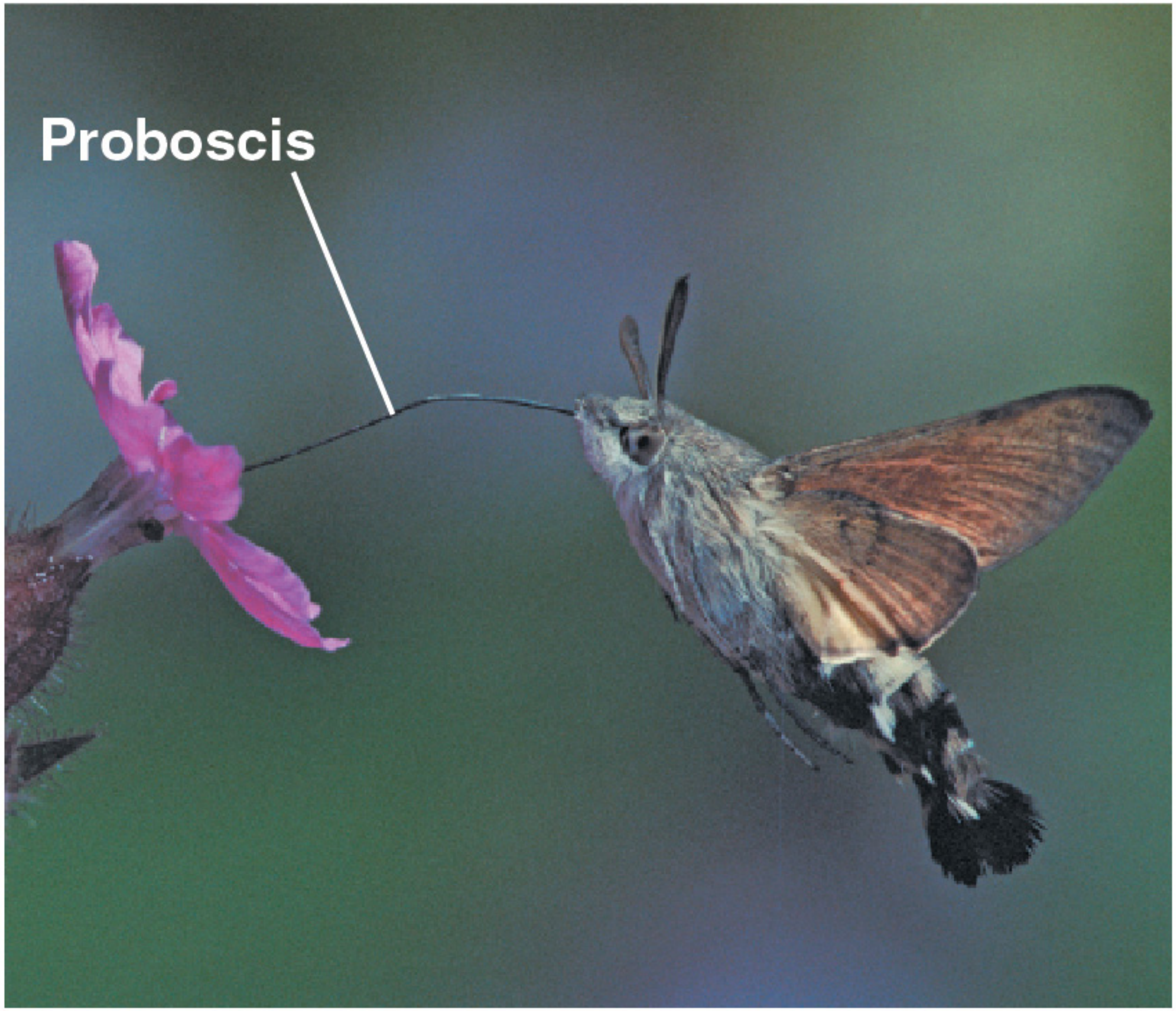


Figure 33.42 Exploring insect diversity: Winged insects, Hemiptera

Hemiptera (85,000 species)

- Hemipterans include “true bugs”, such as stink bugs, bed bugs, and assassin bugs
- They have two pairs of wings, one partly leathery and the other membranous
- They have piercing or sucking mouthparts

Hemiptera (85,000 species)

Figure 33.42 Exploring insect diversity: Winged insects, Orthoptera

Orthoptera (13,000 species)

- Orthopterans are mostly herbivorous insects including grasshoppers, crickets, and their relatives
- Large hind legs are adapted for jumping
- They have two pairs of wings (one leathery, one membranous) and biting or chewing mouthparts
- Many males rub together body parts to make courtship sounds

Orthoptera (13,000 species)

Orthoptera (13,000 species)

- Insects play roles as predators, prey, parasites, and decomposers
- Some are beneficial, such as pollinators; others are harmful, such as crop pests or disease carriers
- In many parts of the world, people eat insects as a protein source

Video: Bee Pollinating

Orthoptera (13,000 species)

- Insects compete with humans for food
  - For example, in parts of Africa, about 75% of crops are lost to insects
- Insects quickly evolve resistance to the many pesticides used to combat them

CONCEPT 33.5: Echinoderms and chordates are deuterostomes

- Echinoderms (phylum Echinodermata) include sea stars and sea urchins
- Vertebrates (animals that have a backbone) are members of phylum Chordata
- Echinoderms and chordates constitute the clade Deuterostomia

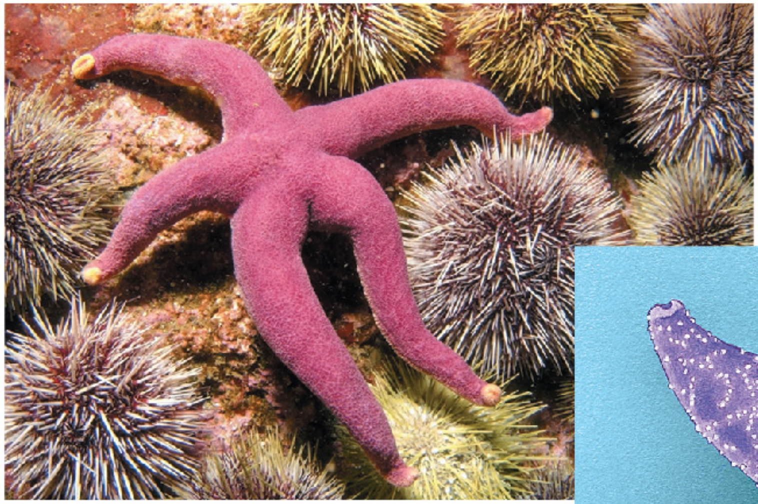
Figure 33.UN05

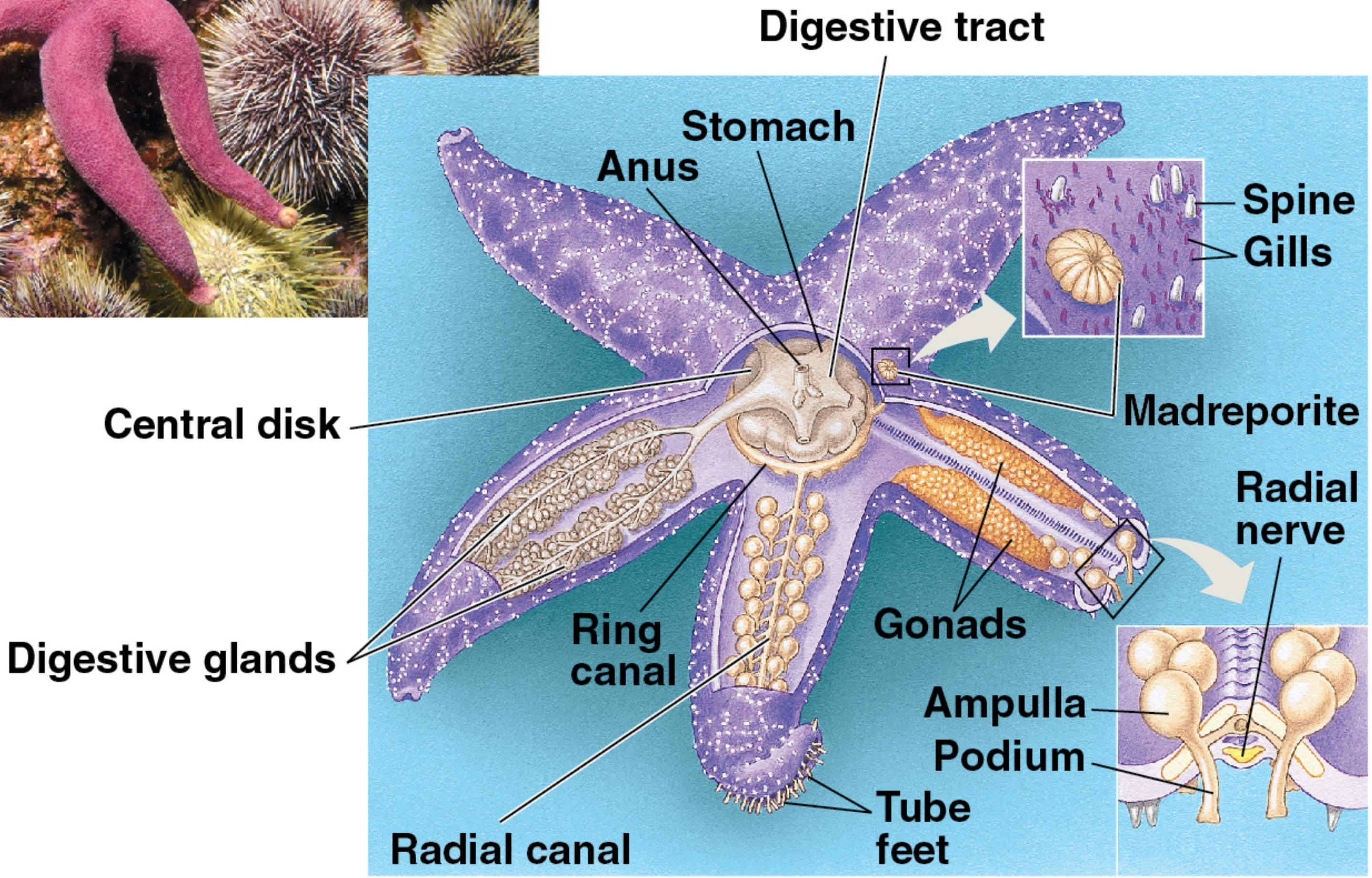
- Deuterostomes share developmental characteristics
  - Radial cleavage
  - Formation of the anus from the blastopore
- These characteristics are also found in other clades
- DNA similarities are used to define deuterostomes

Echinoderms

- Sea stars (starfish) and most other **echinoderms** are slow-moving or sessile marine animals
- They have a coelom and an endoskeleton of hard calcareous plates; most are prickly
- The **water vascular system**, a network of hydraulic canals, branches into **tube feet** that function in locomotion and feeding
- They have separate sexes and external fertilization

Figure 33.43




Digestive tract
Stomach
Anus
Spine
Gills
Central disk
Madreporite
Radial
nerve
Digestive glands
Ring
canal
Gonads
Ampulla
Podium
Tube
feet
Radial canal

Video: Echinoderm Tube Feet

- Most adult echinoderms appear to have radial symmetry with multiples of five
- Their symmetry is not truly radial; the opening of the water vascular system is not central
- Echinoderm larvae have bilateral symmetry

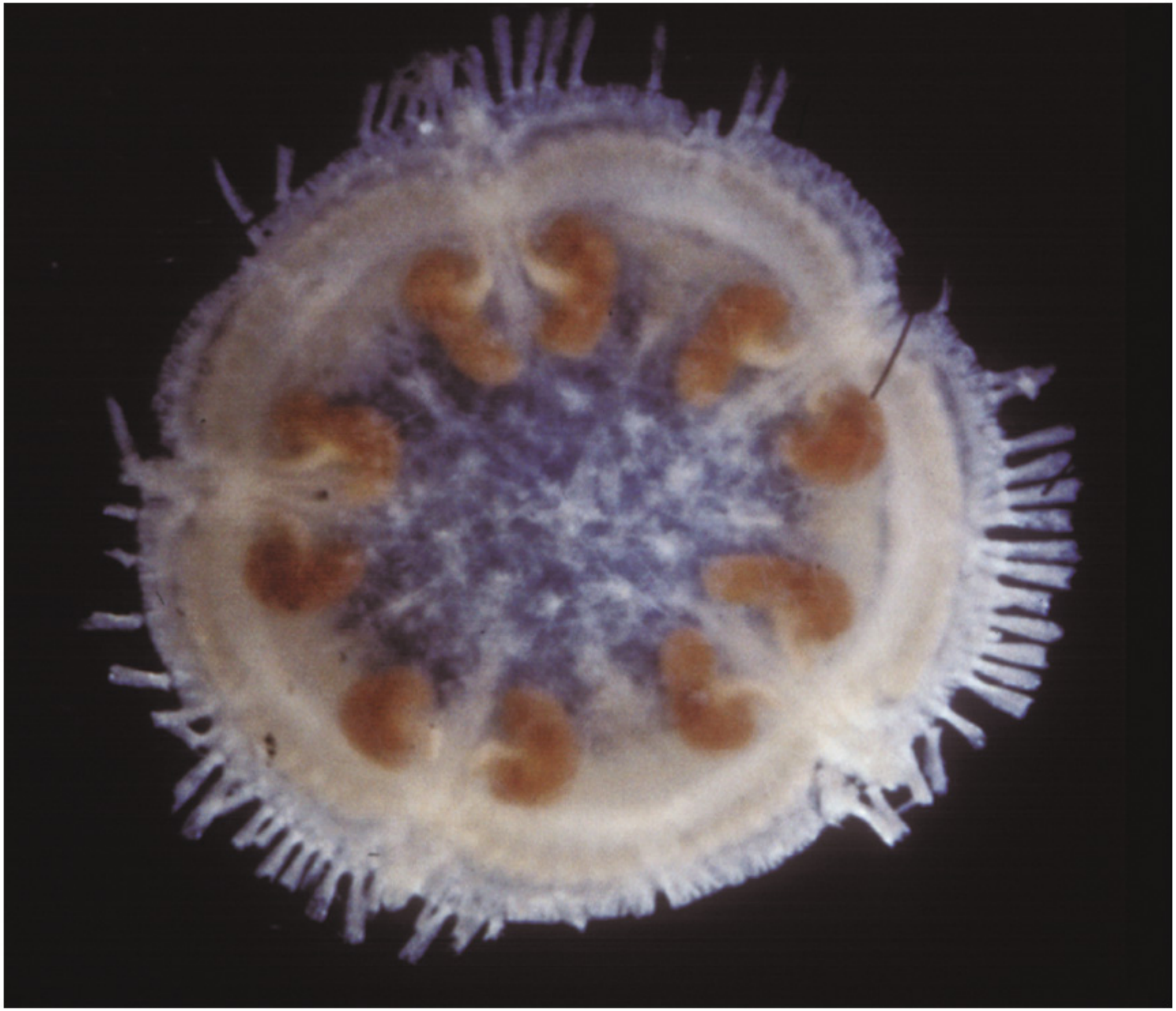
- Living echinoderms are divided into five clades
  - Asteroidea (sea stars and sea daisies)
  - Ophiuroidea (brittle stars)
  - Echinoidea (sea urchins and sand dollars)
  - Crinoidea (sea lilies and feather stars)
  - Holothuroidea (sea cucumbers)

Asteroidea: Sea Stars and Sea Daisies

- Sea stars have arms radiating from a central disk; the undersurfaces of the arms bear tube feed
- Tube feet grip the substrate with adhesive chemicals
- Tube feet are used to pry open bivalves, which are digested externally
- Several echinoderms have regenerative powers
  - For example, sea stars can regrow lost arms

- Sea daisies are a group of three armless species
- They live on submerged wood and absorb nutrients through a membrane that surrounds their body
- The body is usually disk-shaped, with five-sided organization, less than a centimeter in diameter

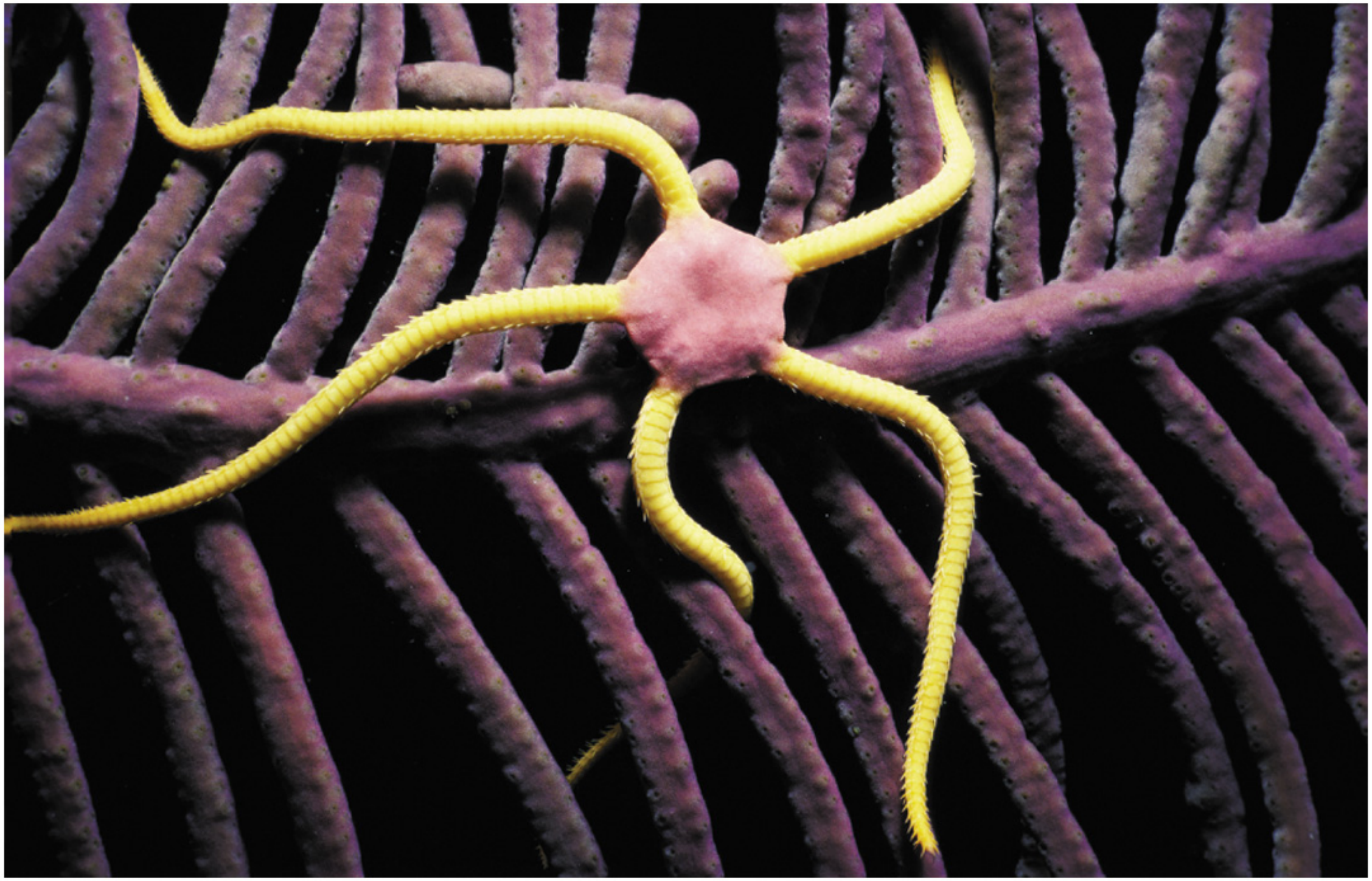
Figure 33.44



Ophiuroidea: Brittle Stars

- Brittle stars have a distinct central disk and long, flexible arms used for movement
- Tube feet are used to grip the substrate
- They may be suspension feeders, predators, or scavengers

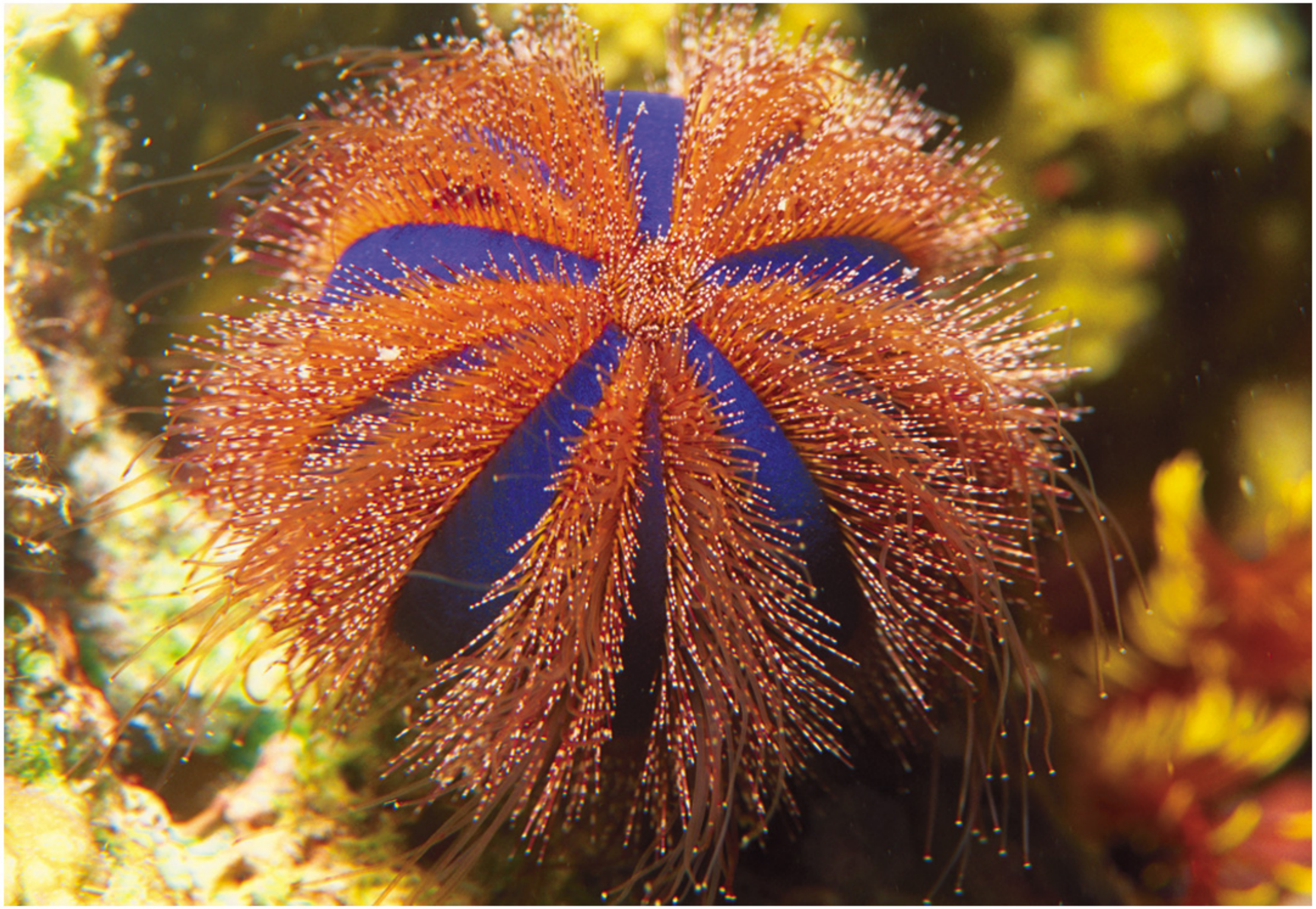
Figure 33.45



Echinoidea: Sea Urchins and Sand Dollars

- Sea urchins and sand dollars have no arms, but have five rows of tube feet used for movement
- Sea urchins are spherical; sand dollars are flat disks
- Sea urchins use spines for movement and protection and feed on seaweed using jaw-like structures surrounding the mouth

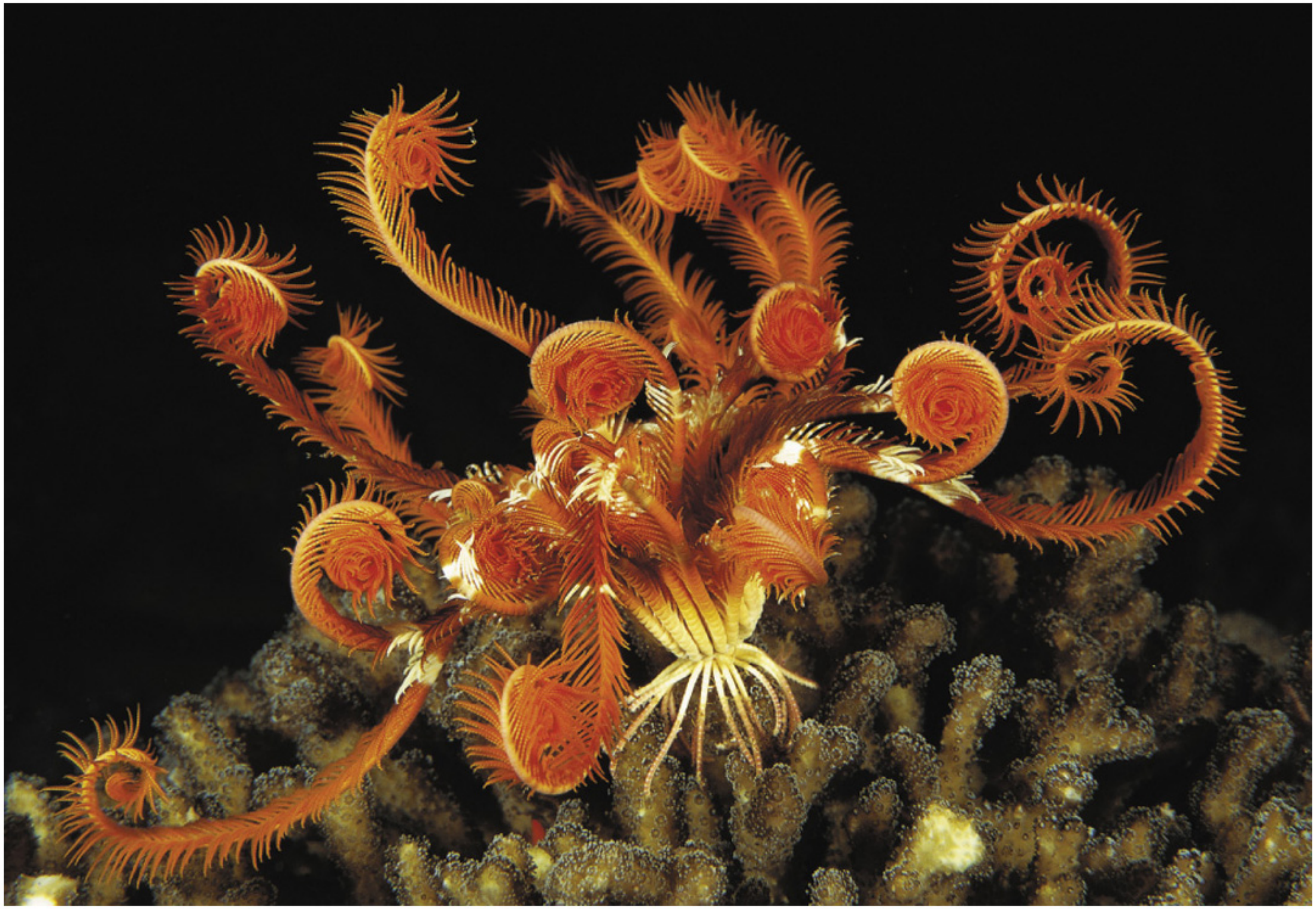
Figure 33.46



Crinoidea: Sea Lilies and Feather Stars

- Sea lilies live attached to the substrate by a stalk
- Feather stars can crawl using long, flexible arms
- Both use their arms in suspension feeding
- Crinoidea have changed little in over 500 million years of evolution

Figure 33.47



Holothuroidea: Sea Cucumbers

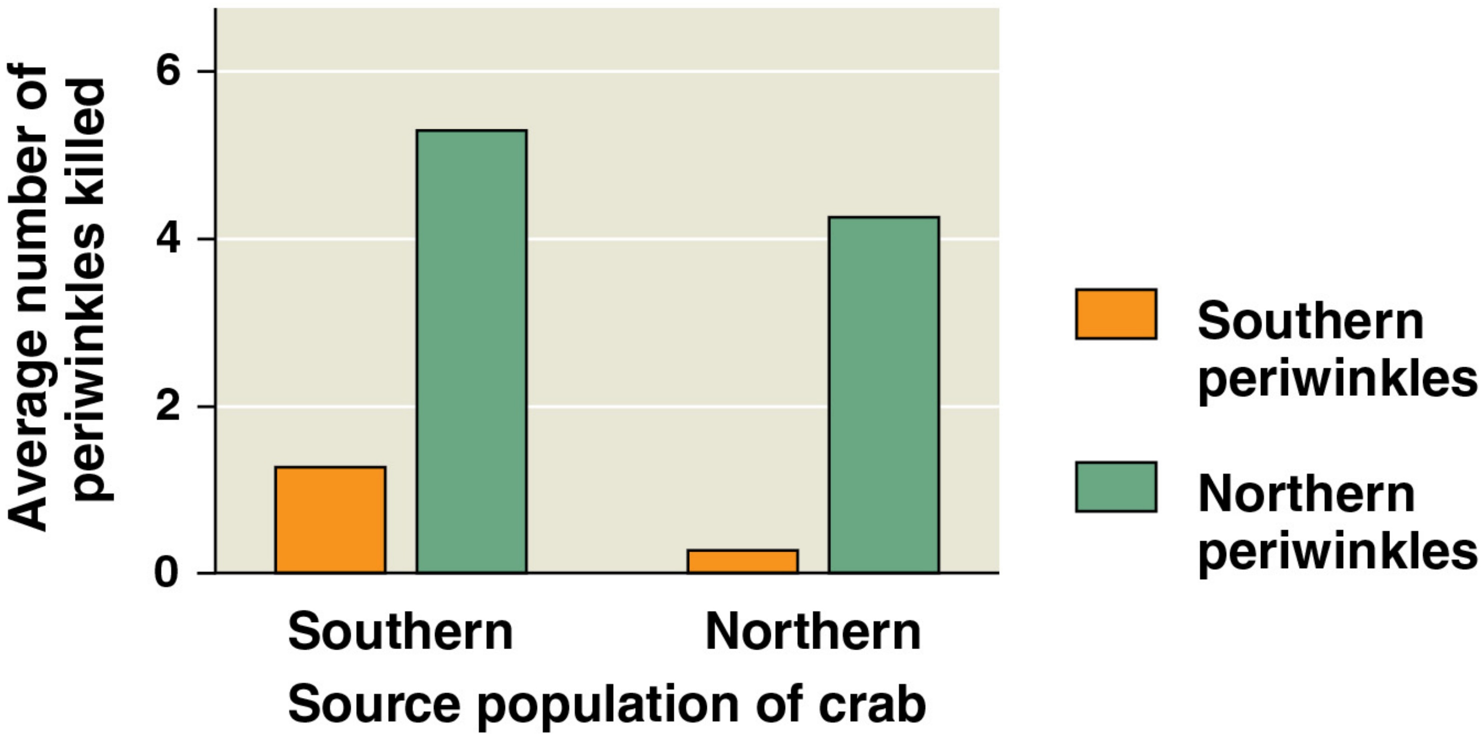
- Sea cucumbers do not resemble other echinoderms
- They lack spines, and have reduced endoskeletons
- They are elongated along the oral-aboral axis
- They have five rows of tube feet, some of which are used as feeding tentacles

Figure 33.48

Chordates

- Phylum Chordata includes vertebrates and two groups of invertebrates (lancelets and tunicates)
- Chordates are bilaterally symmetrical coelomates with segmented bodies
- They are closely related to echinoderms, but have evolved independently for at least 500 million years

Figure 33.UN06a



Data from R. Rochette et al., Interaction between an invasive decapod and a native gastropod: Predator foraging tactics and prey architectural defenses, *Marine Ecology Progress Series* 330:179–188 (2007).

A periwinkle

Figure 33.UN07

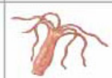
	Phylum		Description
Metazoa	Porifera (sponges)		Lack tissues; have choanocytes (collar cells—flagellated cells that ingest bacteria and tiny food particles)
Metazoa; Eumetazoa	Cnidaria (hydras, jellies, sea anemones, corals)		Unique stinging structures (nematocysts) housed in specialized cells (cnidocytes); diploblastic; radially symmetrical; gastrovascular cavity (digestive compartment with a single opening)
Metazoa; Eumetazoa; Bilateria; Lophotrochozoa	Platyhelminthes (flatworms)		No body cavity; dorsoventrally flattened; gastrovascular cavity or no digestive tract
	Syndermata (rotifers and acanthocephalans)		Hemocoel; rotifers have alimentary canal (digestive tube with mouth and anus) and jaws (trophi); acanthocephalans are parasites of vertebrates
	Ectoprocta and Brachiopoda		Coelom; have lophophores (feeding structures bearing ciliated tentacles)
	Mollusca (clams, snails, squids)		Hemocoel; reduced coelom; three main body parts (muscular foot, visceral mass, mantle); most have hard shell made of calcium carbonate
	Annelida (segmented worms)		Coelom; body wall and internal organs are segmented (except digestive tract, which is unsegmented)
Metazoa; Eumetazoa; Bilateria; Ecdysozoa	Nematoda (roundworms)		Hemocoel; cylindrical body with tapered ends; no circulatory system; undergo ecdysis
	Arthropoda (spiders, centipedes, crustaceans, and insects)		Hemocoel; reduced coelom. Have segmented body, jointed appendages, and exoskeleton made of protein and chitin
Metazoa; Eumetazoa; Bilateria; Deuterostomia	Echinodermata (sea stars, sea urchins)		Coelom; bilaterally symmetrical larvae and five-part body organization as adults; unique water vascular system; endoskeleton
	Chordata (lancelets, tunicates, vertebrates)		Coelom; have notochord; dorsal, hollow nerve cord; pharyngeal slits; post-anal tail (see Figure 34.3)

Figure 33.UN08

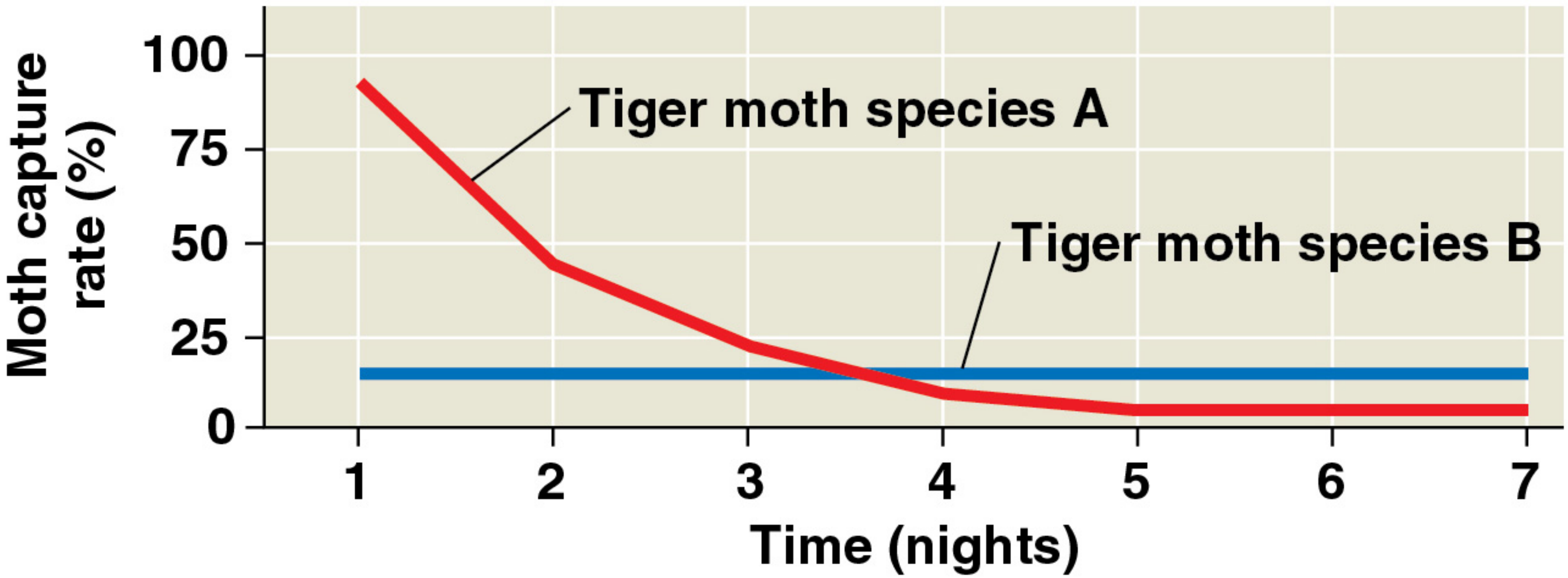


Figure 33.UN09