Chapter 16

Molluscs

Characteristics

- They contain nearly 50,000 living species and 35,000 fossil species.
- They have a soft body and belong to the lophotrochozoa protostomes.
- They include chitons, tooth shells, snails, slugs, nudibranchs, sea butterflies, clams, mussels, oysters, squids, octopuses and nautiluses.
- Some may weigh 450 kg and grow to 18 m long, but 80% are under 5 cm.
- Molluscs include herbivorous grazers, predaceous carnivores, filter feeders and parasites.
- Most are marine, but some are terrestrial or freshwater aquatic.
**Evolution**

- Fossil evidence indicates molluscs evolved in the sea; most have remained marine.
- Some bivalves and gastropods moved to brackish and freshwater.
- Only snails (gastropods) have successfully invaded the land; they are limited to moist, sheltered habitats with calcium in the soil.
- The cephalopods evolved to become relatively intelligent.
- The coelom is limited to a chamber around the heart; some zoologists believe molluscs arose separately from annelids and their coeloms are not homologous.

**Economics**

- Culturing of pearls and pearl buttons is an important industry.
- Burrowing shipworms destroy wooden ships and wharves.
- Snails and slugs are garden pests; some snails are intermediate hosts for parasites.

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**Mollusc Body Plan: Head-Foot and Visceral Mass Portions**

- The head-foot portion contains the feeding, cephalic sensory and locomotor organs.
- The visceral mass portion contains digestive, circulatory, respiratory, and reproductive organs.

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**Mantle Cavity**

- Two folds of skin form the protective mantle or pallium.
- The space between mantle and body wall is the mantle cavity.
- The mantle cavity houses the gills (ctenidia) or a lung.
- In most molluscs, the mantle secretes a protective shell over the visceral mass.

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**Head-Foot**

- Most molluscs have a well-developed head bearing the mouth and some sensory organs.
- Photosensory receptors range from simple to complex eyes.
- Tentacles may be present.
- Posterior to the mouth is the chief locomotor organ, the foot.

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**The Radula**

- The radula is unique to molluscs; it is found in all except bivalves and some solenogasters.
- The radula is a protruding, rasping, tongue-like organ.
- The ribbon-like membrane has rows of tiny teeth—up to 250,000—pointed backward.
- The radula rasps off fine particles of food material from surfaces.
- The radula serves as a conveyor belt to move particles to the digestive tract.
The Radula

- New rows of teeth replace those that wear away.
- The pattern and number of teeth are used in classification of molluscs.
- Some are specialized to bore through hard material or harpoon prey.

The Foot

- The foot is usually ventral.
- It can function for attachment to the substratum or for locomotion.
- Modifications include the attachment disc of limpets, the hatchet foot of clams and the siphon jet of squids.
- Secreted mucus can aid in adhesion or help some molluscs glide on cilia.
- Snails and bivalves extend the foot hydraulically by engorgement with blood.
- Burrowers extend the foot into mud or sand, enlarge the tip as an anchor, and draw forward.
- Free-swimming forms have modified the foot into wing or fin-like swimming agents.

Visceral Mass - The Mantle Cavity

- A mantle is a sheath of skin on each side of the body; it secretes the shell when present.
- The mantle cavity houses the gills or lungs that develop from the mantle.
- The exposed surface of the mantle also serves for gaseous exchange.
- In aquatic molluscs, a continuous flow of water brings in oxygen and food, and flushes out wastes.

The Mantle and Mantle Cavity

- Products of digestive, excretory and reproductive systems empty into the mantle cavity.
- Cephalopods use the head and mantle cavity to create jet propulsion.
- A mollusc gill has leaf-like filaments; cilia propel water across the surface.
- Countercurrent blood movement in a gill absorbs oxygen efficiently.
- In most molluscs, two ctenidia on opposite sides form an incurrent and an excurrent chamber.

The Shell

- When present, the shell is secreted by the mantle and lined by it.
- The periostracum is the outer horny layer, composed of conchiolin, a tanned protein.
- The middle prismatic layer has closely packed prisms of CaCO₃.
- The inner nacreous layer is next to the mantle; the nacre is laid down in thin layers.
- The thick periostracum of freshwater molluscs protects against acid from leaf decay in streams.

Internal Structure and Function

- The open circulatory system includes a pumping heart, blood vessels and blood sinuses.
- Most cephalopods have a closed system with a heart, vessels and capillaries.
- Most molluscs have a pair of kidneys or metanephridia.
- Kidney ducts also discharge sperm and eggs.
- The nervous system has pairs of ganglia but is generally simpler than in annelids.
- In air-breathing snails, the nervous system produces growth hormones.
- Sense organs vary and may be highly specialized.
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**Reproduction and Life History**

- Most are dioecious but some are hermaphroditic.
- The egg hatches and produces a free-swimming larva called a trochophore larva.
- This larva undergoes direct metamorphosis into a small juvenile in chitons.
- In many gastropods and bivalves, an intermediate larval stage—the veliger—is a derived state.
- The trochophore larvae are considered by some to unite molluscs with annelids, marine turbellarians, nemertines, phoronids, etc. in a taxon called Trochozoa.

**Classes of Molluscs**

- Caudofoveata
- Solenogastres
- Monoplacophora
- Polyplacophora
- Scaphopoda
- Gastropoda
- Bivalvia
- Cephalopoda

**Class Polyplacophora: Chitons**

- Chitons are somewhat flattened molluscs with eight dorsal plates.
- The head and cephalic organs are reduced.
- Photosensitive structures (esthetes) similar to eyes pierce the plates.
- Most prefer rocky intertidal surfaces.
- The chiton radula is reinforced with iron mineral; it scrapes algae from the rocks.
- The mantle extends around the chiton margin.
- Gills are suspended from the roof of the mantle cavity and grooves form a closed chamber so water flows from anterior to posterior.

**Chitons - continued**

- A pair of osphradia serves as a sense organ to sample water in the mantle groove near the anus.
- Blood pumped by a three-chambered heart travels through the aorta and sinuses to the gills.
- A pair of metanephridia carries wastes from the pericardial cavity to the exterior.
- Sexes are separate and trochophore larvae metamorphose into juveniles without a veliger stage.
**Class Scaphopoda**

- Tusk or tooth shells are found living on the ocean bottom from the subtidal zone to 6000 m depth.
- The slender body is covered with a mantle; the tubular shell is open at both ends.
- This is a unique body plan: the mantle is wrapped around the viscera and fused to form a tube.
- The foot protrudes from the larger end to burrow into mud; the small end extends into water.
- Foot and ciliary action moves respiratory water through the mantle cavity.
- Gills are absent and gaseous exchange occurs via the mantle.

**Scaphopoda continued**

- Detritus and protozoa are caught on cilia on the foot or the mucus-covered knobs of the tentacles.
- The radula carries food to a crushing gizzard.
- The head or captacula lacks eyes, tentacles or osphradia.

**Class Gastropoda**

- This class is the most diverse and contains 40,000 living and 15,000 fossil species.
- It includes snails, limpets, slugs, whelks, conches, periwinkles, sea slugs, sea hares and sea butterflies.
- They vary from primitive marine forms to air-breathing terrestrial snails and slugs.
- Torsion is a twisting process that diverts the veliger from a bilateral to asymmetrical form.

**Gastropod Shells**

- It is a one-piece univalve, coiled or uncoiled.
- The apex is the smallest and oldest whorl.
- The whorls become larger and spiral around the central axis or columella.
- Giant marine gastropods have a shell up to 60 cm long; some fossil forms are two meters long.

**Torsion**

- Only gastropods undergo torsion.
- Torsion moves the mantle cavity from the posterior to the front of the body.
- This twists the visceral organs through a 90 to 180 degree rotation while in the veliger stage.
- The anus cavity and mantle cavity move from posterior to anterior, opening above the head.
- Gills, kidneys and heart auricles are switched left-to-right; the nerve cords are also twisted.
- Detorsion occurred in opisthobranchs and pulmonates, both are derived from tortured ancestors.
- This allows the possibility of wastes washing back over gills, or “fouling.”
**Torsion**

Coiling or spiral winding of the shell and visceral mass is not the same as torsion.

- It occurs at the same larval stage as torsion but had a separate, earlier evolutionary origin.
- All living gastropods descended from coiled, tormented ancestors even if they now lack this trait.
- A planospiral shell has all whorls in a single plane; it is the primitive state.
- A conispiral shape provides more compactness; each whorl is to the side of the previous one.

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**Coiling**

- Shifting the shell upward and back helped balance the uneven weight distribution.
- However, the gill, auricle and kidney of the right side are lost in most species.
- Loss of the right gill allows one solution to the problem of fouling; wastes expel to the right.

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**Feeding Habits**

- Adaptation of the radula provides much variation in gastropod feeding habits.
- Many are herbivorous and graze, browse or feed on plankton.
- Some scavenge on decaying flesh; others are active carnivores that tear prey using their radula.
- The oyster borer alternates rasping with chemical softening of the shell to bore a hole.

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**Feeding Habits**

- Species of *Conus* can deliver a lethal sting to secure prey; the venom is a conotoxin that is specific for the neuroreceptors of its preferred prey.
- Some molluscs collect debris as a mucus ball to ingest it; sea butterflies secrete a mucus net.
- Digestion is usually extracellular in the lumen of the stomach.

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**Conus**

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Internal Form and Function

- Respiration in many molluscs is performed by ctenidia in the mantle cavity.
- Derived prosobranchs lost one gill and half of the remaining gill; the resulting attachment to the wall of the mantle cavity provided respiratory efficiency.

Respiration continued

- The lung opens to the outside by a small opening, the pneumostome.
- Aquatic pulmonates surface to expel a gas bubble and inhale by curling, thus forming a siphon.

Other Systems

- Most have a single nephridium and well-developed circulatory and nervous systems.
- Sense organs include eyes, statocysts, tactile organs and chemoreceptors.
- Eyes vary from simple cups holding photoreceptors to a complex eye with a lens and cornea.
- A sensory osphradium at the base of the incumbent siphon may be chemosensory or mechanoreceptive.

Gastropod Reproduction

- Gastropods include both monoecious and dioecious species.
- Copulation in monoecious species may involve exchange of spermatozoa or spermatophores.
- Many terrestrial species inject a dart to heighten arousal before copulation.
- Primitive gastropods discharge ova and sperm into water and fertilization is external.
- Eggs are emitted singly or in clusters, and may be transparent or in tough egg capsules.
- Young may emerge as veliger larvae or pass this stage inside the egg.
- Some species, including most freshwater snails, are ovoviviparous.

Major Groups of Gastropods

- **Prosobranchs** - marine snails and some freshwater and terrestrial gastropods
- **Pulmonates** - includes all land and most freshwater snails and slugs.
- **Opisthobranchs** - sea slugs, sea hare, sea butterflies and canoe shells

Class Bivalvia

- Bivalves include mussels, clams, scallops, oysters, and shipworms.
- They range in size from 1-2 mm in length to the giant South Pacific clams.
- Most are sedentary filter feeders dependent on ciliary currents to bring in food.
- Bivalves lack a head, radula or other aspects of cephalization.
Bivalve Life History

- Most are marine; some live in freshwater streams, ponds and lakes.
- Native freshwater clams in the U.S. are the most jeopardized animal group; of more than 300 species once present, 12 are extinct, 42 are threatened or endangered and 88 more are of concern. (Zebra mussel invasion)
- Freshwater clams are sensitive to water quality changes, including pollution and sedimentation.

Form and Function

- The two shells or valves are held together by a hinge ligament.
- The valves are drawn together by strong adductor muscles.
- The umbo is the bulge, the oldest part of the shell with growth occurring outward in rings.
- Pearls are produced when an irritant is lodged between the shell and mantle; layers of nacre are secreted around the foreign material.

Body and Mantle

- A visceral mass is suspended from the dorsal midline; a foot is attached anteroventrally.
- The ctenidia (gills) hang down on each side, each covered by a fold of the mantle.
- Posterior edges of the mantle folds form excurrent and incumbent openings.
- In burrowing clams, the mantle forms long siphons to reach the water above. (See Figure 16.28)

Locomotion

- The slender foot is extended out from between the valves.
- Blood is pumped into the foot; it swells and anchors the bivalve in the mud.
- Shortening the foot then pulls the clam forward.
- Scallops clap their valves to create a jet propulsion; the mantle edges direct the stream.

Gills

- Both the mantle and gills perform gaseous exchange.
- Gills are derived from primitive ctenidia by lengthening the filaments to each side.
- The filaments fused to form plate-like lamellae with vertical water tubes inside.
- Water enters the incumbent siphon, enters the water tubes through pores, and proceeds dorsally to the suprabranchial chamber and then out the excurrent siphon.

Feeding

- Suspended organic matter enters the incumbent siphon.
- Gland cells on the gills and labial palps secrete mucus to entangle particles.
- Food in mucus masses slides to food grooves at the lower edge of the gills.
- Cilia and grooves on the labial palps direct the mucous mass into the mouth.
Internal Structure and Function

- The stomach is folded into ciliary tracts for sorting particles.
- The style sac secretes a crystalline style which is kept whirling by cilia in the style sac.
- This rotating style helps free digestive enzymes and roll up a mucous food mass.
- Dislodged particles are directed to a digestive gland or are engulfed by amebocytes.

Circulation/Respiration/Excretion

- The three-chambered heart has two auricles and one ventricle.
- Some blood is oxygenated in the mantle; it returns to the ventricle through the auricles.
- The rest circulates through sinuses, the kidneys, the gills, and then back to the auricles.
- A pair of U-shaped kidneys is ventral and posterior to the heart.

Nervous System

- The nervous system has three pairs of widely separated ganglia connected together.
- Sense organs are poorly developed: statocysts in the foot, osphradia in the mantle cavity, and some pigment cells on the mantle.
- Some mantle eyes have a cornea, lens, retina and pigmented layer.
- Tentacles may have tactile and chemoreceptor cells.

Reproduction

- Sexes are usually separate.
- Gametes discharged in the suprabranchial chamber are carried out in the excurrent flow.
- Fertilization is usually external.
- Freshwater clams have internal fertilization where sperm enter the incurrent siphon to fertilize eggs in the water tubes of the gills.

Development

- Embryos develop as trochophore, the veliger, and lastly spat larval stages.
- Larvae develop into a bivalved glochidia stage that is discharged and attaches to the gills of passing fish where they live briefly as parasites.
- They eventually sink to begin independent life on the streambed; the “hitchhiking” having helped distribute the species.

Boring

- Burrowing has led some to evolve a mechanism for boring into harder surfaces.
- Shipworms are destructive to ships and wharves; the radula functions as a wood rasp.
- Symbiotic bacteria produce cellulase, which helps digest wood.
- The bacteria also fix nitrogen; the diet is high in carbon but deficient in nitrogen.
- Some clams can bore into rock and produce long burrows.
**Class Cephalopoda**

- This class includes squids, octopuses, nautiluses, devilfish and cuttlefish.
- All are marine predators.
- The foot is in the head region and is modified for expelling water from the mantle cavity.
- They range from 2 cm to the giant squid that is the largest invertebrate known.

**Cephalopods continued**

- The cephalopod fossil record goes back to the Cambrian; earliest shells were straight.
- A *Nautilus* is the culmination of shell coiling; a remaining survivor of nautiloids.
- Octopuses and squids apparently evolved from early straight-shelled ancestors.
- Ammonoids are now extinct but had quite elaborate shells.
- Cephalopods are mostly marine; octopuses are mostly intertidal and squids are deep-sea animals.

**Shell**

- Nautiloid and ammonoid shells had gas chambers allowing them to swim.
- Unlike gastropod shells, the nautilus shell is divided into chambers.
- The living animal only inhabits the last chamber.
- A cord of living tissue, the siphuncle, connects the chambers to the visceral mass.

**Shell - continued**

- The cuttlefish shell is enclosed in the mantle.
- The squid shell is a thin strip called the pen, enclosed in mantle.
- The octopus has completely lost the shell.
- Gas pressure in the nautilus chambers is only one atmosphere compared to the 41 atmospheres of pressure in the surrounding deep ocean.
Locomotion
- Cephalopods swim by forcefully expelling water through a ventral funnel or siphon.
- It can control the direction and the force of the water, thus determining its speed.
- Lateral fins of squids and cuttlefishes are stabilizers.
- The Nautilus swims mainly at night.
- Octopuses mainly crawl on the bottom but can swim backward by spurting jets of water; some with webbing between their arms swim with a medusa-like action.

Respiration and Circulation
- Except for nautiloids, cephalopods have one pair of gills.
- With higher oxygen demands, cephalopods have a muscular pumping system to keep water flowing through the mantle cavity.
- Their circulatory system has a network of vessels conducting blood through gill filaments.
- Blood goes to the systemic circulation before it goes to the gills; accessory or branchial hearts at the base of each gill increase pressure to blood going through gill capillaries.

Nervous and Sensory Systems
- The cephalopod brain is the largest of any invertebrate.
- Squids have giant nerve fibers.
- Sense organs are well-developed; eyes are complex, complete with cornea, lens and retina.
- They can learn by reward and punishment, and by observation of others.
- Cephalopods lack a sense of hearing but have tactile and chemoreceptor cells in their arms.

Convergence?
- Cephalopod and Vertebrate eyes have been used as a "classic" example of convergence for years.
- Details of structure are similar but differ in development.
- Two conserved genes indicate that eyes of all Bilateralia may have been derived from a common ancestral type of photoreceptor.

Communication
- Cephalopods use chemical and visual signals to communicate.
- Chromatophores are cells in the skin that contain pigment granules.
- Contractions of the muscle fibers attached to the cell boundary causes the cell to expand and change the color pattern.

Communication - continued
- Color patterns can be changed rapidly and target individuals in different directions.
- Deep-water cephalopods have elaborate luminescent organs.
- An ink sac empties into the rectum; it contains an ink gland that secretes sepia when the animal is alarmed.
Reproduction

- Sexes are separate.
- In the male seminal vesicle, spermatozoa are packaged in spermatophores and stored.
- One arm of the male is modified as an intromittent organ, the hectocotylus.
- The hectocotylus plucks a spermatophore from the mantle cavity and inserts it into the female.
- Fertilized eggs leave the oviduct and are attached to stones, etc.
- The large, yolky eggs undergo meroblastic cleavage; they hatch into juveniles with no free-swimming larval stage.

Blue-Ringed Octopus


- Beak that can penetrate a wet-suit
- The bite might be painless, but this octopus injects a neuromuscular paralysing venom.
- The venom contains some maculotoxin, a poison more violent than any found on land animals.
  - The nerve conduction is blocked and neuromuscular paralysis is followed by death.
  - The victim might be saved if artificial respiration starts before marked cyanosis and hypotension develops.
- The blue-ringed octopus is the size of a golf ball but its poison is powerful enough to kill an adult human in minutes.
- There's no known antidote.
  - The only treatment is hours of heart massage and artificial respiration until the poison has worked its way out of your system.

Blue-Ringed Octopus - continued

- The venom contains tetrodotoxin, which blocks sodium channels and causes motor paralysis and occasionally respiratory failure. Though with fixed dilated pupils, the senses of the patients are often intact. The victims are aware but unable to respond.
- Although the painless bite can kill an adult

Symptoms

- Onset of nausea.
- Hazy Vision. (Within seconds you are blind.)
- Loss of sense of touch, speech and the ability to swallow.
- Within 3 minutes, paralysis sets in and your body goes into respiratory arrest.
- The poison is not injected but is contained in the octopus's saliva, which comes from two glands each as big as its brain.
- Poison from the one is used on its main prey, crabs, and is relatively harmless to humans.
- Poison from the other gland serves as defense against predators.
- The blue-ringed octopus either secretes the poison in the vicinity of its prey, waits until it is immobile and then devours it, or it jumps out and envelops the in its 8 tentacles and bites it.
Phylogeny

- The 1st mollusc probably arose in Precambrian.
- Mollusca is considered a protostome allied with annelids and arthropods.
- Molecular evidence strengthens the idea that molluscs and annelids are more closely related to each other than either is to arthropods.

The “Hypothetical Ancestral Mollusc”

- It probably lacked a shell or crawling foot.
- It likely was a worm-like organism with a ventral gliding surface.
- It probably possessed a dorsal mantle, a chitinous cuticle and calcareous scales.

The End....