Chapter 17
Segmented Worms

Diversity
- About 15,000 species of segmented worms are classified in the phylum Annelida.
- About two-thirds are the more obscure marine worms.
- Annelids are true coelomates in the protostome branch with spiral cleavage and mosaic development.
- The nervous system is more centralized and the circulatory system more complex than in other worms.

Segmentation
- Body segments are marked by circular grooves called annuli.
- Metamerism is the repetition of organs in segments called metameres or somites.
- Walls, called septa, separate segments.
- Metamerism is found in arthropods, which is probably homologous with annelids, and in vertebrates, where it evolved independently.
- Metamerism is not limited to annelids, but is shared by arthropods and vertebrates, in which it apparently evolved independently.

Other Characters/Distribution
- Except for leeches, annelids have tiny chitinous bristles called setae.
  - Short setae anchor a segment in an earthworm so it prevents slipping backward.
  - Long setae help aquatic worms swim.
- Polychaetes are mainly marine and usually benthic.
- Oligochaetes and leeches are in freshwaters, or terrestrial soils; many leeches are predators.

Metamerism (Segmentation)
- A serial repetition of body parts arranged longitudinally down the body.
- In annelids it affects all of the organ systems, except the usually tubular digestive tract (even here often find paired series of glands on the gut wall).
- Major blood vessels extend the length of the body above and below the digestive tube, but give rise to segmentally arranged lateral branches in each segment.
- Each segment contains a pair of nephridia (but, some segments may lose them in adults). Segmental ganglia and segmental nerves give the nervous system a metameric character.
- External rings, parapodia and setae give the external surface a metameric character.

Metamerism
- The appearance of segmented, coelomate animals with a straight digestive tube was major event in evolution of animals. The traditional view is that out of this stem two of the largest and most important invertebrate phyla, the Annelida and Arthropoda, eventually developed.
  - For an alternate view see http://tolweb.org/tree?group=Bilateria&contgroup=Animals
How Did Metamerism Evolve?

- Metamerism involves the compartmentalization of the wormlike body into segments marked off by septa (membranous structures separating one septum from another).
- Newest evolutionary theories suggest that septa evolved in order to allow the development of blood vessels running transversely (sideways). A highly complex blood vascular system became advantageous with the development of lateral appendages, the parapodia. If you have such appendages it becomes necessary to supply them with nutrients.

Metamerism

- Once metamerism developed it provided an aid to locomotion in long animals who could burrow. Contrary to the traditional view, the ability to use metamerism for locomotion is a secondary development.
- Can burrow with peristaltic waves if segmented. Coelom and body wall probably became segmented and rest of body parts followed.

Evolutionary Significance of Metamerism

(Summary)

- No satisfactory explanation for the origins of metamerism and the coelom has gained acceptance.
- A coelom may have evolved independently in chordates and probably twice in the protostomes.
- The coelom may have been very advantageous as a hydrostatic skeleton.
- Coelomic fluid would have acted as a circulatory fluid and reduce the need for flame cells everywhere.
- A coelom could store gametes for timed release; this would require nervous and endocrine control.
- Metamerism would increase burrowing efficiency; this would favor evolution of the nervous system.

Body Plan

- The anterior tip is the prostomium; the terminal portion bearing the anus is the pygidium.
- The prostomium and pygidium are not considered metameres like the other segments.
- New metameres form just in front of the pygidium; thus the newest segments are at the posterior.
- Strong circular and longitudinal muscles underlie the body wall.
- The surface is covered with an epidermis and a thin outer layer of non-chitinous cuticle.
Coelom

- The coelom develops embryonically as a split in mesoderm on each side of the gut (schizocoel).
- Peritoneum (mesodermal epithelium) lines the body wall and forms dorsal and ventral mesenteries.
- Peritonea of adjacent segments meet to form the septa.
- The gut and longitudinal blood vessels extend through the septa.

Hydrostatic Skeleton

- Except in leeches, the coelom is filled with fluid and serves as a hydrostatic skeleton.
- The fluid volume remains constant.
- Therefore contraction of longitudinal muscles causes the body to shorten and fatten.
- Contraction of circular muscles causes the body to narrow and lengthen.
- By separating this force into sections, widening and elongation move the whole animal.
- Alternate waves of contraction, or peristalsis, allow efficient burrowing.
- Swimming annelids use undulatory movements.

Diversity

- Polychaeta is the largest class of annelids with more than 10,000 species, mostly marine.
- They vary from 1 mm to 3 meters long.
- Polychaetes can tolerate a wide range of salinity.
- Warmer regions have more freshwater polychaetes.
- Some live in crevices; others inhabit tubes or are pelagic.
- Sedentary polychaetes are mainly tube-living.
- Errant polychaetes may be free-moving, burrowing or crawling.

Class Polychaeta

- Polychaetes have a well-differentiated head with sense organs.
- Paired appendages called parapodia are on most segments.
- They have no clitellum.
- Many setae are arranged in bundles on the parapodia.
- They have differentiation of some somites.
- There is more specialization of sensory organs than in clitellates.

Characteristics

- A head or prostomium may or may not be retractile; it often bears eyes, tentacles and sensory palps.
- The first segment or peristomium surrounds the mouth and may have setae, palps or chitinous jaws.
- Ciliary feeders may bear a tentacular crown that opens like a fan but can be withdrawn into the tube.
- Most segments of the trunk bear parapodia with lobes, cirri, setae and other parts.
- Parapodia help crawl, swim, and anchor the worm in a tube.
Nutrition

• A polychaete has a foregut, midgut and hindgut.
• The **foregut** has a stomodeum, pharynx and anterior esophagus lined with cuticle.
• The **midgut** derived from mesoderm secretes enzymes and absorbs nutrients.
• The short hindgut is derived from ectoderm and leads to the anus on the pygidium.
• Errant polychaetes are predators or scavengers.
• Sedentary polychaetes feed on suspended particles or particles in sediment.

Circulation and Respiration

• Most have parapodia and gills for gaseous exchange; some lack them and use the body surface.
• Circulation varies; *Nereis* has a dorsal vessel that carries blood forward and a ventral vessel that carries blood posteriorly.
• Blood flows across between these major vessels in networks around the parapodia and intestine.

Excretion

• Excretory organs vary, from protonephridia to metanephridia, and mixed forms.
• There is one pair per metamere; the inner end (nephrostome) opens into the coelomic cavity.
• Coelomic fluid enters the nephrostome; selective resorption occurs along the nephridial duct.

Nervous System and Sense Organs

• Dorsal cerebral ganglia connect to subpharyngeal ganglia by a circumpharyngeal commissure.
• A double ventral nerve cord runs the length of the worm with ganglia in each metamere.
• Sense organs include eyes, nuchal organs and statocysts.
  - Eyes vary from simple eyespots to well-developed image-resolving eyes similar to mollusc eyes.
  - Nuchal organs are elliptical sensory pits that are probably chemoreceptive.
  - Some burrowing and tube-building polychaetes use statocysts to orient their body.

Reproduction and Development

• In contrast to clitellates, polychaetes have no permanent sex organs and are monoecious.
• Gonads appear as simple temporary swellings of the peritoneum.
• Gametes are shed into the coelom and exit by gonoducts, metanephridia or rupturing of the body.
• Fertilization is external and the early larva is a trochophore.
Epitoky

- A reproductive individual, an epitoke, is formed from a worm and leaves bottom burrows, tubes and other habitations and becomes pelagic.
- Epitokal modifications include changes in the formation of the head, the structure of the parapodia and setae, the size of the segments and the segmental musculature, among others.
- Often only gamete-bearing segments are affected, so worm looks like two different worms in one. Can get epitoke from non-epitokus worm by direct transformation of entire individual or by transformation and separation of the posterior end from the atoke (anterior end remains behind and regenerates).
- Epitoke segments are crammed with gametes and often branch so that even more gametes can be produced.

Epitoke Swarming

- Usually epitokous polychaetes swim to the surface during the shedding of the eggs and sperm.
- Congregates sexes and increases probability of fertilization.
- Female produces pheromone to attract male and stimulates shedding of the sperm. The sperm, in turn, stimulate shedding of eggs.
- To be effective, swarming must be synchronized. Not fully understood how such precise synchronization occurs. Changes in light intensity in some. Lunar cycles in others.

Palolo Worm

- South pacific Palolo worm swarms at dawn one week after the November full moon. “The sexual pieces rise to the surface in countless millions, and the appearance of the water at this time has been compared to vermicelli soup. Later it appears milky from the eggs and sperms that are discharged. The anterior part of the worm, which remains hidden in some crevice in the coral rock when the posterior piece breaks off, regenerates the missing parts. On the corresponding day of the next year, the regenerated posterior end, laden with sex cells, breaks away.”

Palolo Worms

- The natives of the Samoan and other islands are familiar with the habits of the palolos. They consider them a great delicacy and look forward to their breeding season. When the day arrives, they scoop them up in buckets and prepare a great feast, gorging themselves just as we do on thanksgiving day, knowing that there will not be another treat like it until exactly the same day of the next year.”
Class Oligochaeta

- **Diversity**
  - Over 3000 species occur in habitats from soil to freshwater; a few are marine or parasitic.
  - Nearly all bear setae; although highly varied, setae are fewer than in polychaetes.

Earthworms

- Earthworms burrow in moist, rich soil; they emerge at night.
- In wet weather they stay near the surface; in dry weather they burrow deep and become dormant.
- Darwin studied earthworms and estimated 10-18 tons [9-16 metric tonnes] of dry earth passed through earthworm intestines per acre [0.4 hectares] annually.
- Earthworms have an important role in churning the soil, mixing materials and adding nutrients.
- Giant tropical earthworms may reach 4 meters long and live in interconnected tunnels.

Form and Function

- The prostomium overhangs the mouth at the anterior end.
- In most earthworms, each segment bears four pairs of chitinous setae; some may bear over 100.
- Each seta is a bristlelike rod set in a sac and moved by tiny muscles.
- Setae anchor segments during burrowing.

Nutrition

- Most oligochaetes are scavengers feeding on decayed organic matter.
- Food is moistened by the mouth and drawn in by sucking action of muscular pharynx.
- Soil calcium produces a high blood calcium level; calciferous glands along the esophagus keep down the calcium ion concentration in the blood and are ion-regulatory rather than digestive in function.
- Food passes the esophagus to be stored in a thin-walled crop.
- The muscular gizzard grinds food into small pieces.
- Digestion and absorption occur in the intestine; an infolded typhlosole increases surface area.
- Chloragogen tissue surrounds the intestine and synthesizes glycogen and fat; cells full of fat float free in the coelom as eleocytes.
- Chloragogen cells also function in excretion.
Circulation and Respiration

- Both coelomic fluid and blood carry food, wastes and respiratory gases.
- Blood circulates in a closed system with five main trunks running lengthwise in the body.
- The dorsal vessel above the alimentary canal has valves and functions as a true heart.
- The dorsal vessel pumps blood anteriorly into five pairs of aortic arches.
- The aortic arches maintain steady pressure into the ventral vessels.
- A ventral vessel serves as an aorta, delivering blood to body walls, nephridia and digestive tract.
- Blood contains colorless ameboid cells and dissolved hemoglobin.
- Earthworms have no special gaseous exchange organs; the moist skin handles all exchanges.

Excretion

- Water and Osmotic Regulation
  - Most marine invertebrates are in osmotic equilibrium with their seawater environment.
  - With body surfaces permeable to water and salts, the internal and external concentrations are equal.
  - Such animals that cannot regulate osmotic pressure of their body fluids are called osmotic conformers.
  - This functions for open ocean organisms because the open ocean is stable.
  - Animals that must live within a narrow salinity range are stenohaline.
  - Organisms that can tolerate the wide variations found in estuaries are euryhaline.

- How Terrestrial Animals Maintain Salt and Water Balance
  - Animals carried their watery composition with them as they evolved within a terrestrial existence.
  - They continued to adapt to the threats of desiccation and became abundant in arid areas.
  - Animals lose water across respiratory and body surfaces, excretion of urine and elimination of feces.
  - Water is gained from water in food, drinking water and metabolic water.

Protonephridium

- This tubular structure is the most common (and simplest) design to maintain osmotic balance.
- Fluid enters the system through specialized “flame cells” and passes through tubules to exit the body.
- Rhythmic beating of a flagellar tuft creates negative pressure that draws fluid into tubes where water and metabolites are recovered; wastes are left to be expelled.
- Nitrogenous wastes, mainly ammonia, diffuse across the surface of the body.
- This system is a closed system since the fluid must pass across flame cells.

Metanephridium

- A metanephridium is an open system found in molluscs and annelids.
- The tubule is open at both ends; fluid is swept into the tubule through a ciliated funnel-like opening.
- A network of blood vessels to reclaim water and valuable solutes surrounds a metanephridium.
- The basic process of urine formation in the tubule remains the same: withdraw valuable solutes and add waste solutes.
Excretion in Oligochaetes

- Each somite, except the first three and last one, have a pair of **metanephridia**.
- Each unit occupies parts of two adjacent somites.
- A ciliated funnel, the nephrostome, draws in wastes and leads through the septum.
- These coil until the nephridial duct ends at a bladder that empties outside at the nephridiopore.
- Wastes from both the coelom and the blood capillary beds are discharged.
- Aquatic oligochaetes excrete toxic ammonia; terrestrial worms excrete the less toxic urea.
- Chloragogen cells that break and enter the nephridia produce both urea and ammonia.
- Salts pass across the integument, apparently by active transport.

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**Nervous System**

- Earthworms have both a central nervous system and peripheral nerves.
- A pair of cerebral ganglia connects around the pharynx to the ganglia of the ventral nerve cord.
- Fused ganglia in each somite contain both sensory and motor fibers.
- Neurosecretory cells in the brain and ganglia secrete neurohormones to regulate reproduction, secondary sex characteristics and regeneration.
- Earthworms lack eyes but have many photoreceptors in the epidermis.
- Free nerve endings in the tegument are probably tactile.

**General Behavior**

- Although they lack specialized sense organs, they are sensitive to many stimuli.
- They avoid light unless it is very dim.
- Chemical stimuli are important to find food.
- Earthworms have limited learning ability; it is mostly trial-and-error learning.

**Reproduction and Development**

- Earthworms are monoecious.
- In *Lumbricus*, reproductive systems are in somites 9 through 15.
- Immature sperm from testes mature in seminal vesicles and then pass into sperm ducts.
- Eggs are discharged by ovaries into the coelomic cavity; ciliated funnels carry them outside.
- Two pairs of seminal receptacles receive and store sperm during copulation.
- Earthworms mate at night during warm, moist weather.
- They mate by aligning in different directions with ventral surfaces together.
Reproduction and Development

- Mucus secreted by the clitellum holds them together.
- Sperm travel to the seminal receptacles of the other worm along seminal grooves.
- After mutual copulation, each worm secretes a mucus tube and chitinous band to form a cocoon.
- As the cocoon passes forward, eggs, albumin, and sperm pour into it.
- Fertilization and embryogenesis takes place in the cocoon; young worms emerge.

Freshwater Oligochaetes

- These oligochaetes are generally smaller with longer setae than on earthworms.
- Aquatic oligochaetes are important food for fishes; a few are ectoparasites.
- A wide variety occur in water, mud, and moist soil.

Class Hirudinea: Leeches

- Diversity
  - Most leeches live in freshwater but a few are marine or in moist terrestrial environments.
  - They are more common in the tropics than temperate zones.
  - Leeches vary in color: black, brown, red and olive green.
  - Most are flattened.
  - Some are carnivores on small invertebrates; others are temporary or permanent parasites.
  - Leeches are hermaphroditic and have a clitellum during the breeding season.
  - The clitellum secretes a cocoon for reception of eggs.
  - They have lost setae and developed suckers for attachment while sucking blood.
  - The gut is specialized for storage of large quantities of blood.

Form and Function

- Leeches usually have 34 somites, but appear to have more due to superficial annuli.
- Leeches lack distinct coelomic compartments and septa have disappeared.
- In most, the coelomic cavity is filled with connective tissue and spaces called lacunae.
- The lacunae channels may serve as an auxiliary circulatory system.
- Most leeches use suckers to attach so they can "inchworm" along the surface.

Nutrition

- Although popularly considered parasites, many are predaceous.
- Freshwater leeches have a proboscis for ingesting small invertebrates as well as to suck blood.
- Some terrestrial leeches feed on insect larvae, earthworms and slugs.
- Other terrestrial leeches climb trees or bushes to reach warm-blooded vertebrates such as baby birds.
- Most are fluid feeders that prefer tissue fluids and blood pumped from open wounds.

Nutrition

- Association between leech and "host" brief so may be more accurately called predators than parasites.
- Not species specific as are most parasites. Class specific instead.
  - Leech that preys upon a reptile such as a turtle may also prey upon an alligator, but probably would not prey on an amphibian such as a frog or on a fish.
Nutrition

• Some parasitic leeches leave a host during breeding season; some fish leeches remain on a host.
• Medicinal leeches were originally used when it was wrongly believed disorders were caused by excess blood. Now used to aid in promoting circulation for reattachment of severed digits or limbs.

Respiration and Excretion

• Some fish leeches have gills; all other leeches exchange gases across the skin.
• There are 10 to 17 pairs of nephridia; coelomocytes and other special cells may assist in excretion.

Nervous and Sensory Systems

• Leeches have two “brains”; the anterior fused ganglia form a ring around the pharynx.
• Seven pairs of fused ganglia are at the posterior.
• 21 pairs of segmental ganglia are in between along a double nerve cord.
• The epidermis contains free sensory nerve endings and photoreceptor cells.
• A row of sensillae is in the central annulus of each segment.
• Pigment-cup ocelli are present.

Reproduction

• Leeches are hermaphroditic and cross-fertilize during copulation.
• Sperm are transferred by hypodermic impregnation.
• The clitellum secretes a cocoon to receive the sperm and egg.
• The cocoons are buried in mud or damp soil, and development is similar to that of oligochaetes.

Circulation

• The coelom has been reduced by invasion of connective tissue and chloragogen tissue.
• This forms a system of coelomic sinuses and channels.
• Some leeches have a typical oligochaete circulatory system; the coelomic system is auxiliary.
• Some leeches lack blood vessels and the coelomic sinuses are the only vascular system.