INTRODUCTION TO ANIMAL EVOLUTION

OUTLINE

I. What is an Animal?

II. An Overview of Animal Phylogeny and Diversity

A. Parazoans lack true tissues
B. Evolution of body cavities led to more complex animals
C. Coelomates branched into protostomes and deuterostomes

III. The Origins of Animal Diversity

A. Most animal phyla originated in a relatively brief span of geological time
B. Developmental genetics may clarify our understanding of the Cambrian diversification

OBJECTIVES

After reading this chapter and attending lecture, the student should be able to:

1. List characteristics that distinguish animals from organisms in the other four kingdoms.
2. Distinguish between radial and bilateral symmetry.
3. Outline the major phylogenetic branches of the animal kingdom, which are based upon grade of organization; symmetry and embryonic germ layers; absence or presence of a body cavity; and protostome-deuterostome dichotomy.
4. Distinguish among acoelomate, pseudocoelomate and coelomate.
5. Distinguish between spiral and radial cleavage; determinant and indeterminate cleavage; schizocoelous and enterocoelous.
6. Compare developmental differences between protostomes and deuterostomes including:
   a. Plane of cleavage
   b. Determination
   c. Fate of the blastopore
   d. Coelom formation
7. Compare and contrast two hypotheses about animal origins from unicellular ancestors: syncytial hypothesis and colonial hypothesis.
8. Explain why it is difficult to resolve what the first animals looked like.
9. Describe two views about discontinuities between Ediacaran and Cambrian fauna.

KEY TERMS

ingestion	bilateral symmetry	archenteron	deuterostomes
cleavage	dorsal	mesoderm	spiral cleavage
blastula	ventral	diploblastic	determinate cleavage
gastrulation	anterior	triploblastic	radial cleavage
larva	posterior	acoelomates	indeterminate cleavage
metamorphosis	bilateria	pseudocoelom	blastopore
parazoa	cephalization	pseudocoelomates	schizocoelous
eumetazoa	germ layers	coelomates	enterocoelous
radial symmetry	ectoderm	coelom	Ediacaran period
radiata	endoderm	protostomes	Cambrian explosion

LECTURE NOTES

Over one million species of animals are living today; 95% of these are invertebrates.

- Grouped into about 35 phyla depending on the taxonomic view followed.
- Most are aquatic.
- The most familiar belong to the subphylum Vertebrata of the phylum Chordata. This is only about 5% of the total.

I. What is an Animal?

Although there is great animal diversity, most animals share the following characteristics:

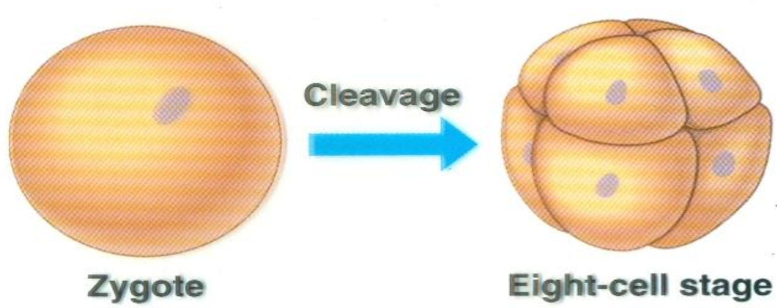
- Multicellular, eukaryotic organisms
- Heterotrophy is by ingestion.
  - *Ingestion* = Eating other organisms or decomposing organic matter (detritus). This mode of nutrition distinguishes animals from the plants and fungi.
  - Carbohydrate reserves generally are stored as glycogen.
- No cell walls are present, but animals do have intercellular junctions: desmosomes, gap junctions, and tight junctions.

- Highly differentiated body cells which are organized into tissues, organs and organ systems for such specialized functions as digestion, internal transport, gas exchange, movement, coordination, excretion, and reproduction.
- Nervous tissue (impulse conduction) and muscle tissue (movement) are unique to animals.
- Reproduction is typically sexual with flagellated sperm fertilizing nonmotile eggs to form diploid zygotes. A diploid stage dominates the life cycle.
  - The zygote undergoes a series of mitotic divisions known as *cleavage* which produces a *blastula* in most animals.
  - *Gastrulation* occurs after the blastula has formed; during this process, the embryonic forms of adult body tissues are produced.
  - Development in some animals is direct to maturation while the life cycles of others include *larvae* which undergo *metamorphosis* into sexually mature adults.
  - *Larva* = Free-living, sexually immature forms
- Figure 32.1 shows the early embryonic development in animals.

The seas contain the greatest diversity of animal phyla, although many groups live in fresh water and terrestrial habitats.

Figure 32.1 Early embryonic development in animals

Layer 1



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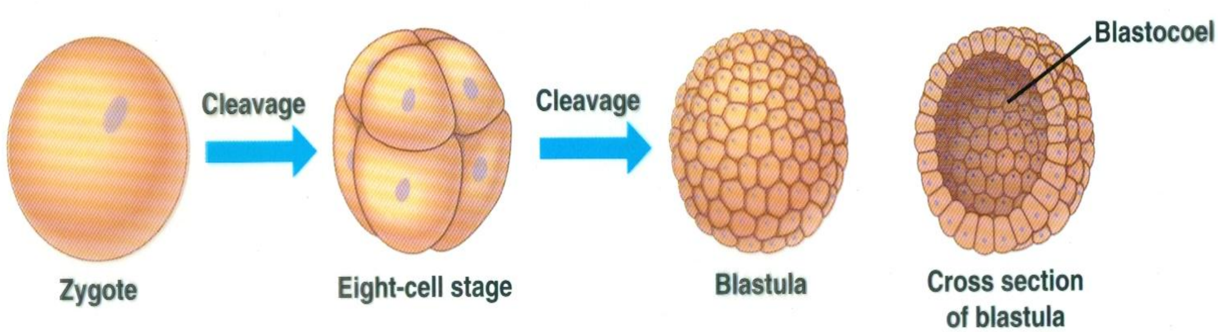

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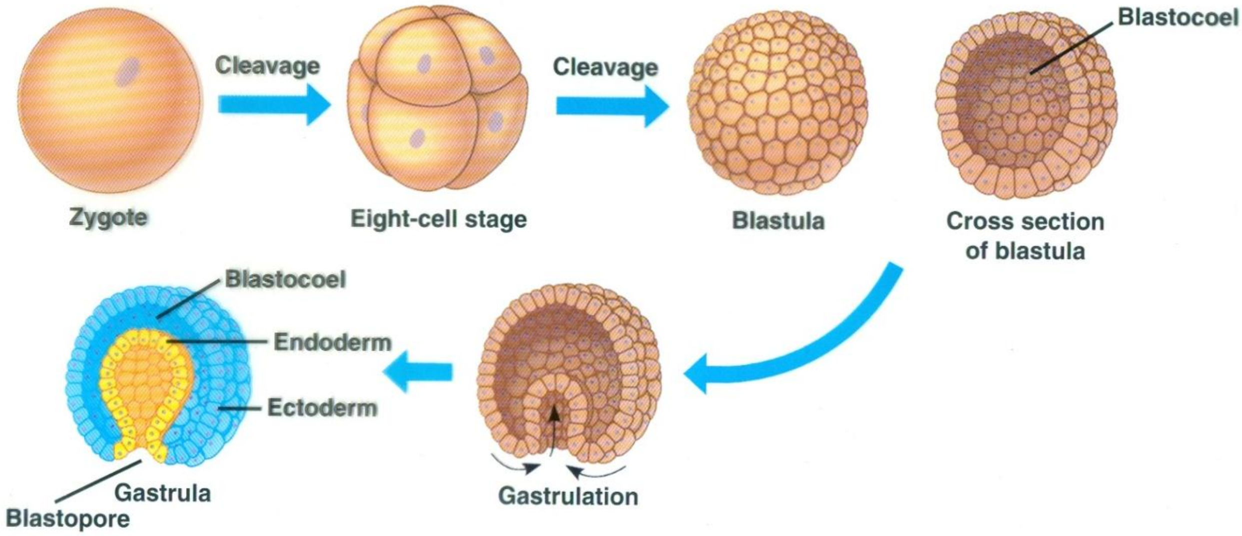


II. An Overview of Animal Phylogeny and Diversity

Animals diversified so rapidly during the late Precambrian and early Cambrian periods that it is difficult to determine the exact sequence of branching from the fossil record.

Figure 32.2 shows hypothesis of animal phylogeny

- To reconstruct the evolutionary history of the animal phyla, zoologists use information from comparative anatomy, embryology of living animals, and molecular systematics.
- Most zoologists agree that the animal kingdom is monophyletic and that the ancestral organism was probably a colonial flagellated protist related to choanoflagellates (Figure 32.3).

Figure 32.3 One hypothesis for the origin of animals form a flagellated protist

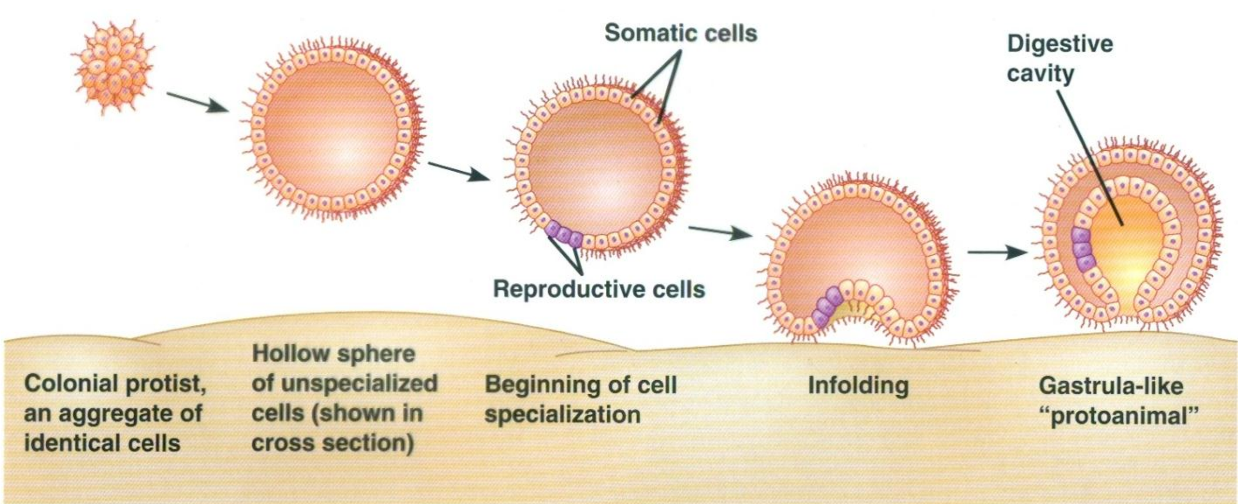


Figure 32.2a One hypothesis of animal phylogeny based mainly on morphological and developmental comparisons

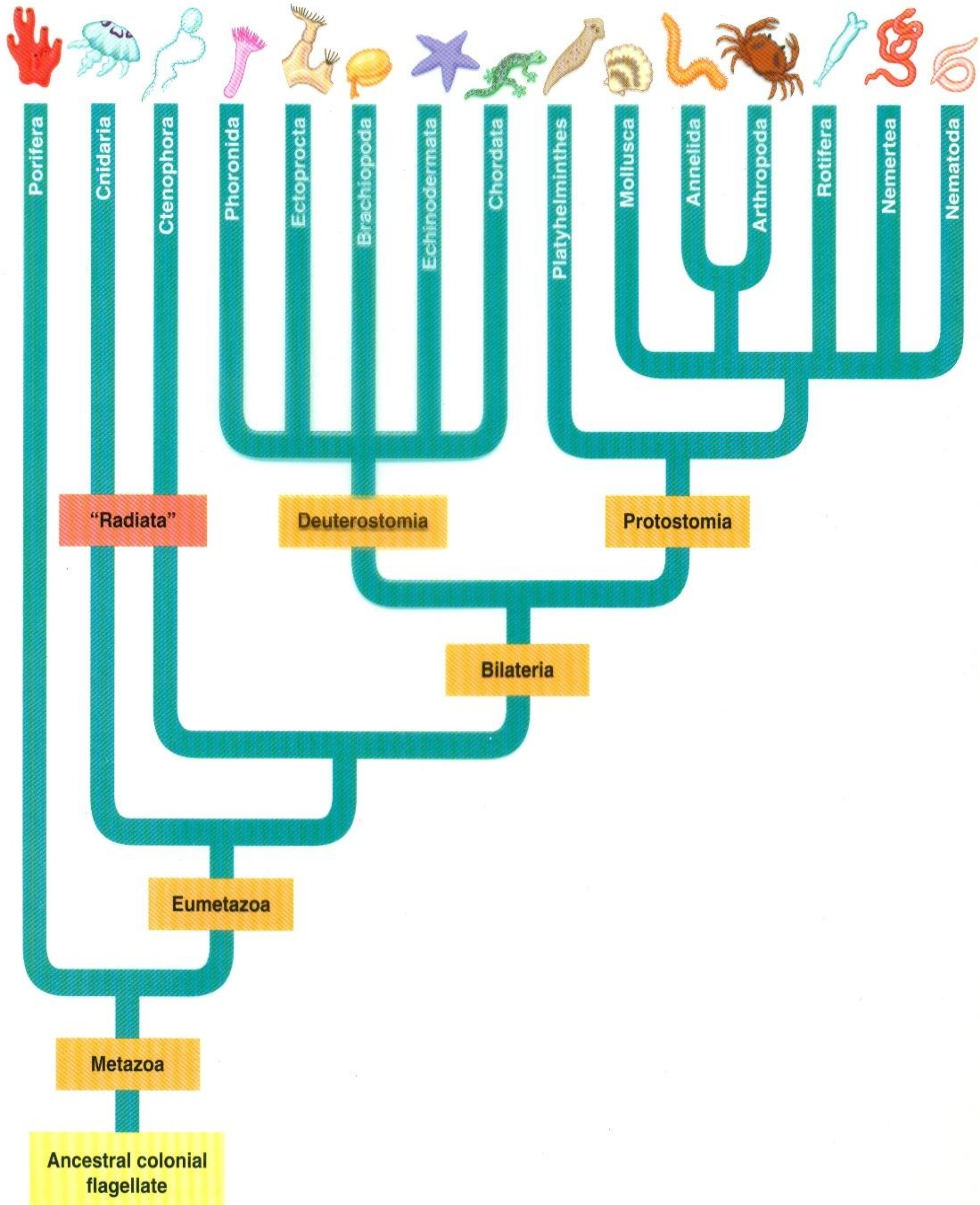
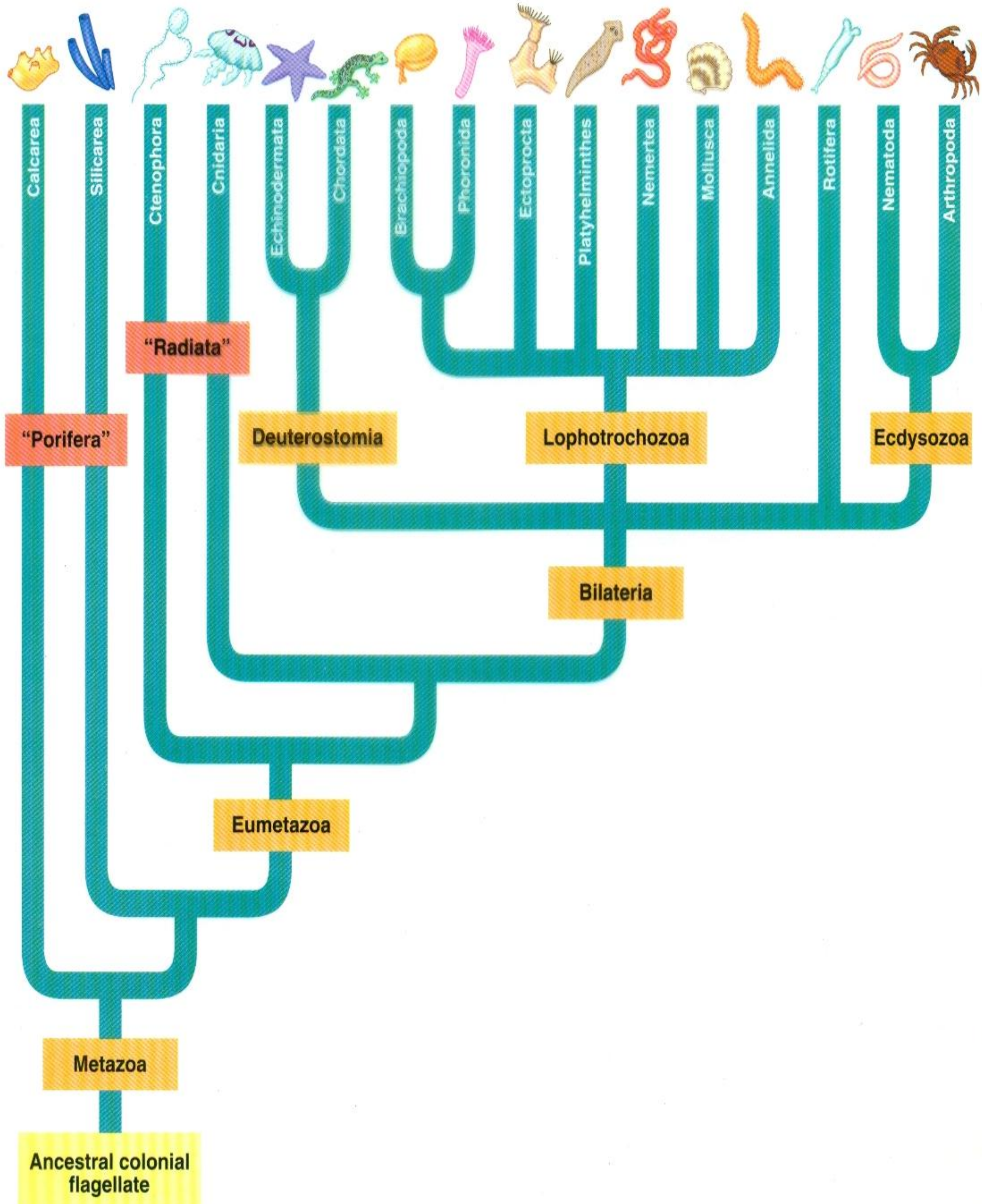


Figure 32.2b One hypothesis of animal phylogeny based mainly on molecular data



A. Parazoans lack true tissues

Sponges (Phylum Porifera) represent an early branch of the animal kingdom.

- Have unique development and simple anatomy that separates them from other animals
- Lack true tissues, therefore, they are called parazoa ("beside the animals")

The presence of true tissues is characteristic of nearly all the other groups of animals, collectively known as *eumetazoa.* True tissues permitted the evolution of a more complex anatomy.

B. Radiata and bilateria are the major branches of eumetazoans

The division of eumetazoans into two branches is based partly on body symmetry.

- *Radiata* exhibit *radial symmetry* (Figure 32.4a).
  - These animals have an oral (top) and aboral (bottom) side, but no front, back, left, or right sides.
- *Bilateria* exhibit *bilateral symmetry* (Figure 32.4b).

  → Bilaterally symmetrical animals have *dorsal* (top), *ventral* (bottom), *anterior* (head), *posterior* (tail), left and right body surfaces.

  → These animals exhibit *cephalization* (an evolutionary trend toward concentration of sensory structures at the anterior end).

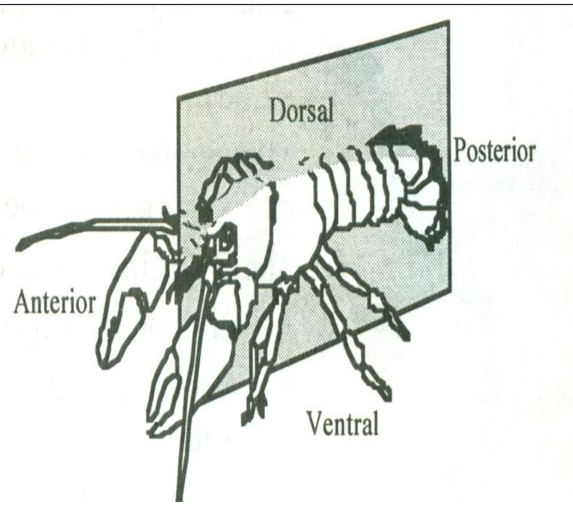
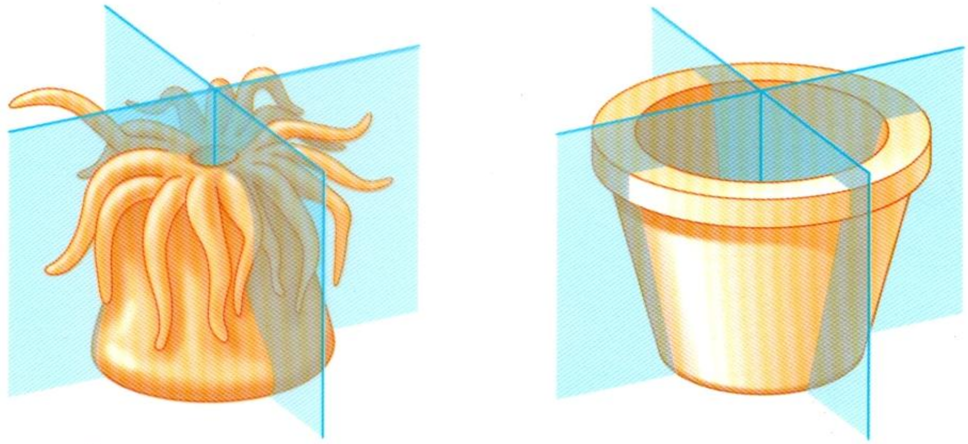
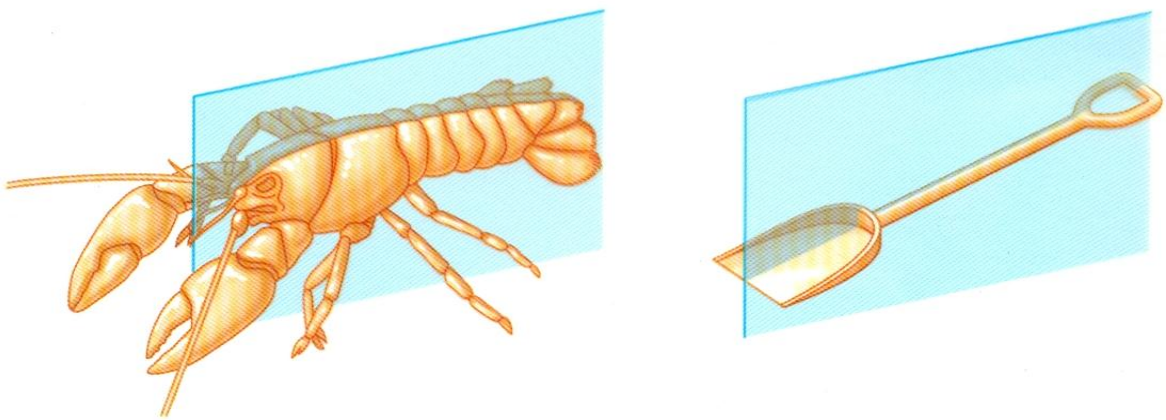
	
Radial Symmetry	Bilaterally Symmetry

Figure 32.4 Body Symmetry



(a) Radial symmetry



(b) Bilateral symmetry

Care must be taken when assigning an animal to an evolutionary line as symmetry may change between the larval and adult forms. The phylum Echinodermata shows a secondary radial symmetry in adults, which evolved as an adaptation to their sedentary lifestyle. They are actually in the bilateria.

Examination of development and body plan can define the radiata-bilateria split better than symmetry.

- The early embryo of all eumetazoans undergoes *gastrulation*. Concentric germ layers develop which form the various tissues and organs as development continues.

  → The radiata (e.g., Phylum Cnidaria, Phylum Ctenophores) develop only two germ layers (*ectoderm* and *endoderm*) and are termed *diploblastic*.

→ The bilateria (e.g., all eumetazoan phyla except Phylum Cnidaria and Phylum Ctenophores) develop three germ layers (ectoderm, endoderm, and *mesoderm*) and are termed *triploblastic*.

The germ layers of an early embryo include:

1. Ectoderm
    - Covers the surface of the embryo
    - Forms the animal's outer covering and the central nervous system in some phyla
2. Endoderm
    - Innermost germ layer which lines the *archenteron* (primitive gut)
    - Forms the lining of the digestive tract, and outpocketings give rise to the liver and lungs of vertebrates
3. Mesoderm
    - Located between the ectoderm and endoderm in triploblastic animals
    - Forms the muscles and most organs located between the digestive tract and outer covering of the animal

C. Evolution of body cavities led to more complex animals

Triploblastic animals can also be grouped on the basis of whether a body cavity develops and how that cavity develops.

Animals in which no body cavity develops are termed acoelomate.

- *Acoelomate* = An animal body plan characterized by no body cavity present between the digestive tract and the outer body wall (Figure 32.5c)

The area between the digestive tract and outer wall is filled with cells, producing a solid body (e.g., Phylum Platyhelminthes).

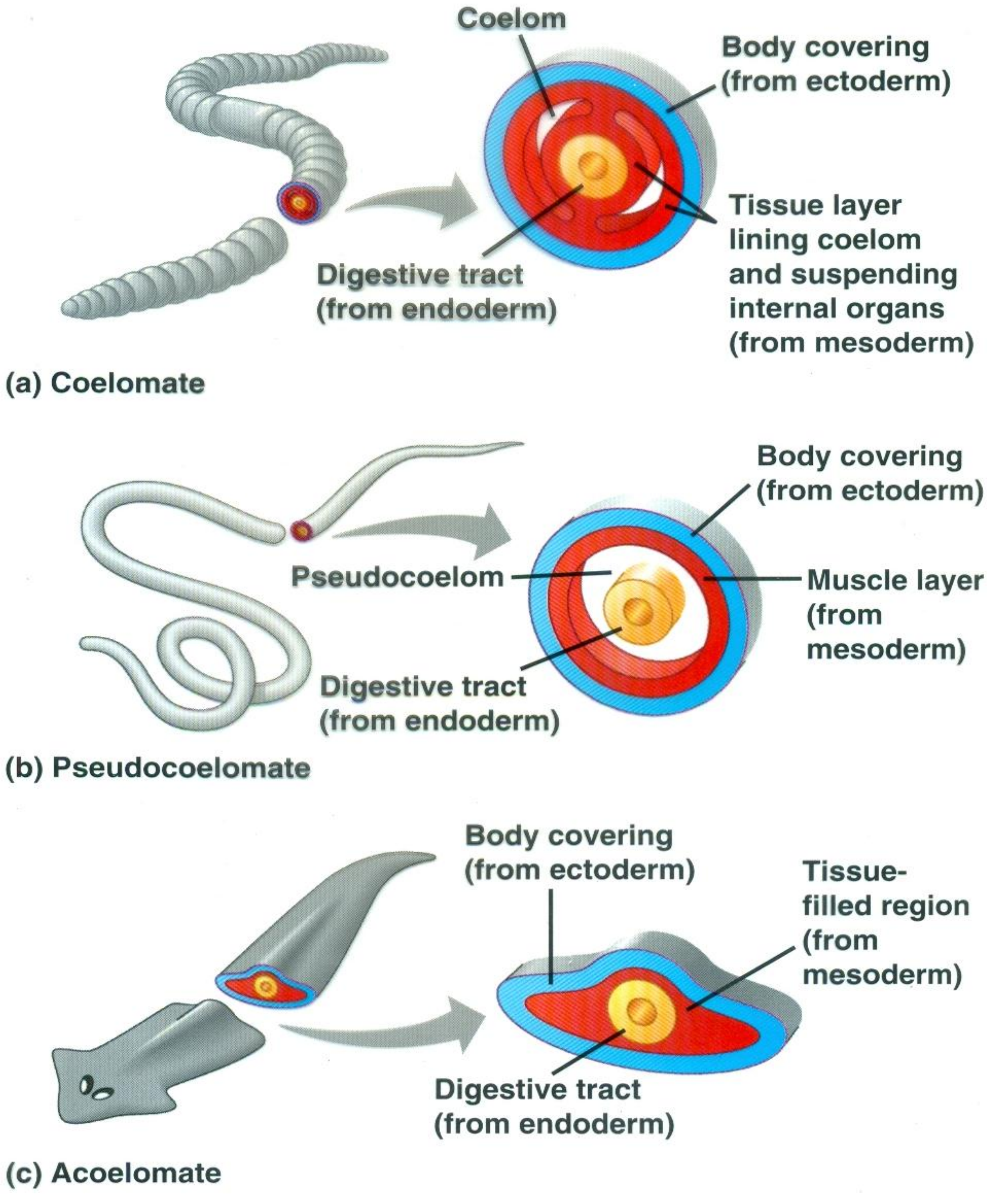
Animals in which a body cavity develops may be termed pseudocoelomate or coelomate, depending on how the cavity develops.

- *Pseudocoelomate* = Animal body plan characterized by a fluid-filled body cavity that separates the digestive tract and the outer body wall. (Figure 32.5b.)
- This cavity (the *pseudocoelom*) is not completely lined with tissue derived from mesoderm (e.g., Phylum Nematoda).
- *Coelomate* = Animal body plan characterized by a fluid-filled body cavity completely lined with tissue derived from mesoderm (the *coelom*) that separates the digestive tract from the outer body wall (Figure 32.5a)
- Mesenteries connect the inner and outer mesoderm layers and suspend the internal organs in the coelom (e.g., Annelida).

- The fluid-filled body cavities:
  - Cushion the organs, thus preventing injury
  - Allow internal organs can grow and move independently of the outer body wall.
  - Serve as a hydrostatic skeleton in soft bodied coelomates such as earthworms.

In addition to the presence of a body cavity, acoelomates differ from pseudocoelomates and eucoelomates by not having a blood vascular system.

Figure 32.5 Body plans of triploblastic animals



D. Coelomates branched into protostomes and deuterostomes

Distinguished by differences in development, the coelomate phyla can be divided into two distinct evolutionary lines:

1. *Protostomes* (e.g., mollusks, annelids, arthropods)
2. *Deuterostomes* (e.g., echinoderms, chordates)

Developmental differences between protostomes and deuterostomes include: cleavage patterns, coelom formation, and fate of the blastopore.

1. Cleavage

Most protostomes undergo spiral cleavage and determinate cleavage during their development.

- *Spiral cleavage* = Cleavage in which the planes of cell division are diagonal to the vertical axis of the embryo.
- *Determinate cleavage* = Cleavage in which the developmental fate of each embryonic cell is established very early; a cell isolated from the four-cell stage of an embryo will not develop fully.

Deuterostomes undergo radial cleavage and indeterminate cleavage during their development.

- *Radial cleavage* = Cleavage during which the cleavage planes are either parallel or perpendicular to the vertical axis of the embryo
- *Indeterminate cleavage* = Cleavage in which each early embryonic cell retains the capacity to develop into a complete embryo if isolated from other cells; this type of cleavage in the human zygote results in identical twins.

2. Coelom formation

Schizocoelous = Descriptive term for coelom development during which, as the archenteron forms, the coelom begins as splits within the solid mesodermal mass; coelom formation found in protostomes.

Enterocoelous = Coelom development during which the mesoderm arises as lateral outpocketings of the archenteron with hollows that become the coelomic cavities; coelom formation found in deuterostomes.

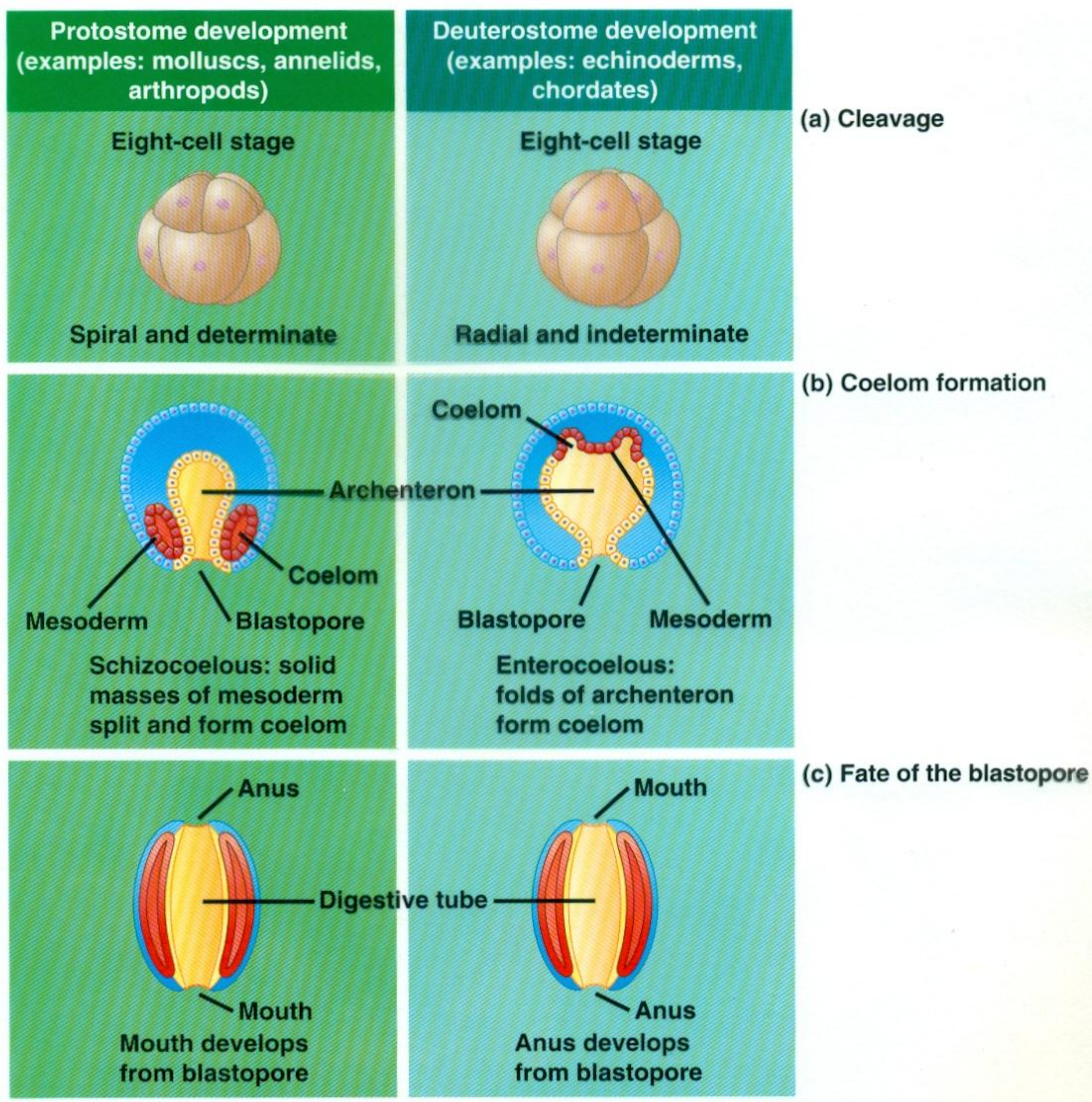
3. Blastopore fate

Blastopore = The first opening of the archenteron which forms during gastrulation

- In protostomes, the blastopore forms the mouth.

- In deuterostomes, the blastopore forms the anus.
- Figure 32. 7 shows the differences in the development of protostomes and deuterostomes.

Figure 32.7 A comparison of protostome and deuterostome development.



SUMMARY OF PROTOSTOME - DEUTEROSTOME SPLIT	
PROTOSTOMES	DEUTEROSTOMES

Spiral cleavage	Radial cleavage
Determinate cleavage	Indeterminate cleavage
Blastopore forms the mouth	Blastopore forms the anus
Schizocoelous coelom formation	Enterocoelous coelom formation

III. The Origins of Animal Diversity

A. Most animal phyla originated in a relatively brief span of geological time

The animal kingdom probably originated from colonial protists related to choanoflagellates. The diversification that produced many phyla occurred in a relatively short time on the geological scale. This evolutionary episode is called the *Cambrian explosion.*

The Cambrian explosion encompassed a 20-million-year time span at the beginning of the Cambrian period (ca. 545 to 525 million years ago).

- Nearly all of the major animal body plans seen today evolved during this time.
- New taxa appeared later but were variations on the basic plans already evolved. For example, mammals evolved about 220 million years ago, but are only a variation of the chordate body plan which evolved during the Cambrian explosion.

A much less diverse fauna preceded the Cambrian explosion.

- This Precambrian fauna dated back to the *Ediacaran period* (700 million years ago).
  - → This period is named for the Ediacara Hills of Australia where Precambrian animal fossils were first discovered.
  - → Fossils similar in age to these have since been discovered on other continents.
- Most Ediacaran fossils appear to be cnidarians although bilaterial animals are also indicated by fossilized burrows probably left by worms.

The diversity of Cambrian animals is represented in three fossil beds:

- The Burgess Shale in British Columbia is the best known.
- A fossil bed in Greenland and one in the Yunnan region of China predate the Burgess Shale by 10 million years.

Two contrasting interpretations of Burgess Shale fossils have been proposed:

1. The Cambrian explosion resulted in a large number of phyla which included the current phyla, many of which are now extinct.

   → During the mass extinction at the end of the Cambrian, only the base stock of 35 or so extant phyla survived.

2. The diversity of the Cambrian fossils represents ancient variations within the taxonomic boundaries of extant phyla.

   → As these fossils undergo continued study, many are classified into extant phyla. Thus, the number of exclusively Cambrian fossils is decreasing.

B. Developmental genetics may clarify our understanding of the Cambrian diversification

Several hypotheses about external factors have been proposed as explanations for the Cambrian explosion and the lack of subsequent major diversification.

1. The Cambrian explosion was an adaptive radiation resulting from the origin of the first animals.

   → These early animals diversified as they adapted to the various, previously unoccupied, ecological niches.

2. Predator-prey relationships emerged and triggered diverse evolutionary adaptations.

   → Various kinds of shells and different forms of locomotion evolved as defense mechanisms against predation.

   → Predators also evolved new mechanisms to capture prey.

3. Major environmental change provided an opportunity for diversification during the Cambrian explosion.

   → The accumulation of atmospheric oxygen may have finally reached a concentration to support the more active metabolism needed for feeding and other activities by mobile animals.

Other hypotheses for the Cambrian explosion have emphasized internal changes in the organisms.

1. The origin of mesoderm may have stimulated diversification of the body plan.

→ This third tissue layer permits development of more complex anatomical structure.

2. Variation in genes that control pattern formation during animal development may have played a role in diversification.

   → Some of the genes that determine features such as segmentation and placement of appendages and other structures are common to diverse animal phyla.

   → Variation in expression of these genes during development results in morphological differences that distinguish the phyla.

   → This same kind of variation in expression may have resulted in the relatively rapid origin of diverse animal types during the Cambrian explosion.

   → The phyla, once developed, may have become locked into developmental patterns that permitted subtle variation to allow speciation and the origin of lower taxa, but prevented large scale morphological evolution resulting in new phyla.

The hypotheses presented for external and internal factors are not mutually exclusive.

A combination of factors may have combined to produce the Cambrian explosion.

REFERENCES

Brusca, R and Brusca, G. *Invertebrates*. 2nd ed. Sunderland, Massachusetts: Sinauer Associates, 2003.

Campbell, N., et al. *Biology*. 10th ed. Menlo Park, California: Benjamin/Cummings, 2013.

Harris, C.L. *Concepts on Zoology*, 2nd ed. New York, NY: HarperCollins, 1996.