

Lecture 2- The 'New Phylogeny'

Determining animal relationships

Two assumptions have influenced thinking about the relationships between animal groups:

1. Animals that look (or develop) more like one another are more closely related
2. Animal complexity has increased over evolutionary time within lineages

Question: Are these assumptions always justified?

Often, but not always

Animals are often similar due to convergence

Increases in 'complexity' within animal lineages are not, in fact, inevitable (some examples are given in the following lectures).

Assumption/principle/concept that continues to inform our understanding of animal relationships:

Parsimony

- Hypotheses (i.e. trees) that explain the evolution of the 'observed' animal diversity in the fewest evolutionary steps are preferred
- We work on the assumption that if a tree can explain the animal diversity out there in a fewer number of evolutionary changes then its more likely to be true than one that requires a large number of evolutionary changes
- That in itself is an assumption - may not always be true

Evolutionary change- doesn't give the amount of change or the direction of the change, it can be a gain or a loss of a trait can be increase or loss of complexity

Morphological phylogenies

2 misconceptions:

Morphological phylogeny - trees of animal relationships based on morphological characteristics

Molecular phylogeny - trees of animal relationships based on molecular characteristics

You can now have trees that are based on both characters together

- Morphological trees are based on extinct animals (fossils) and extant (living) animals
- Morphological characters are identified and scored (usually as present/absent).
- These data are then used to construct trees of animal relationship following defined principles (one example being parsimony).
- Compare them by the number of characters the animals share with each other
- Subjective- characters you choose and processes you use to construct trees

Characters that unite a particular group of animals (i.e. that are not present in more ancestral animals) are assumed to have arisen once shortly prior to the radiation of that group.

Synapomorphies- shared, derived characters

Animals that share more- the assumption is that they're more closely related

The character evolved in the ancestor of the group and has been retained by all members of that group

- Apomorphy- a newly evolved character
- Synapomorphy- apomorphy that is shared by multiple different groups of animals

Most animals look different to each other

Embryological characters are often used since the major morphological differences between animals arise during their embryonic development

An example of a 'traditional' morphological phylogeny

Potential

1. Synapomorphy:

- a. Protostomy
- b. Deuterostomy

2. Coelom (unites Coelomates)

3. Segmentation (unites Arthropod + Annelids into the Articulata)

- Closely related groups of animals
- Puts animals together based on their segmented body plan
- Earthworms and marine polyps have segmented body plan
- Arthropods, insects, millipedes, spiders- closely related - segmented body plan down anterior posterior axis

Early animal embryogenesis

- Gastrulation leads to the formation of two (diploblast animals) or three (triploblast animals) embryonic cell layers.
- Inner endoderm and outer ectoderm in diploblasts.
- In triploblasts a third cell layer forms between the ectoderm and endoderm - the mesoderm.
- Mesoderm can give rise to skeleton and muscle.

- Egg
- Complete cell division- 8 cell stage
- More divisions which gives rise to a ball of cells - blastula
- Cells cover the outside of the cell
- The inside of the ball is hollow - blastocoel
- Contains yolk which is feeding the cells
- Gastrulation happens
- Cells come into the interior of the cell and form a hole- blastopore
- Cells inside- endoderm - mid-gut
- Cells outside- ectoderm- epidermis and the lining of foregut and hindgut

1. Protostomy vs. Deuterostomy

Protostome

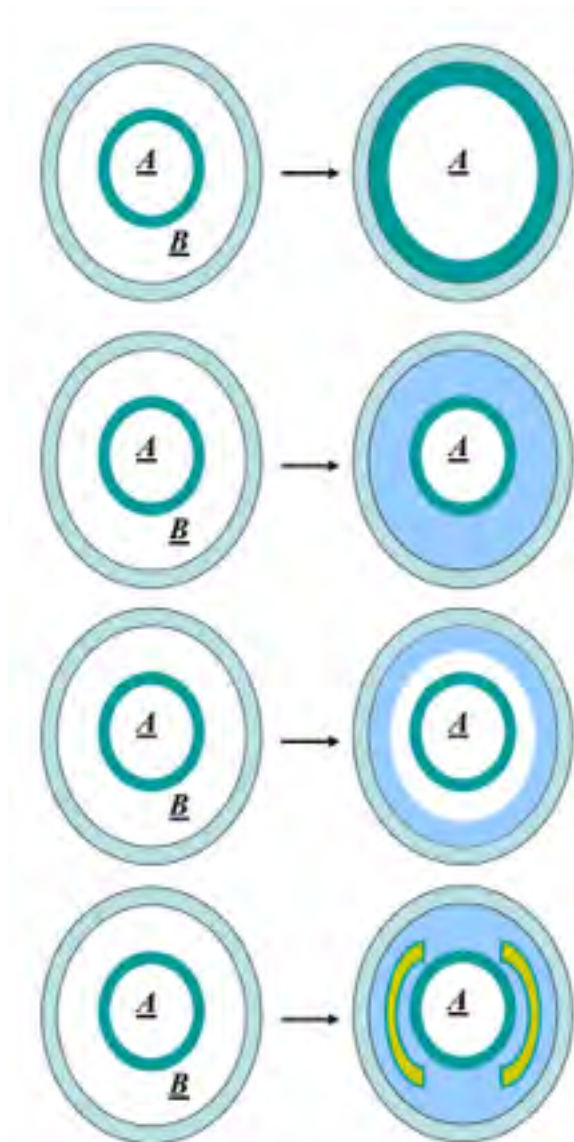
- 'First mouth'
- The blastopore becomes the mouth

Deuterostome

- 'Second mouth'
- The blastopore becomes the anus, and the mouth forms secondarily by fusion of ectoderm/ endoderm

2. Acoelomates vs. Coelomates

Body cavity vs no body cavity



Diploblasts (Acoelomates):

2 layers

Blastocoel (B) largely disappears

Endoderm comes up against the ectoderm

Archenteron (A) becomes the 'gut' (diploblastic)

Small gap

In jellyfish- there are some cells that function and some nerves that function within this gap- newly understood

E.g. Cnidaria, such as anemones, jellyfish).

Triploblastic (Acoelomates):

3 layers

A solid mesoderm (M) replaces the blastocoel

E.g. platyhelminth, flatworms)

Triploblastic, (Pseudocoelomate):

3 layers

A mesoderm partially replaces the blastocoel

Cavity is said to be 'disorganised' and lacks a membrane delimiting it – a peritoneum

E.g. nematodes

Triploblastic, (Coelomate):

3 layers

A mesoderm forms, itself invaded by a body cavity (coelom)

E.g. polychaete annelid

Muscle fibres forming within there that work against the body wall and allow these within the body cavity to work against the limbs

Allows the animal to put pressure against the outside world
Animals historically would be quite passive and responsive to water currents and movement on the sediment

Whereas with the evolution of a body cavity the animal is much more likely to be able to interact with its environment

3. Segmentation (The Articulata hypothesis)

Coelomates:

- Annelid -Marine Polychaete
- Centipede-Terrestrial arthropod

Grouping of annelids and arthropods on the basis of their body segmentation

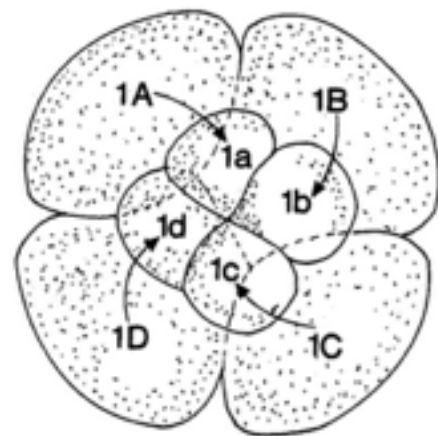
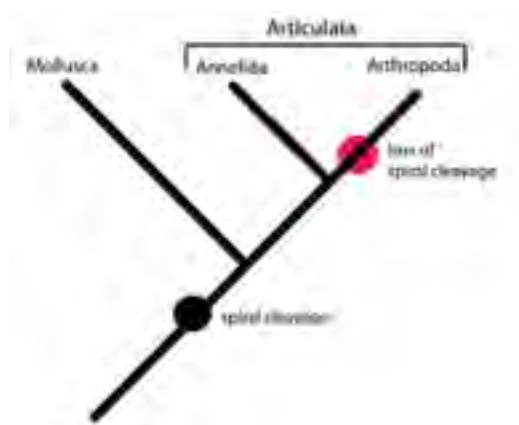
Early embryogenesis -spiral cleavage- third cell division which gives rise to 8 cells –cells twist – big macro cells on outside and micro cells

Assumption of putting these animal together based on their segmentation:

- Arthropods lost their spiral cleavage

OR

- Molluscs and annelids gained this independently which is less parsimonious- assuming 2 changes rather than 1



Molecular Phylogenies

Observed and compared molecules as well as morphology

Gene (nucleotide) and protein (amino acid) sequences have been used to determine animal relationships

Phylogenomics- whole genome sequences have been sequenced and compared to determine animal relationships with much more confidence (i.e. more data)

- Molecular characters are identified by making alignments of the sequence of conserved molecules (genes or proteins) and scoring similarities and differences between them at each conserved position
- Where divergence has occurred in the DNA or protein sequence of the animals
- You can count differences and calculate the level of similarity in the molecular sequence across animals

- You put animals that have sequences that are more similar – group together on the tree
- Ones that have diverged more are more separated on the tree

The use of molecules has given rise to the 'New Animal Phylogeny'

An example of an informative molecular alignment - chaetognaths group with protostomes

- Doesn't have many distinguishing features that make it an ally to any other phylum of animals
- Prior to being able to get molecular sequencing it was a mystery as to where this animal belonged on the animals tree
- When mitochondrial DNA was sequenced- Nad5
- Arrow worm belongs to protostomes
- A lot of divergence in this group of animals
- Diverging for long time

Sources of gene/protein sequences used to construct molecular phylogenies

Ribosomal RNA (rRNA) molecules

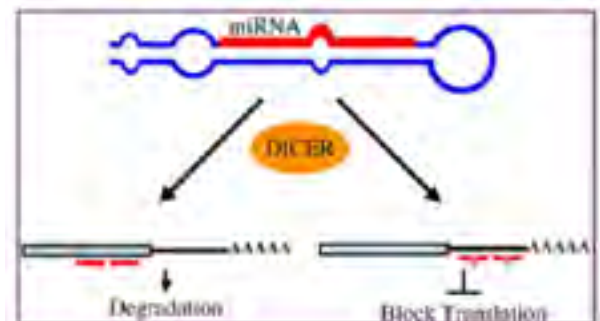
- Ribosomal small/large subunit

Mitochondrial genomes

- Mitochondrial genes/proteins (sequence/ order)

microRNAs (miRNAs)

- Genes that aren't translated- remain as mRNA and fold into loops
- Trigger process of whole degradation of other genes
- Involved in gene regulation but don't make proteins
- If one of these exist in 2 animals – likely to be related because microRNAs tend not to evolve more than once



EST (Expressed sequence tags) datasets

- The sequences of transcripts that are expressed in a given tissue or whole animal
- Take mRNA being expressed in animals and reverse transcribe them into DNA
- Use those sequences

Many genes selected from complete genome sequences (Initially *Drosophila*, *C. elegans* & humans, but now many are available)

Why might molecules be better than morphology?

One assumption is that many positions within gene/protein sequences change/evolve neutrally (i.e. aren't subject to selection pressures) and are therefore less prone to homoplasy/convergent evolution (i.e. unrelated animals evolving in similar ways in similar ecological situations).

This is particularly true for 'housekeeping genes' (genes involved in fundamental processes; e.g. respiration) whose functions are unlikely to change over time.

- Redundancy at the level of the genetic code
- For every amino acid there are multiple different codes which code for that amino acid
- Can change third position in the sequence and amino acid won't change
- No selection pressure from stopping this position in DNA from changing position
- Happens randomly through mutation
- No chance that this can happen thorough convergence through selection pressures driving similar change through natural selection

- Some redundancy at the level of amino acid sequence
- 'conservative' amino acid changes are unlikely to alter protein function and so can occur neutrally
- Chemical make up of that amino acid is more or less the same as the other one
- For example, Glu (E) can often change to Asp (D) (and vice versa) without changing protein function.
- Natural selection isn't selecting for or against it – neutral change

- One assumption is that gene/protein sequences behave like a 'molecular clock' - changes occur (on average) at a relatively fixed rate, in a consistent way, over time and across lineages.
- The longer these animals have been diverging from each other the more changes they've picked up
- Can be used as a guide to see how long animals have been evolving separately from each other
- Diverged recently or a long time ago
- This is called neutral evolution

Groups exhibiting deuterostomy placed within the traditional protostomes

1. Lophophorates

- Animals that have a clear deuterostome form of development
- Molecules were putting them in the protostomes

- Lophophore- Filter feeding structure looks like fingers

2. Chaetognatha

- Not sure where in the protostomes they belong
- Could be basal protostome

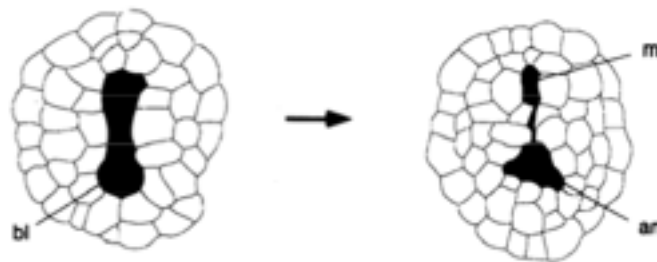
3. Priapulida

- Based on gene expression studies in an ecdysozoan priapulid worm (above), Martin-Duran et al. (Current Biology, 2012)
- The common ancestor of Protostomia exhibited deuterostomy (and by extension also the common ancestor of all bilaterally symmetrical animals - Urbilateria)

Groups exhibiting amphistomy are also placed within the traditional protostomes

Polychaete annelids

- Some animals didn't quite fit into the idea of protostomy vs. deuterostomy
- Amphistomy- cells pinch over and form a tube – tube stays open at both ends
- Produce mouth and anus in a simultaneous process

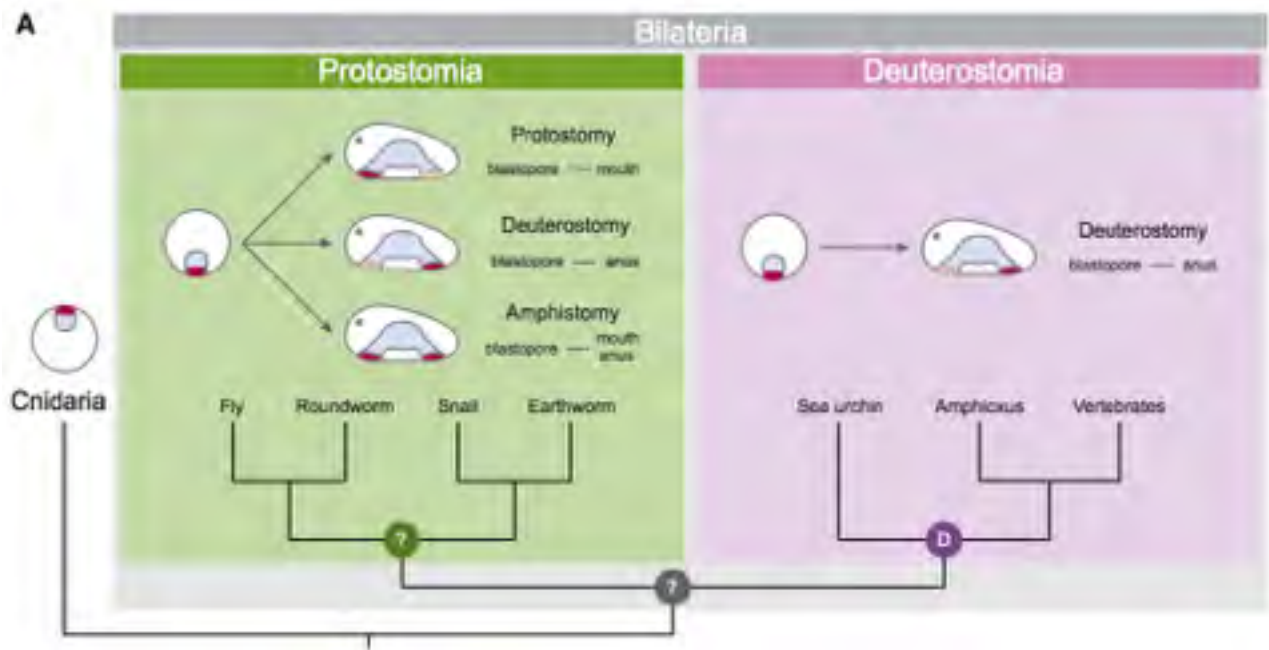


- Can look at genes that are expressed very early around the blastopore – *cdx* and *bra*
- Look at genes expressed away from the blastopore – *foxA* *gsc*
- Can follow through development
- Introvert stage
- Can see anus forming
- Genes expressed at the blastopore are still expressed where the anus is
- Can trace events through embryogenesis through gene expression
- Proof that blastopore forms the anus
- Genes expressed away from this end up being expressed where the mouth is formed later in embryogenesis

it is no longer clear if the common ancestor of traditional protostomes (Ecdysozoa + Lophotrochozoa) exhibited protostomy, deuterostomy or amphistomy

- Traditional protostomia was filled with animals which might shown protostomy

- Very little embryonic evidence that protostomy actually happens
- Due to advances in technology assumption about blastopore are being challenged
- Questionable as to how many animals actually show protostomy
- A lot of animals were clearly deuterostomes
- Call them protostomes but they do deuterostomy
- Puts doubt in what early ancestor was doing
- ? Not clear what was happening out of the 3 choices



A recent model for the evolution of deuterostomy and protostomy

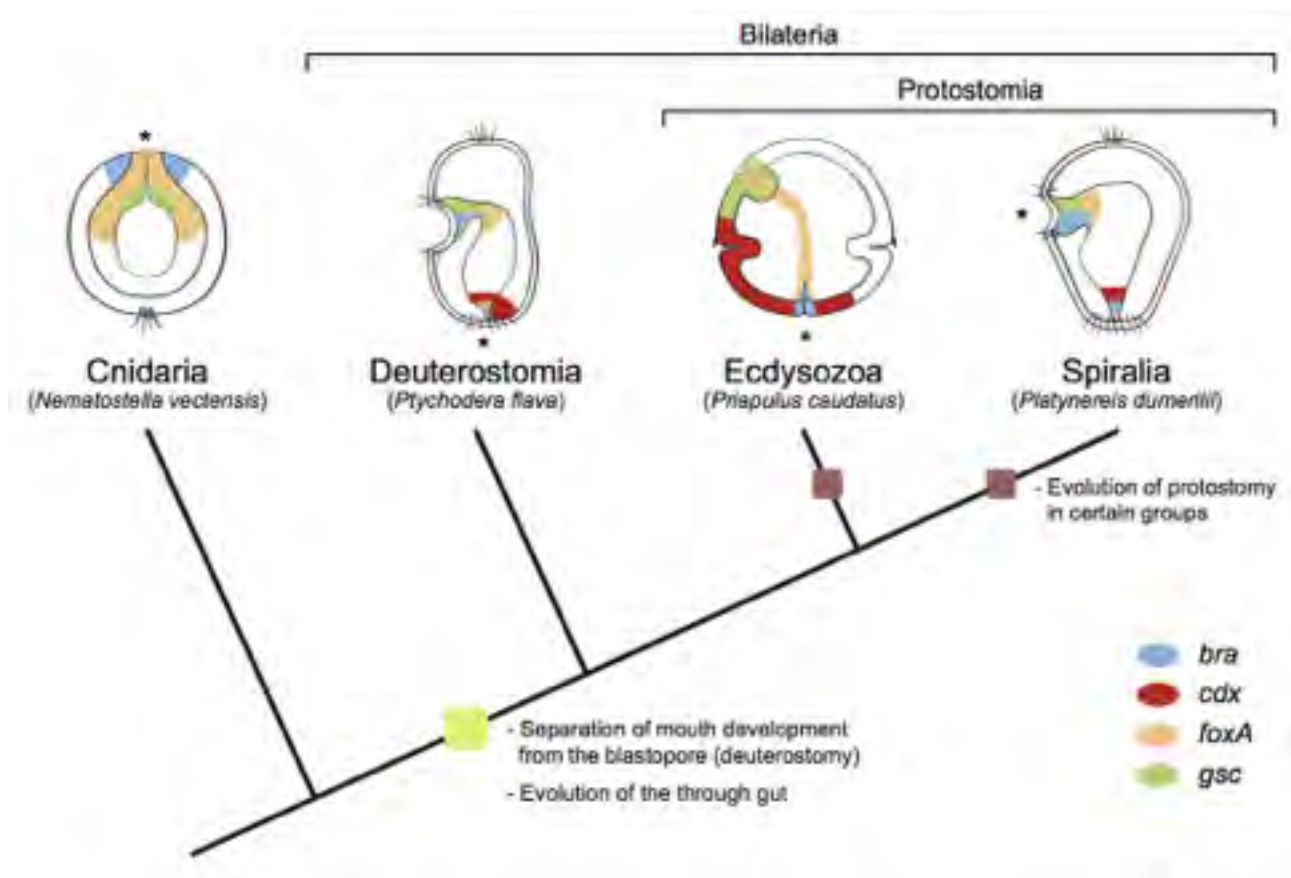
Hypothesis:

- In cnidarians they have one opening not 2 – mouth
- Everything that comes in goes out the same way
- In bilaterians (not all) have 2 opening to the body – mouth, anus, digestive tract
- Some genes involved in developing the mouth move away and form the mouths somewhere else
- Genes responsible for forming the blastopore stayed where they were
- Separation of functioning forming 2 holes rather than 1

Idea:

- This has been the base plan for bilaterians
- Blastopore becoming anus- deuterostomy
- Separate mouth forming through movement of these genes away

In traditional protostomes which were ancestor deuterostomes – some have evolved protostomy secondary



1st implication of 'The New Phylogeny'

Protostomy is not a synapomorphy of Lophotrochozoa + Ecdysozoa (i.e. Protostomia)

Protostomy is rather likely to be an:

- Apomorphy (a derived characteristic) of particular lophotrochozoan and ecdysozoan clades

- ◆ Evolves in random lineages within tradition protostomes

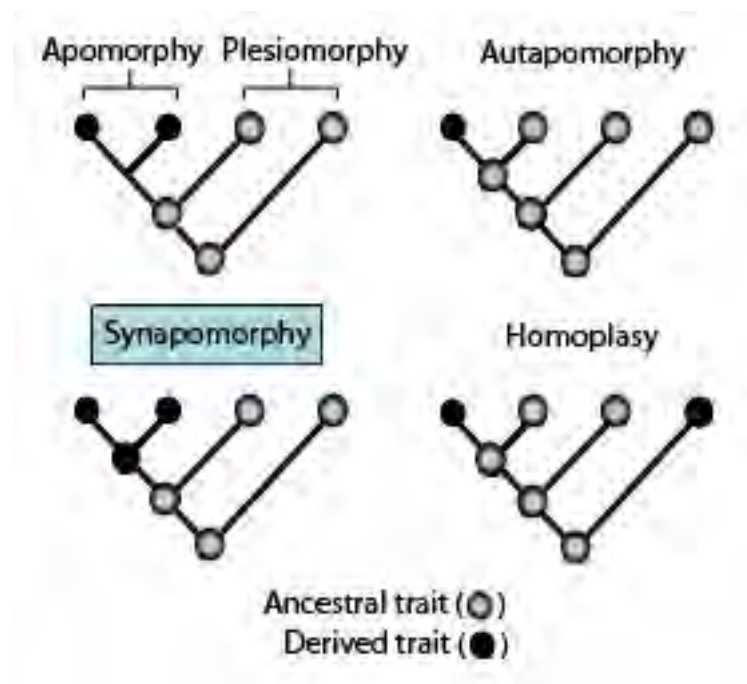
OR

- Example of homoplasy (convergence)

- ◆ Trait that has evolved convergently within tradition protostomes a few times but the ancestor was a deuterostome

Deuterostomy is likely to be a symplesiomorphy

- ◆ An ancestral trait retained by many animals.
 - ◆ In this case bilaterally symmetrical (bilaterian) animals



Acoelomates

- A solid mass of internal tissue replaces it – we have seen this in the case of the platyhelminthes.
- This is the mesoderm.
- These animals are referred to as acoelomate – without a coelom.

Phylogenomics now suggest acoelomate platyhelminths group within the major coelomate lophotrochozoan group

Group of animals that don't have body cavity in the middle of a group that do

Explanations:

- Platyhelminths used to have a body cavity but lost it- one change (most parsimonious)

OR

- All of these group have independently evolved complex body cavities in their evolution

Molecular sequencing is putting early superficially simpler animals amongst complex ones is suggesting that they are not simple because they've always been simple but because they've lost traits over time

2nd implication of 'The New Phylogeny'

- The coelom (or its absence) is an example of homoplasy
- Either coeloms have evolved multiple times convergently in different triploblast lineages, or coeloms have been lost multiple times independently during the radiation of bilaterian animals, or perhaps more likely a bit of both has happened