Invertebrate Zoology

BIOL 3408
Dr. Christopher M. Ritzi
MWF 11:00 – 11:50

Outline

- Review Syllabus
- Course Introduction
- Chapter 1 and Review

Syllabus

- Dr. Christopher M. Ritzi
- Office: WSB 216
- Office hours: M&W 8:30-10:30am, T 2-3pm or appt.
- Phone: 837-8420
- Email: critzi@sulross.edu
- Webpage: http://bbsrsu@sulross.edu & http://faculty.sulross.edu/critzi/
- Lecture: 11:00-12:15 MW WSB 101
  - Lab: 1-3:00pm Monday WSB 109

Syllabus

- A contract between you and me
- Information on the course webpage
- Exams and grading policy
- Attendance policy
- Lecture notes

Course Objectives

- A comprehensive look at the diversity of animals:
  - Functional morphology
  - Ontogeny
  - Phylogeny
- Learn the language of comparative organismal biology:
  - The Glossary
- Build a foundation for introspection, discovery, innovation, and public policy

A Word About the Text

- B & B: Readings are listed on the syllabus
- Chapters 1—4 & 24 are very important – consult them throughout the term
- Familiarize yourself with the drawings & images in the remaining chapters
- DO NOT overwhelm yourself with too many details – the text is a resource
- Focus on the specific topics & terms highlighted in your lecture notes

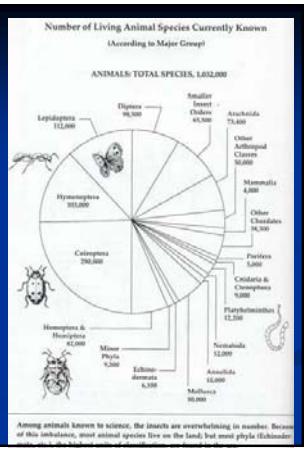
Why Study Inverts?

- Diversity
- Importance
- Interesting
- Ecological Models of the "Big Picture"

Why Inverts?

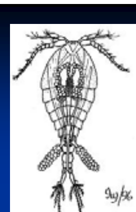
- Most animals are invertebrates
- 97% of all species
- 99% of all individual animals

- In fact: 2 new phyla have been discovered in the past 20 years.



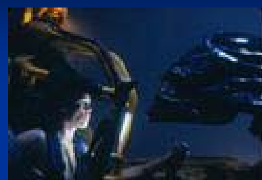
Why Inverts?

- They are ecologically, environmentally, and medically important
- Copepods are the most numerous animals on earth
- Stream inverts are used as water-quality indicators
- Parasites – like this tapeworm, can impact human and domestic animal health.



Why Inverts?

- They have inspired awe and inspiration in those who behold them.



Why Inverts?

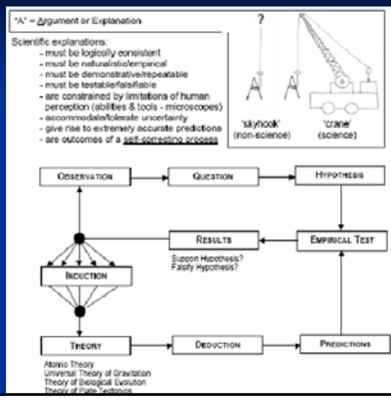
- **Invertebrates reveal the nature of biological diversity by providing "the big picture"**
  - e.g. Some phyla cut across ecological boundaries while others do not. Why?
- **Some ecological terms:**

 * sessile
 * planktonic (zooplankton and phytoplankton)
 * suspension-feeding
 * parasite versus predator

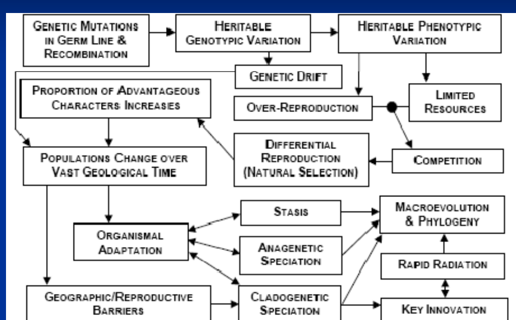
Background

- The Scientific Method
- Biological Evolution via Natural Selection
- Diversity of Eukaryotes
- Diversity of the Eukaryotic Cell
- Laws of Thermodynamics
- Phylogeny

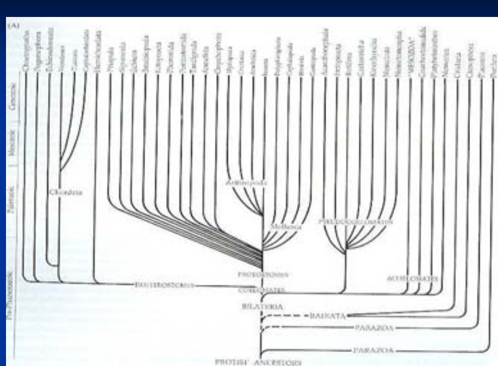
Scientific Method



BIOLOGICAL EVOLUTION (VIA NATURAL SELECTION)



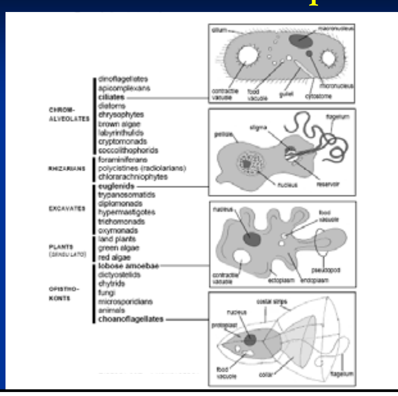
The Diversity of the Eukaryotes



Diversity of the Eukaryotic Cell

- Tools of discovery
  - Light microscopy
  - Transmission electron microscopy
  - Scanning electron microscopy
  - Molecular biology

Overview of Groups

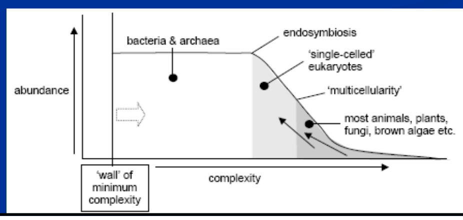


Laws of Thermodynamics

- ENTROPY measures the dispersal of energy as a function of temperature. In other words, entropy measures the relative state of disorder in a system: positive entropy = more disorder; negative entropy = more order.
- SECOND LAW OF THERMODYNAMICS: energy disperses from being localized to spread out, if it is not hindered by outside influences. In other words, within a closed system, net entropy is always positive until a state of equilibrium is met.

Entropy

- A popular but misguided criticism of Biological Evolution is that the Theory contradicts the Second Law of Thermodynamics, because through evolutionary processes, organisms have become more ordered – moving away from the 'wall' of minimum complexity:
  Life = negative entropy.



Entropy

- In light of the fact that the Second Law applies only to closed systems (e.g., the entire universe), it cannot apply to biological processes on Earth – an open system fueled by the Sun. The continuous bombardment of the Sun's energy creates a state of extreme disequilibrium on Earth and promotes a localized 'pocket' of negative entropy in the universe, within which Life is a manifestation. As required by the Second Law, the net entropy in the universe remains positive; localized 'pockets' of negative entropy are offset and exceeded by the production of positive entropy elsewhere (e.g., the bursting of stars).

What are Phyla?

- **'Phylogeny'** is the evolutionary relationships among organisms; the patterns of lineage branching produced by the true evolutionary history of the organisms being considered.

  'Taxon' - group of similar and related invidividuals

- **The hierarchical system of classification:**
  Kingdom
  Phylum
  Class
  Order
  Family
  Genus
  Species -a group of organisms that can potentially breed with one another

- The phylum concept is based on grouping of organisms with a similar basic **'body plan'**
  Based on such things as development sequences, tissue layer arrangements, segmentation, symmetry, physiological systems, morphological structures…
  Question: *Should species be divided fairly equally among taxa?*

Teleology

- An archaic, non-scientific (anthropocentric) idea asserting that the diversity of organisms is purposeful and is directed toward optimum design or perfection. Teleological thinking gave rise to the SCALA NATURAE (advocated by Aristotle, 384-322 B.C.) – a viewpoint that is pervasive even today:

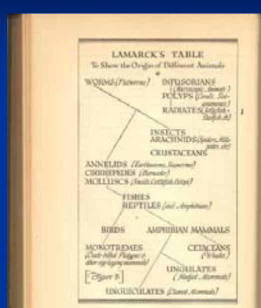
CREATOR
PRINCIPALITIES
ANGELS
BUGS-----PEOPLE
PLANTS
GLOP/SLIME
DIRT

Higher
Lower

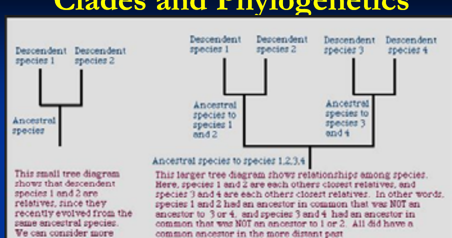
- **Avoid using teleological language** to express yourself on exams or in class.

Classification

- The basis of modern classification was developed by Carl Linnaeus (1707-1778).
- *Why classify organisms?*
- From similarity and differences of body plans, zoologist have constructed 'phylogenetic (evolutionary) trees' (who is most closely related to who, analogous to a family tree)



Clades and Phylogenetics



A **clade** (or **monophyletic** group) is a group of species that includes an ancestral species and <u>all</u> of its descendants

Do species 1 and 2 make up a distinct clade?

Do species 1, 2, and 3 make up a distinct clade?

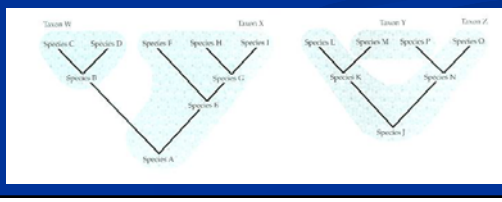
Do species 1, 2, 3,and 4 make up a distinct clade?

If a grouping excludes a taxon (or taxa) that has a more recent common ancestor with some members but not all of that grouping, then it is said to be **paraphyletic**?

What would be an example of this in the above diagram?

What Makes a Group?

- Monophyletic – group contains the ancestor and all descendants (ie. A natural group)
- Paraphyletic – group contains the ancestor and some, but not all, descendants.
- Polyphyletic – group that arose from two different ancestors.



Classical Criteria for Homology

- Homologous Character
  - Any trait present in 2 or more different lineages that was also present in their most recent common ancestor.

1. Unique similarity in form
2. Corresponding position within a common body plan
3. The existence of intermediate states (developmental or paleontological)

Looks can be Deceiving

- Convergent evolution, reversals, and parallel evolution can confuse phylogeny.
- Important of polarizing character states.
- What are the various character states:
  - Primitive character state (ancestral) or plesiomorphy
  - Advanced character state (derived) or apomorphy
- These states are **relative** according to placement in the tree.

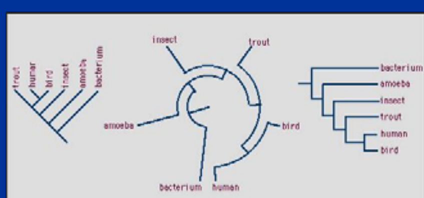
Categorizing Characters

- When forming trees, plesiomorphys and apomorphies become further distinguished.
  - Autapomorphy – unique derived character
  - Synapomorphy – shared derived character
  - Symplesiomorphy – shared primitive character
- Each node, or branching point, of a tree should be based on synapomorphies.

Now let's look at some trees.

Types of Trees

- Some trees merely express order of divergence (cladograms). All 3 of these trees express the exact same information:



More Trees

- Some trees can indicate estimated time of divergence (some people consider trees that represent time as 'phylogenetic trees' reserving the term 'cladogram' for those trees that only express order of divergence)

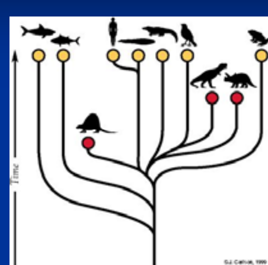
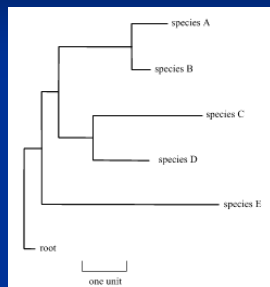


Figure 5. Phylogenetic tree congruent with cladogram in Figure 4. Redrawn from Carlson, 1995.

Even More Trees

- Some trees can indicate amount of divergence (or convergence) for a particular set of characteristics



Be sure you know how to 'read' a phylogenetic tree!

- *In the tree below: What taxon is most closely related to birds?*
  Are reptiles (which include lizards, crocodiles, and dinosaurs) a monophyletic group?
  Which taxon is least closely related to humans?
  Which taxon diverged first (longest ago) from the lineage that gave rise to humans?
  Which taxon has the least recent shared ancestors with humans?
  Of the organisms represented in this tree, do humans, whales, and demitrodons form a monophyletic group?

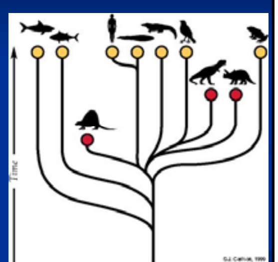
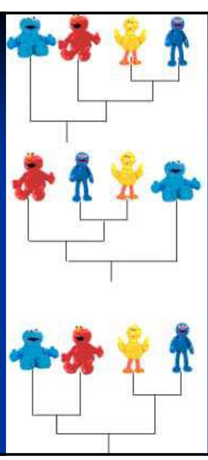
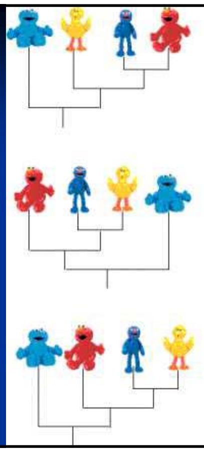


Figure 5. Phylogenetic tree congruent with cladogram in Figure 4. Redrawn from Carlson, 1995.



Quiz

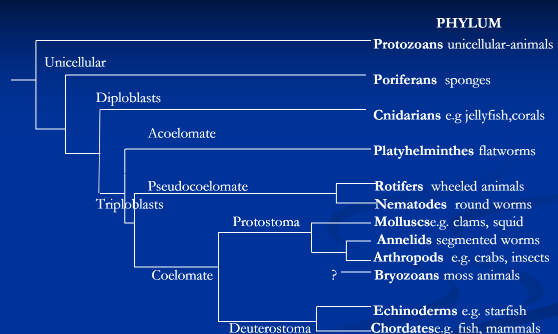
- *In terms of order of divergence, which of these trees is not like the others?*



Quiz Cont.

- *In terms of order of divergence, which of these trees is not like the others?*

A Traditional Tree

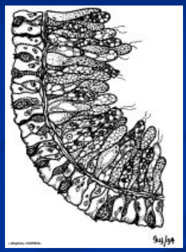


This tree is based largely on:

- Tissue organization
- Body symmetry
- Body cavity
- Development
- Other morphological characters

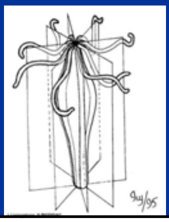
Tissue Organization

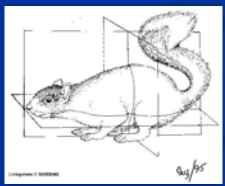
* **acellular** (unicellular)
* **diploblastic** - Animals whose body parts are organized into layers that are derived embryologically from two tissue layers: ectoderm and endoderm.
* **triploblastic** - Animals whose body parts are organized into layers that are derived embryologically from three tissue layers: ectoderm, mesoderm, and endoderm.



Body symmetry

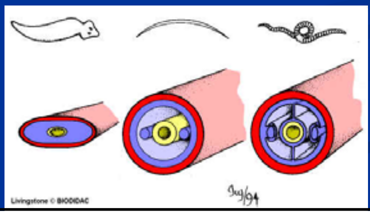
* **radial** - Animal body plan in which more than one imaginary plane through this axis yields halves that are mirror images of each other.
* **bilateral** - Animal body plan with mirror image left and right sides.





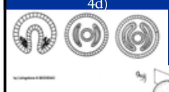
Body cavity

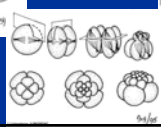
* **aceolomate** - having no body cavity (coelom) between the body wall and internal organs
* **pseudoceolomate (blastoceolomate)** - having a body cavity between the mesoderm and endoderm; a persistent blastocoel that is not lined with peritoneum
* **ceolomate** - having a fluid-filled body cavity between the gut and the outer body wall musculature that is lined with derivatives of the embryonic mesoderm.



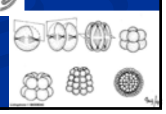
Development

* **Protostome**: animals whose development is characterized by: the mouth is derived from the blastopore
  - spiral determinate cleavage
  - schizocoelic coelom formation
  - the mesoderm is formed from a particular blastomere (called 4d)



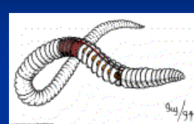


* **Deuterostome**: animals whose development is characterized by:
  - the mouth is not derived from the blastopore
  - radial indeterminate cleavage
  - often characterized by enterocoelous coelom formation
  - dipleurula-like larval stage



Other Morphological Characteristics

* **segmentation** (metamerism) - Division of the body along the anteroposterior axis into a serial succession of segments.



* **lophophore** - Tentacle-bearing ridge or arm within which is an extension of the coelomic cavity

Question

- The importance of many of the above characteristics in distinguishing evolutionary relationships among invertebrates has recently been seriously questioned.
- A question for future lectures: *Why might such characteristics not be useful (in fact, may be downright misleading) when constructing a phylogenetic tree?*

Problems

- The older phylogenetic tree (discussed in the previous lecture) has never satisfactorily placed the phyla that have a mixed set of deuterostome and protostome characteristics.
  - For example in the **Phylum Phoronida** where the blastopore forms the mouth (as in protostomes), but clevage is radial and indeterminate (as in deuterostomes).
- By 1990, many other characteristics traditionally used to construct this phylogeny were called into question. For example (based on Willmer's 1990 book, "Invertebrate Relationships") many of these traditional groupings could not easily be distinguished based on:
  - distinctive biological molecules (e.g. collagen, chiton, hemoglobin, sialic acid…)
  - larval types
  - structure of the cuticle
  - segmentation

A Tree???

- The final tree appearing in Willmer's 1990 book is quite unsatisfactory:

- While this tree is too "lawn-like" to be of value, the traditional invertebrate tree may be too linear where each more primitive group gives rise to the next more advanced group (not "bushy").

Does time truly tell?

- Linnaeus proposed his hierarchical classification scheme well before Darwin proposed natural selection.

What then was Linnaeus' system based on?

What is the advantage of an evolutionary-based classification system?

What are reasons why the old ways may not work?

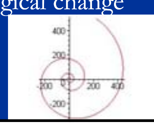
- Rates of evolution are not always constant
- Direction of evolution is not one way
- Traditional groups may be biased by the way we classify

Rates of Evolution

(Are closely related organisms always similar in appearance?)

- * Rapid environmental change should lead to rapid rates of evolution

- * Small changes in genes can lead to major morphological change



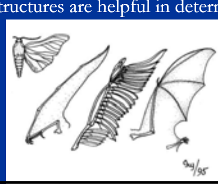
Evolution not always "forward"

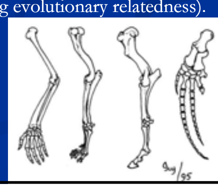
* **Convergent evolution**

(*Are organisms that appear similar always closely related?)*

Analogous structures - structures that are independently similar between two species that are not closely related; attributable to convergent evolution.

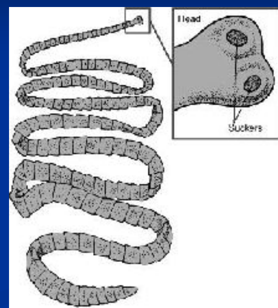
(as opposed to **Homologous structures** - structures in different species that are similar because of common ancestry - such structures are helpful in determining evolutionary relatedness).





Forward and yet Backward

* evolution sometimes results in structures becoming less complex rather than more complex. And some lineages have never evolved complexity



Traditional groups may be biased

<u>**“Schools” of classification:**</u>

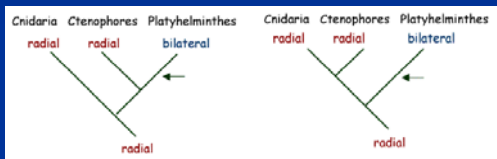
- **Phenetics** (numerical taxonomy)
  - Is not concerned with evolutionary relationships in its purest form and is based solely on numerous similar (shared characters) using computer algorithms to determine which groups are most alike. All characteristics are weighted equally regardless of whether analogous or homologous.
- **Evolutionary systematics** (classical taxonomy)
  - Characters are weighted differently based on suspected evolutionary value. Closeness of relationships is based on <u>both</u> **shared derived** and **shared primitive** characteristics
- **Cladistics** (phylogenetic systematics)
  - Similar to evolutionary systematics in that characters are weighted differently based on suspected evolutionary value, however closeness of relationships <u>based solely on **shared derived** characteristics</u>. Strict rules are applied (multiple trees are calculated with sophisticated computer algorithms and the one that uses the least number of convergent evolutions is considered best). The method is dependent on correctly identifying the true ancestral conditions from which other characteristics are **derived** (apomorphic) versus **primitive** (plesiomorphic).

Tests of Phylogenies

- Methods of phylogenetic analysis:
  - Maximum Parsimony
  - Distance (ie Neighbor joining)
  - Maximum likelihood
  - Bayesian analysis

Application

- If shared <u>primitive</u> characteristics are used, for example symmetry:

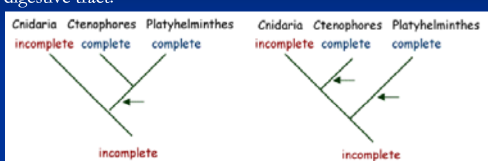


*Where did **bilateral** symmetry evolve and how many times?*

Which of the two trees above is a simpler (most parsimonious) explanation?

More Application

- If shared <u>derived</u> characteristics are used, for example complete digestive tract:



Where did a complete digestive system evolve and how many times?

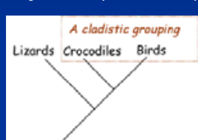
Which of the two trees above is a simpler explanation?

Therefore, which is better to use, shared <u>primitive</u> or shared <u>derived</u> characteristics?

This assumes that we are sure incomplete digestive tract is truly primitive. *How do we know this?*

Cladists

- Cladists insist that boundaries for groupings be based strictly on evolutionary sequence of divergence produced by cladistic analysis.



i.e. A cladistic classification system attempts to group organisms together only into **monophyletic** taxa. Even though lizards and crocs share a lot of primitive characteristics, shared derived characteristics indicate a more recent common ancestor between crocs and birds. "Reptiles" as a group are **paraphyletic** in that some members have a more recent shared ancestor with a group outside that taxon than with some members within that group. A cladist would object to such a taxonomic grouping.

The Cladist's Argument

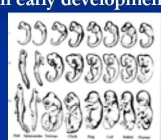
And because cladistic analysis can produce different (and cladists might say 'truer') phylogenetic trees, traditional invertebrate groupings (that were not based on cladistics) may contain paraphyletic groupings that do not correctly represent evolutionary relationships.

In other words, some of the problems with the traditional phylogeny may have arisen from basing groupings on shared primitive traits.

For example, can we assume protostomes are all more closely related to each other than to dueterostomes given that protostome characteristics are considered more primitive? Can we assume dueterostomes are all more closely related to each other than to protostomes given that dueterostomes characteristics are considered more derived?

Can we really tell?

- ***How can analogous and homologous structures be distinguished (as well as primitive and derived)?***
- **Concentrate on early developmental characteristics.**



- Ernst Haeckel's - "Ontogeny recapitulates Phylogeny" While rejected in its purest form, it has been considered a reasonable assumption that evolution will less successfully modify early stages of development.
- Therefore, early developmental characteristics should be more useful.

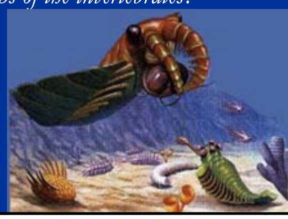
Warning on use!

- However, may not always be a good assumption for two reasons:
  - Genes regulating early development can undergo evolution - Only "less likely", not impossible
  - Genes regulating later development can be de-activated (not expressed) - **Neotony**

Another way to polarize

- **Examine paleontological (fossil) evidence of ancestors**

Why not turn to the fossil record to resolve all evolutionary relationships of the invertebrates?



Tools to Build Trees

- Improved fossil record
- Molecular sequence data
- Amino acid sequence data
- Regulatory gene data
- Morphological/Behavioral data

Improved Fossil Data

- **Improved fossil data**
  From Cambrian fossil bed that preserved soft bodied animals. Very specialized conditions lead to fossilization of soft-bodied. Major soft-body beds:
- Burgess Shale - Canada
- Chengjiang - China

Anomalocaris

Misszhouia longicaudata

Molecular Sequence Data

- Molecular phylogeny is based on comparing the sequence of molecular subunits (e.g. nucleotides of RNA or DNA)

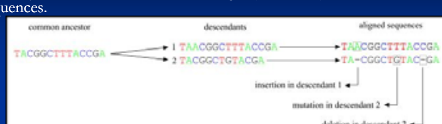
  Sp. 1: **ACTGCGCTG**
  Sp. 2: **ACTGCGCAG**
  Sp. 3: **CCTCCGCAG**

  Molecular phylogenetics is no different in principle from inferring phylogeny from the similarities in morphology. Many of the same methods are applied to both molecules and morphology.

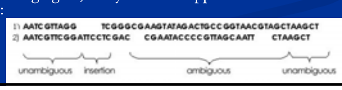
Advantages to DNA

- An 'independent' method to compare to results from other methods
- Relatively easy to generate large data sets
- May, in particular cases, be able to resolve in morphological uncertainties due to problems such as:
  - **Convergent evolution** (there are many molecular ways to produce the same adaptation and because natural selection is based on random mutation, it is unlikely that the same exact molecule will evolve twice - e.g. bioluminescence).
  - Major morphological change that have little genetic basis.
  - Genes not expressed, as in neotony, are still present.
- Molecule of choice in many in invertebrate studies has been **18S rRNA** (or 18S rDNA) b/c there are sufficient base pairs (~1800) and it evolves at an appropriate rate for studying distant relationships.

Problems

- Convergence can still occur
- Not easy to determine number of changes (mutations) between two sequences.
- 

- Numerous mutations are possible (reversals, substitutions, insertions, and deletions of bases) make alignment difficult. What might initially appear as two very different sequences may be the result of a single mutation.
- For example:
- **ACTGCGCTG**
  ATCGCGTCG
-
  In the following figure, many mutation appear to confound attempts to align sequences:



DNA is not everything

- Nucleotide sequences are not necessarily related to morphological differences so that tells us nothing of the appearance of ancestral forms or how variations in form arose. *Is one DNA sequence simpler than another?*

  "Molecular phylogenetics does not necessarily provide the correct phylogeny, but it can help eliminate incorrect ones and can suggest alternative hypotheses that otherwise might not have been considered." - C. Leon Harris, Department of Biological Sciences, State University of New York

Amino Acid Sequences

- Analyzed in much the same way as DNA/RNA
- Has many of the same advantages and disadvantages.
- Some argue that the functionality of proteins makes them more useful, while others argue that proteins lose clarity due to redundancy in the code.

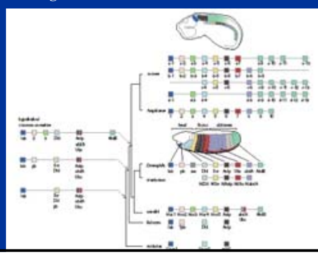
Regulatory Gene Data

- Important morphological features are not necessarily associated with the particular differences in DNA measured in above studies (and not likely to be). **Hox genes** provide a way to examine genetic changes that are related directly to major morphological (body plan) differences.

  How does the sequence of nucleotides of DNA differ among cells within a multicellular organism?
  What is the challenge in making a multicellular organism?
  sticking cells together?
  directing cells to develop differently?

Hox genes

- In recent years, researchers have identified as class of regulatory genes (homeobox) known as ***Hox* genes** (developmental regulatory genes that occur in clusters; they are best characterized in segmented animals, where they control the identity of each successive body region depending on anterior-posterior position).
- *Hox* genes occurring across most animal phyla have the same basic arrangement indicating a common multicellular ancestor from which these groups arose.



Hox genes

- *Hox* genes appear to provide flexibility of design because the basic (original) gene has been repeated and modified within organisms to initiate very different development sequences along each body region of an organism,
- *Hox* genes only designate and <u>initiate</u> a body region's development and other later regulatory genes determine the details of develop with that region.

- *i.e. organisms that share some Hox genes for a given region are not identical for that region*
- "Thus the striking changes in body plans have been accompanied by relatively modest tinkering with the machinery of early development of that long-extinct precursor".

Importance of *Hox* genes

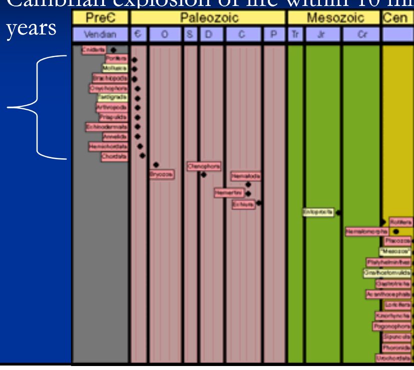
- By understanding the connection between molecular and morphological differences, this line of study preserves the advantages of molecular phylogeny while potentially resolving orders of divergence and reconstructing ancestral stages. *Hox* gene analysis can objectively separate out basic differences in major body plans that might be obscured by morphological features determined by later regulatory genes along the developmental cascade.
- May explain quickness of Cambrian explosion and why new body plans have been slow to arise every since.

Bottom line when constructing phylogenies

- All available evidence must be considered and weighed. **Confidence comes when there is significant agreement among independent evidence for a particular phylogenetic scheme.**
- Using multiple techniques reveals a preponderance of homologous structures in some taxa (indicating relatedness), and scattering of analogous structures that are 'built' differently (indicating the importance of certain adaptations to solve certain environmental problems in a limited number of ways).

Early History of Evolution

- Cambrian explosion of life within 10 million years



Important Discoveries

- Recently, several important fossils discoveries have extended the length of time over which this diversification occurred .
- They will follow in reverse order in which they occurred in the record.

Cambrian Macrofauna

- First fully skeletonized organisms and organisms with distinct limbs became more and more abundant during the Early Cambrian
- First appearance of mineralized skeletons of such phyla as:
  - Mollusca,
  - Brachiopoda
  - Arthropoda
  - Echinodermata
  - Cnidarans

- Furthermore, soft-bodied phyla, also make their appearance such as:
  - Annelida - Polychaeta and Priapulida
  - Onycophora
  - Ctenophora
  - Porifera
  - Chordata

- As well as other taxa that can not be confidently placed into modern phyla (*is this a problem?*).

First shelly faunas

- The first evidence of animals with hard parts are fossils that are small (generally 1 to 5 mm) and only parts of organisms that appear in the middle part of the Early Cambrian.

- Later small shelly fossils - sclerites of worm-like animals or as early representatives of the major fossil groups.
- Early small shelly fossils - tiny tubes, spines, cones and plates that are not clearly allied with modern groups.

Earliest "trace" fossils

- Burrows and intense disturbance of sediment layers (as far back as the late Neoproterozoic; clear indications of trace fossils as early as 570 million years ago and indication of the origin of bilateral symmetry at 555 mya with a rapid increase in size and the presence of vertical movement at ~544 mya). Burrowing would require a level of body differentiation and coordination associated with many phyla known today.

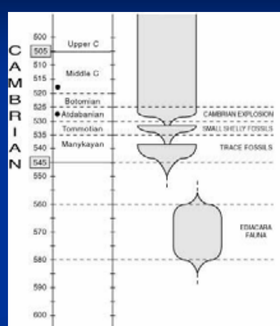
- Trace fossils support rapid diversification though they suggest that diversification was spread out over a longer time period than indicated by typical hard-bodied Cambrian fossil assemblages.

Ediacara “fauna” (Vendobionta)

- Quilt-like body plans forming feathery fronds, pouches, disk and worm-shapes, without heads or obvious circulatory, nervous or digestive systems (Late Proterozoic to the Middle Cambrian).

Current “Explosion” a little longer

- 40 million years now considered by many as the length of time from first multicellular animals to appearance of most major phyla.
- This is still relatively short in geological terms.
- *Given that diversification appears to have occurred over a scant 40 million years (over 600 million years ago), can we reconstruct the relationship among these phyla?*



What does phylogeny tell of evolution?

- **Taxonomically**, *could life today have been very different if past circumstances had been slightly different? Does the bizarre diversity of the Burgess shale and the subsequent branching of major taxa suggests that life on earth as it is today may have been very contingent on past extinctions* (Gould’s “Wonderful Life”)?

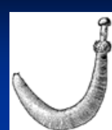
- *Or did most major body plans (i.e. phyla) arise early in multicellular evolution and survive to today? If so what does this suggest about constraints on evolution (Simon Conway Morris's The Crucible of Creation)?*

What does phylogeny tell about evolution?

- **<u>Ecologically</u>**, life today and in the past has change very little. Regardless of the potential taxa available, general niche space in ecological systems appears limited as indicated by similarity of fauna <u>ecologically</u> but not taxonomically over history of animals and by the commonness of convergent evolution. For example:
  - Reef buildering taxa differ depending on geologic era (sponges, algae, bryozoans, brachiopods, corals)

- Burgess fauna <u>ecologically</u> similar to modern day aquatic environments (from SC Morris' "Crucible of Creation").

  Mud-dwellers (infuana , modern equivalents - polychaete worms…):



  Mud-stickers (sessile epifauna, modern equivalents -sponges, oysters, bryozoans…):

  Strollers, walkers, and crawlers (mobile epifauna, modern equivalents - crabs, shrimp…):

  Swimmers and floaters (nekton and plankton, modern equivalents -fish, jellyfish…):

The Bottom Line

- Populations are opportunistic, but constrained within ecological and evolutionary boundaries (but some body plans have allowed some taxa to jump across such boundaries).