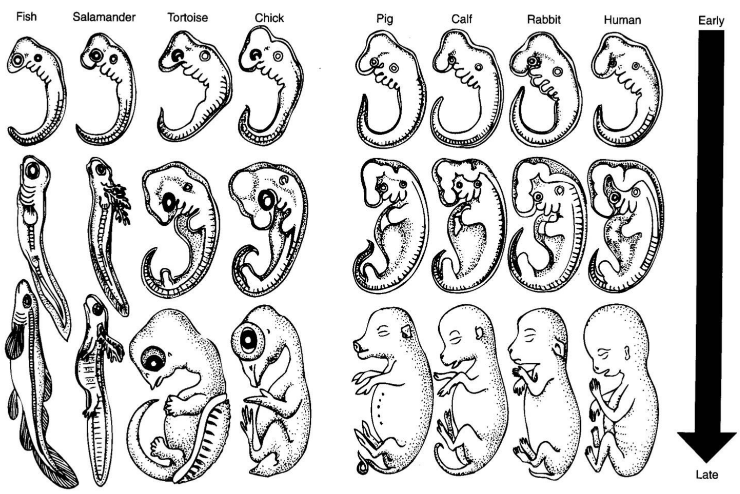
Evolution

From Level 1:

1. History of evolutionary ideas – long before Darwin (from Plato to Lamarck)
2. Darwin's key contribution - Providing credible mechanism for process of evolution: Natural Selection
   - Differential survival of phenotypes (diff forms within species), how many offspring do they produce
3. Examples of selection in action from breeding domestic livestock, industrial melanism, Darwin's finches
4. Geological time and context of evolution (environmental change)
5. Major radiations (e.g. Cambrian, Paleozoic, Modern) and mass extinction (e.g. Cretaceous)
6. Mechanisms of evolutionary change (evolution of diversity in natural pops, genetic drift)
7. Types of selection (directional, balancing, disruptive)
8. Speciation (allopatry - barrier, parapatry - neighbour, sympatry - same area)

Molecular Control of Evolutionary Change

Interaction between developmental bio and evolution



Back to Basics: Intro to Pop Genetics, Genotypes and Hardy-Weinberg Equilibrium

Variation in phenotypes is what drives change - How does it work on a mathematical level

Fundamental Process: Genetic Drift (random process - change), Natural Selection

Understanding radiation of species - Phylogenetics

- Seq. of events involved in evolutionary development of species or taxonomic group of orgs
- Evolutionary development and diversification of species or group of orgs, or of particular feature of an organism
- Relationships discovered through phylogenetic inference methods that evaluate observed heritable traits, such as DNA sequences or morphology under a model of evolution of these traits

Species Radiations and Relevant Processes

Why scientific names -
Scientific names track scientific discussion about taxonomic classification and evolution – that is, you can tell from the scientific name who the close relatives are thought to be, and something about the degree of relatedness between them (e.g. same subspecies or same genus or same family…etc.)
Scientific names sometimes honour those who discovered the species in question, but even that can be useful, as it tells you when the classification was made.

What is a species and how to define and classify them - How do new species evolve ?

Invertebrate Radiations - Evolution of the Metazoans (animals and early invertebrates)

The evolutionary origin of land plants from algal ancestors

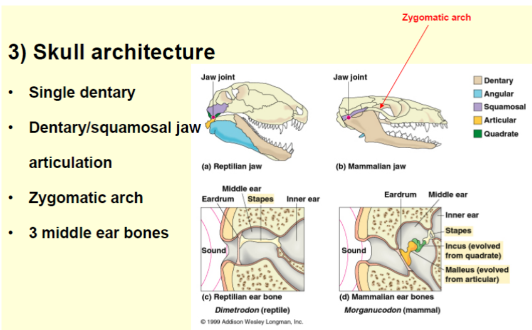
Role of P/S

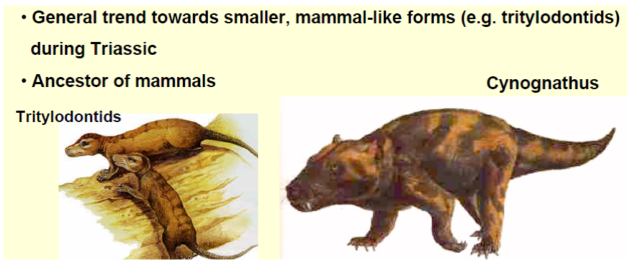
Endosymbiosis - Theory explain origin of eukaryotes cell from prokaryotes -> Several key organelles of eukaryotes originated as symbiosis between separate single-celled orgs

Co-Evolution - Angiosperm flower and pollinators (insects and plants)

Why did Sex Evolve - Why so complicated in plants ??

Earliest Vertebrates
- Radiation of fish
- Radiation of reptiles
- Evolutionary origin of birds – how new fossils and innovative research techniques settled an old controversy
- Evolution of mammals
- Mamalian Radiaiton - Ear and jaw shape defining characteristics





Evoltion of Marine Mammals - From sea -> land -> back to sea evolution

Sexual selection and male comp

How to Understand Evolution

1. Understand key processes
2. Be able to illustrate your understanding with relevant examples (either from the lectures or from reading)
3. Be able to integrate information from across the course – e.g. to understand pattern based on process
4. Be able to demonstrate understanding of key points of inference based on relevant details

Tetrapod Evolution

Macroevolutionary Processes - Major evolutionary change (we evolved from bony fish)

Have legs – will travel! The evolution of land-dwelling vertebrate tetrapods from fish

Ordovician (488-444 MYA):

- Continued marine evolutionary radiation
- Lil change on land and freshwater
- Lacked multicellular plants
- Particular radiation of molluscs (including large cephalopods - head-feet), Brachiopods (phyla) and Echinoderms
- Massive glaciers over Gondwana (sea lvl drops by 50 m - water cooled)
- Mass Extinction - 75% animal species

Silurian (444-416 MYA):

- Marine life rebounds
- Marine vertebrates - Jawless fish abundant

- Late Silurian: First terrestrial vascular plants with roots and leaves
- Provided vegetation and food (habitats and food), soil develops
- First terrestrial arthropods - Scorpions, Millipedes
- More habitats and resources for animals to utilise

Devonian:

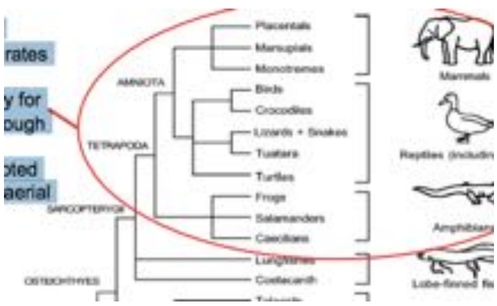
- More diversity and complexity of early plant life
- Terrestrial fungi and small arthropods - Creates simple food webs
- Spread further inland and away from water

- Middle Devonian - More derived plans established
- Expansion of arthropods and insects (millipedes, springtails and scorpions)

- Late - Terrestrial vertebrates appear
- Utilise land if get out of marine envi
- Significant plant life with large leaves (Giant horsetails and club mosses)

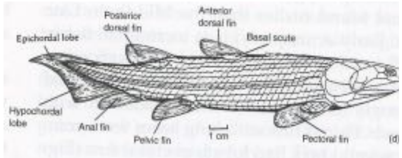
Envi Changes:

- Drop in CO_2 atmospheric levels
- Devonian dry periods (droughts) - Reduce shallow water areas
- Oxygen: shallow coastal lagoons
- Subject to changes in water level as temp change

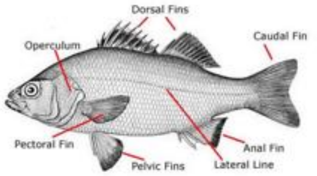


Fish Classification and Diversity

Early Osteichthyes (Bony fish):

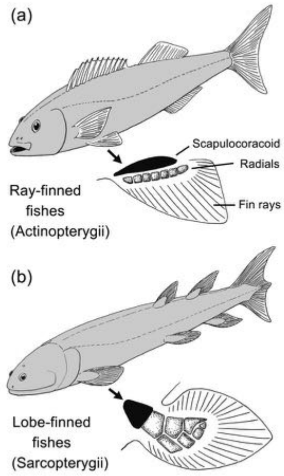


Devonian - Long periods warm, shallow brackish seas and swamps, much organic material deposited in shallow areas - Low O2 availability



Evolution of air-breathing for oxygen - Vascularised pouches off foregut = Simple lungs
- Esp. in sarcopterygiian (lobe-finned) retained functional gills, supplying much oxygen

2 Major Groupings in Bony Fish



1. Ray Finned - Fine bones linked to pectoral girdle
2. Lobe Finned (Sarcopterygiian)
   - Abundant in Devonian
   - Additional substantial limb like bones to pectoral girdle (key feature - limb like)
   - All tetrapods are sarcopterygians or descendants of them

4 Existing Genera of Sarcopterygiian:

Protopterus, lepidosiren, neoceratodus (all dipnoi) and latimeria (coelacactinistia)

Sub-Class: Dipnoi (lung fish - paired fins)

- Paired simple lungs - From highly vascularised invaginations from oesophagus
- Skull - No transverse joint (tetrapod fossils, living amphibians do)
- Ossification (bone-formation) reduced - Less protected, lighter
- Specialised crushing fan-like teeth
- Exhibit aestivation (hibernation)
- Paired openings in top mouth like internal nostrils (found in amphibians)
- Lack similarity between paired fins and tetrapod limbs - highly derived

Sub-Class: Coelacanthinii

- Early relatives had lungs and lived in shallow waters
- Inhabits deep sea locations

Extant Coelacanths (pre-historic):
- Free-swimming, marine predators
- Dorsoventral flexion skull
- Possess paired lobed fins (and distinctive tail anatomy)
- Moves limbs same order as tetrapods, forelimbs alternatively - Humerus, radius and ulna
- No internal nostrils (choanae)
- Coelacanth DNA less similar to Amphibia than lungfish
- Similar to terrestrial organisms

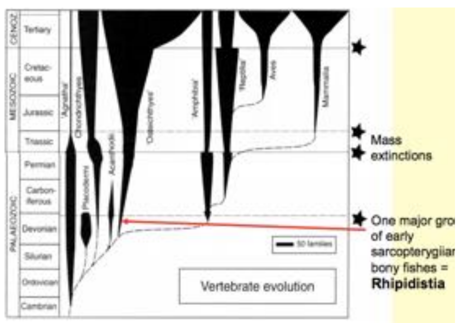
Vertebrate and Early Tetrapod phylogeny from fossil record

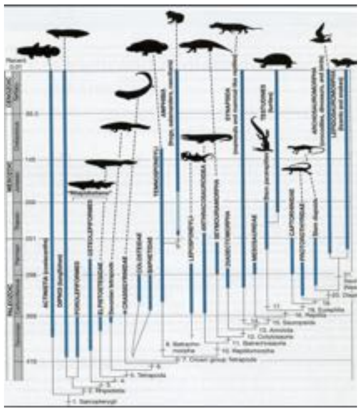
- Fish to amphibians
- Lobed fins sister groups to amphibia (first tetrapod groups)

Consensus Cladogram of Main Extant Vertebrate Groups

Tetrapoda – Air breathing vertebrates, 4 limbs, adapted for terrestrial life [though some secondarily adapted to aquatic or aerial lifestyle)

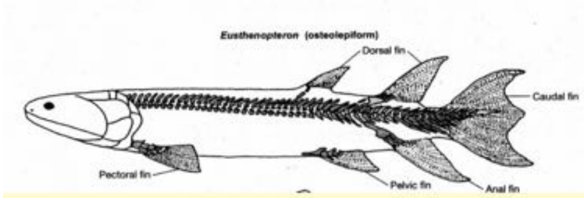
Rhipidistia (early sarcopterygiian bony fishes)





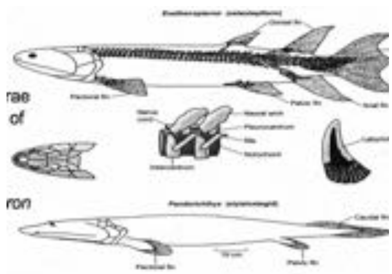
- Simple lungs and internal nostrils (choanae - like amphibia)
- Likely link between tetrapods and aquatic envi
- Free-swimming predators
- Heart - Separate pulmonary and systemic circulations (link with lung evolution)
- Lobe fins (paired pectoral / pelvic 'limbs' and girdles)
- Dorso-ventral flexion of skulls and amphibian-like teeth like extant Amphibia

Phylogentic Relationships of Sarcopterygiian fishes and tetrapods



<u>Devonian Rhipidistian Lungfishes (ca. 390 MYA)</u>

<u>Eusthenopteron (Osteolepiform):</u>
- Cylindrical body
- Short snout
- 4 unpaired fins and paired pectoral and pelvic fins
- Paired, crescent-shaped vertebrae
- Teeth with labyrinthine infolding of enamel



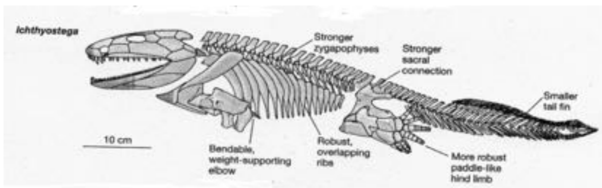
<u>Panderichthys (Elpistostegid - More recent):</u>
- More derived than Eusthenopteron for shallow water life - (aka. terrestrial life)
- Eyes on top of head
- Flattened skull
- Lose dorsal and anal fins
- Reduced tail fin
- Body and head flattened dorsoventrally
- Sister-group to tetrapods

<u>Hypotheses for origins of first tetrapods….</u>

<u>Drying Pond Scenario - Theory:</u>

- Tetrapods arose from lobe-finned fishes
- Devonian droughts -> Driven evol. of air breathing in fishes -> Onto land
- Natural selection favours more terrestrial fish (locomotion, capacity to breathe/live there)
- Lungs for air breathing - Longer survival out of water for longer (no gills)
- Early movement onto land —> Evolution to tetrapods
- Terrestrial - Bear weight, no support by aquatic medium
- Fish-like tail

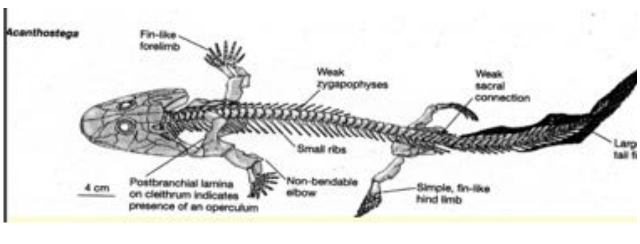
Fossil Ichthyostega (Devonian) - Well-developed limbs like carboniferous amphibians, no gills, fish-like tail

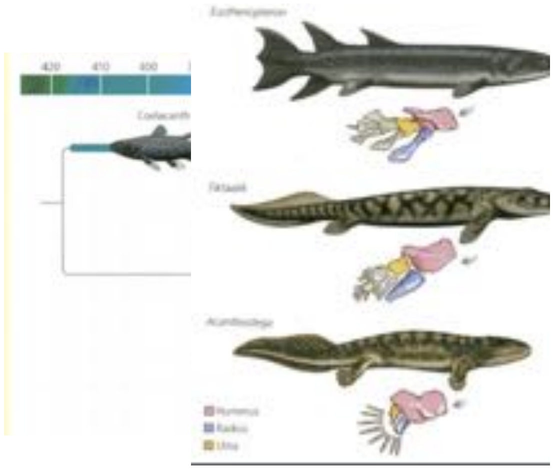


<u>Fish With Legs Scenario - Theory:</u>

Gradual change of adaptations from aquatic forms before colonisation of land during stable habitats

- Discovery fossil skull - Acanthostega
- Fossils (ca. 360-365 MYA) contemporaneous with Ichthyostega





- Acanthostega clearly tetrapod - Not well-adapted for land-life
- Retained internal fish-like gills - 'Fishapod'- Fish with legs
    - Smaller ribs - less weight carrying capacity
    - Knee and elbow joints not bendable
    - Vertebrae weaker
    - Large fish-like tail

Harsh unstable freshwater/terrestrial habitats of mid-Silurian and parts of Devonian succeeded by favourable ones with stable terrestrial habitats (with food)

<u>Missing link - Tiktaalik (intermediary form)</u>

- Clear link with full terrestrial forms and ancestors
- Intermediary form
  - Strengthening humerus (upper-arm bone)
  - Large pectoral fins - support
  - Flexibility in neck - Looking out of water
  - Shallow pond-like areas - hunts
  - ***Fish with legs more likely process for evolution***

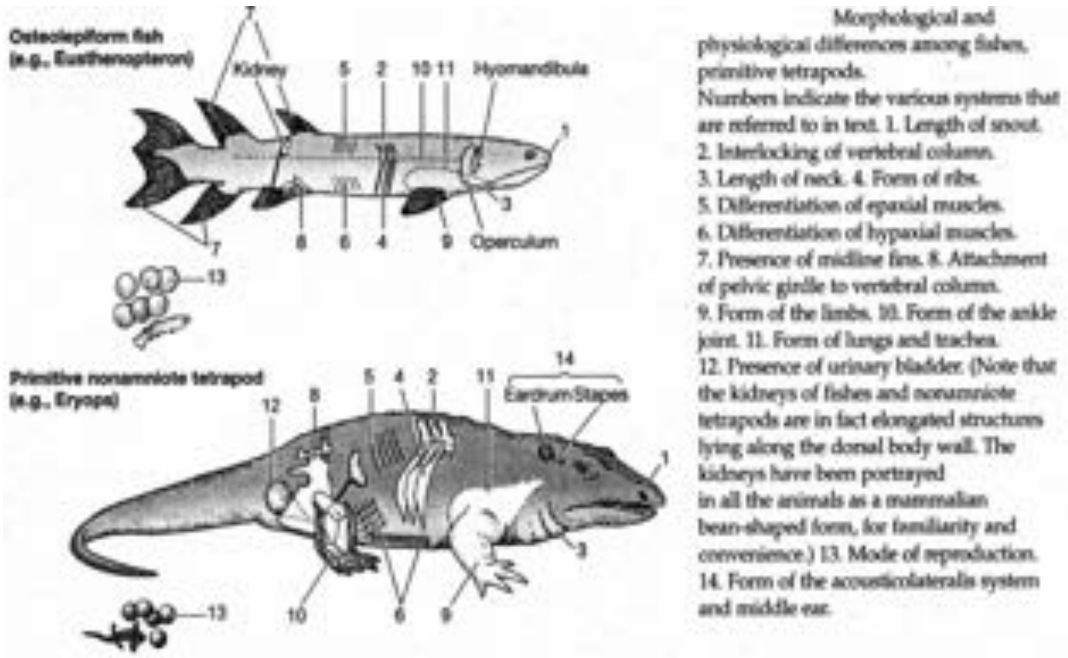
Late Devonian - Early stem tetrapods (aquatic) close to sarcopterygiian (lobe-fin) fish ancestors

Carboniferous - Most subsequent early tetrapod radiation, terrestrial conditions more favourable
- Late Devonian fishapod (highly derived elpistostegid) - 10+ M years before Ichthyostega and Acanthostega
- Lungs and gills, retained fins, lost opercula (gill cover bones) - Neck flexibility

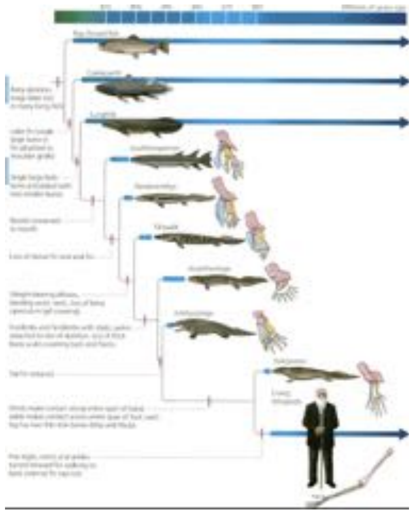
Evolution of Simple Lungs - Change from purely aquatic envi -> shallow ponds -> land (carboniferous)

<u>Key Evolutionary Diffs between fish ancestors and tetrapods</u>

Morphological and Physiological Diffs among Fishes and primitive tetrapods



- Stronger interlocking vertebrate - More robust skeleton framework for skeleton
- Larger more robust ribs

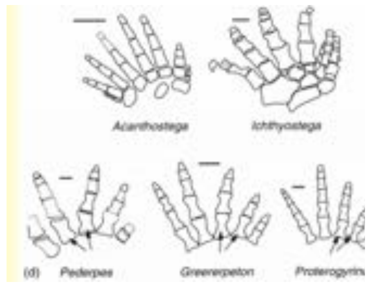


- Weight support
- Lobe fins into limbs (change bone structure)
- Sensory Capability - positioning of eyes and performance, hearing capacity (diff on land), ear bones
- Increased breathing ability - lungs
- Urinary bladder - excretion of waste

Development of Hands and Feet

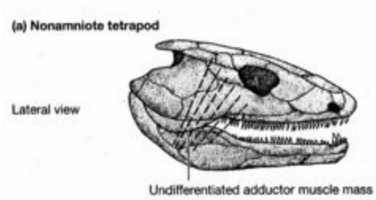
- Greater mobility and weight bearing capacity
- Change in regulating pattern of gene - HOX genes (limb development)
- All jawed vertebrates have 4 HOX clusters (A-D)
- Limb development - Expression of 5' Hox genes at posterior part of clusters (tips/feet/hands)
- Similar expression in fish/tetrapods at proximal part of limb/fin
- Regulation, rather than evolution of new genes
- Absence of genes in most bony fish - secondary loss

Bone Changes - Formation of Neck Region in Tetrapods



- Neck for head mobility - Greater range of movement - For land
- Aquatic medium - Flex body to move head
- Terrestrial - Body anchored to ground, head must move independently (flexibility in neck - lighter connection)
- Frees up skull (limb and shoulder girdle changes too)

Jaws and Muscle Attachment in Early Tetrapods

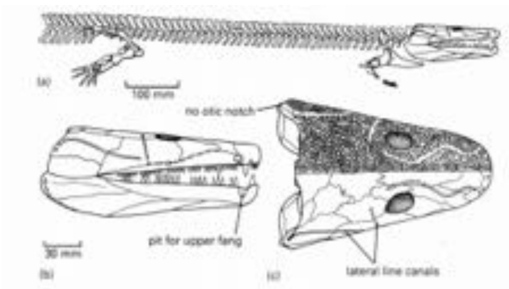


- Non-amniote tetrapod jaw limited force generating "snapping" undifferentiated adductor muscle mass
- Change skull form and more forceful static pressure bite in amniotes
- Jaws and muscle attachment in early tetrapods - weak jaws
- Greater muscular attachment -> More powerful jaw operation

Non-amniotic Tetrapod (i.e. Amphibian) Reproduction:

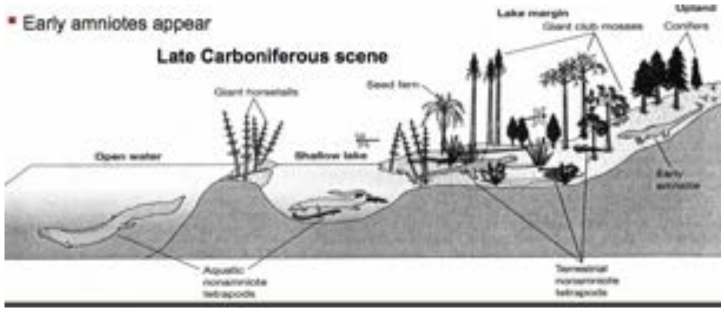
- Breathes air, forages
- Eggs permeable membranes - No protective barrier against desiccation
- Lifecycle completion depends on water or damp envi - Need moist /wet envi for egg laying
- Development dependent into aquatic medium - Larvae have gills
- Larval development in water (gas exchange across gills + integument), then metamorphosis to adult form (lungs + integument)

Divergence in Tetrapod Evolution…



A basal Tetrapod: Greereropteron (a Colosteid)

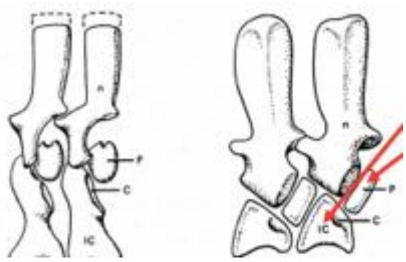
From lower Carboniferous
• Elongate body
• Broad tail
• Short limbs



- Skull & lower jaw flat
- Lateral line canals - sensing environment in aquatic medium and some weight support
- Aquatic?

Tetrapods diverged - Temnospondyls lie on the line to Lissamphibia and Lepospondyli lie on amniote line

Lisamphibia —> Modern Amphibians

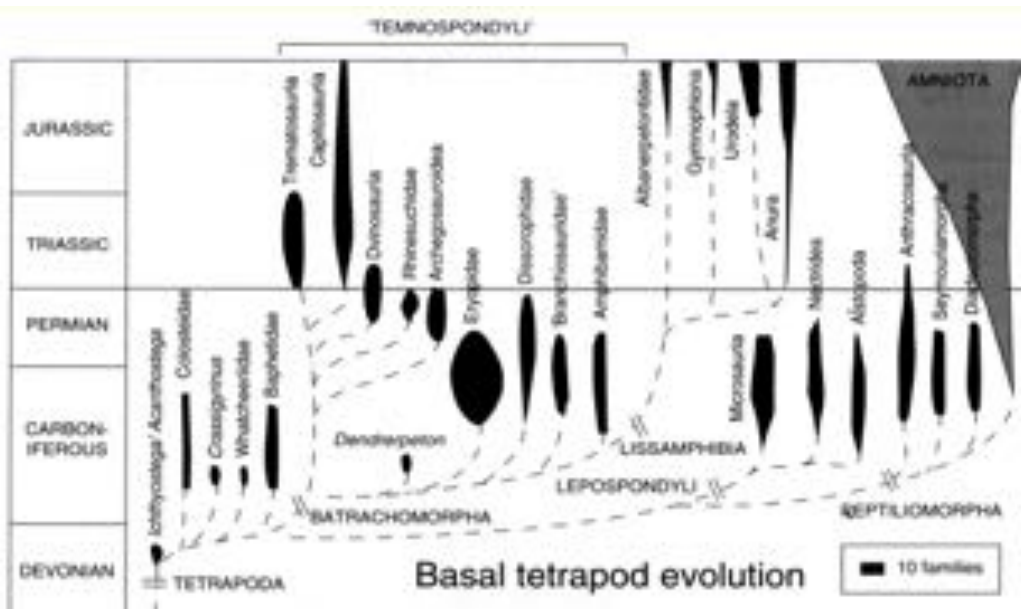


Intercentrum - Main element in Lissamphibia and temnospondyls

Pleurocentrum - Main element in Lepospondyli reptiliomorphs and amniotes

IC = Intercentrum; P = Pleurocentrum
N = neural arch; C = Rib articulation

Postulated relationships of basal tetrapod groups



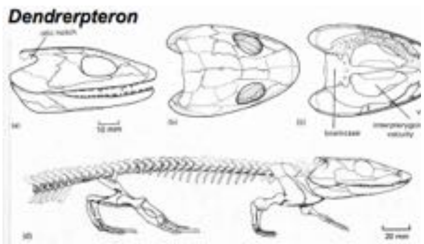
The Carboniferous

- Most preserved habitats represent swamp environs.
- Coal measures laid down
- Most land plants (not modern angiosperms) evolved
- Global drying in Late Carboniferous and Permian
- Conifers replace the spore-bearing plants.
- Terrestrial invertebrates diversify from early

- Carboniferous: Increased oxygen levels.
- Early Amniotes appear
- Selective advantage in amniotes
- Eggs protected in shell

Carboniferous Ecosystems

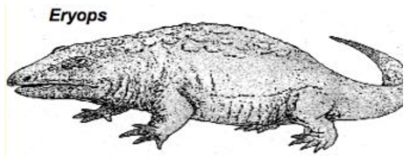
- Coal measures of midland valley between Edinburgh and Glasgow
- Hot springs heated by nearby volcanoes.
- Contains large collection of plants, arthropods, fishes and tetrapods.
- Contrasts with less abundant and less diverse late Devonian fauna
- Wide range of tetrapods including temnospondyls and some non-amniote
- Reptiliomorphs (e.g. Westlothiana) ancestry close to amniotes (reptiles & descendents)
- Documents a terrestrial vertebrate community & associated ecosystem



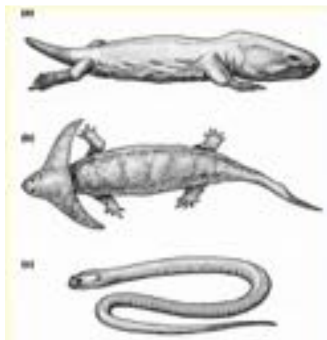
Temnospondyli

Main Carboniferous tetrapod group – survived through to Triassic after Permian, and with reduced diversity until early Cretaceous (150 MYA)

Dendrepteron / Tulerpeton:
- Broad, rounded skull
- Arms stout, Girdles strong
- Stapes (ear) present
- All indicate largely terrestrial animal



Eryops
- Well known Permian temnospondyl
- Heavier limbs, more massive skeleton, 2m long
- Short skull, Large orbits, Large ear-drum
- Fully terrestrial, top carnivore on smaller tetrapods (also fishes?).

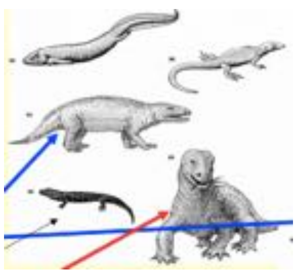


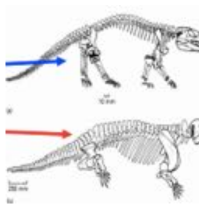
Lepospondyl and Reptiliomorph Tetrapods

Lepospondyls: Smaller tetrapods on evolutionary line to amniotes (reptiles +)

Abundant until mid Permian

a) Pantylus - Terrestrial early Permian microsaur. Microsaurs: largest group, variable life-styles – some were burrowers
b) Diplocaulus - Aquatic, early Permian. Newt-like appearance. Some with dramatically expanded skulls – hydrofoils for lift?
c) Ophiderpeton - An aquatic or burrowing form. Aistopod group.





Tetrapod reptiliomorphs (nonamniotic), closely related to reptiles

a) Poliderpeton (an aquatic species)
b) Gephyrostegus a terrestrial late Carboniferous species
c) Seymouria, a terrestrial early Permian carnivorous species
d) Diadectes, a terrestrial early Permian herbivorous species
e) Westlothian

Extant Amphibian Groups – Lissamphibia, 3 orders

Order: Urodela (Caudata) – salamanders and newts ~350 species; most with external fertilisation and aquatic larvae

Order: Anura – frogs and toads ~ 3500 species; most with external fertilisation but some with direct development (hatch from egg as miniatures of adult form) / internal fertilisation

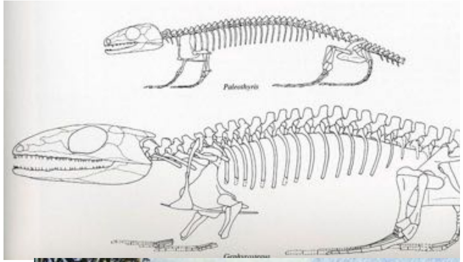
Order: Gymnophiona – caecilians ~ 170 species; many terrestrial with aquatic larvae, some terrestrial and viviparous (give birth to live young) or oviparous (animal lay eggs - little or not other embryonic development within mother) (DD) with internal fertilisation

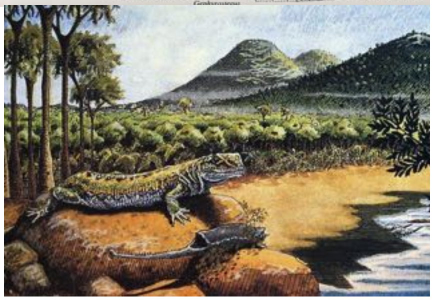
Modern Amphibians - Extinction and conservation

Amphibia appear one of most sensitive groups to widespread extinction in recent times, with a wide variety of species having become extinct or very rare, especially in the tropics where they are most diverse.

Causes:
- Habitat damage, exploitation
- Non-native species introductions
- Climate change and UV radiation
- Disease; transfer of new disease
- Endocrine disruption effects
- = Anthropogenic causes

Reptilian Evolution





Rise of Reptilian - Conquering land

What macroevolutionary traits enabled reptiles to conquer terrestrial habitats?

How did reptiles radiate and colonise water and air?

Is 'Big and Bad' evolutionarily more successful than 'Small and Meek'?

> Example - Marine reptiles (mostly extinct), Stem Reptile, Dinosaurs, Extant Reptile

Consensus cladogram of main extant (existing) vertebrate groups

Reptiles - Part of tetrapods (first four-limbed vertebrates) and amniotes

Including Birds - Birds, Crocodiles, Lizards + Snakes, Tuatara

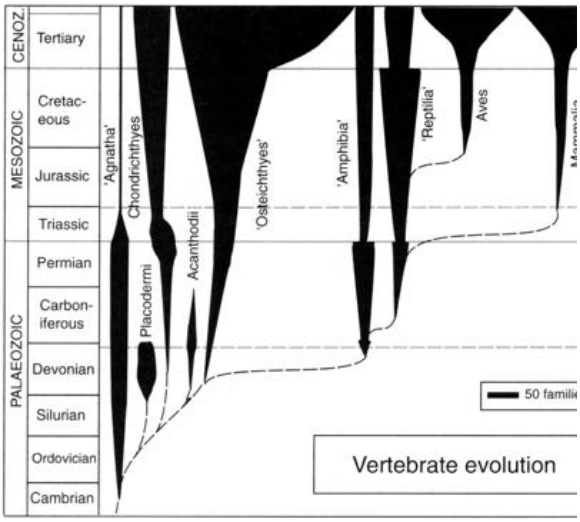
Amniotic, air breathing vertebrates with 4 limbs, adapted primarily for terrestrial life, phylogenetically include birds, but often separated because modern reptiles are ectothermic but birds are endothermic

Amniotes - Lay eggs on land or retain fertilised egg with mother, tetrapods, characterised by having egg equipped with an amnios (adaptation to lay eggs on land rather than in water as anamniotes)

Ectothermic - Org which internal physiological sources of heat relatively small or negligible (cold blooded), depend on external source of body heat

Endothermic - Warm blooded animals, maintain constant body temp independent of envi (birds, mammals and some fish)

Vertebrate Phylogeny From Fossil Record



2 Mass Extinctions occurred

1. End of cretaceous
2. End of permian

Radiation occurred after second extinction (following cretaceous)
Gaps partially filled by rapid radiation of birds and mammals

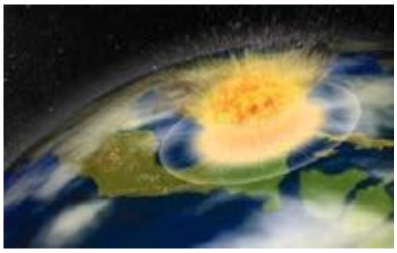
What is a Reptile?

- Ectothermic ("cold-blooded") tetrapod craniates (skulled) breathe using lungs
- Dry scaly skin (impermeable integument), less water loss
- Lay large, shelled amniotic (=cleidoic) eggs, shells protects eggs and prevents desiccation

- Present in all types of terrestrial biome, mostly in tropics (warm envi); many secondarily freshwater and marine species
- Secondary adaptation to freshwater and marine environments
- Colonise drier envis

- About 6,500 living species

- Fossil record from early Carboniferous, with peaks in Jurassic and Cretaceous (Mesozoic Era). Abrupt decline in diversity at end of Cretaceous….. (K-T event)



Fossil Reptile - Top
Amphibian - Bottom

Greater articulation at back of reptile skull

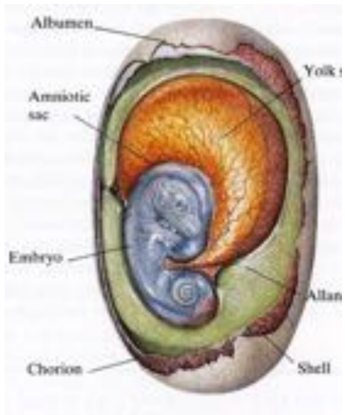
<u>Adaptation to Life on Land</u>

Improved skeleto-muscular arrangement

- Improved skeletal arrangement
- Greater head articulation at neck; neck elongation
- Skeleton giving greater support, including modification of pectoral and pelvic girdles to provide more upright stance, enabling body to be raised off ground and to walk/run more efficiently
- For foraging and hunting
- More support of limbs by skeleton
- Connection of limbs to pelvic and shoulder joints
- Upright posture - More rapid movements and diversity

Waterproof Skin

- Multiple-layered skin produced by division of epidermal cells, with waterproof keratinized older cells forming scales impervious to water
- Rate of water loss through skin greatly restricted, compared with amphibian skin
- Waterproof skin also adaptation to aquatic and marine life.



Amniote Egg

- Allowed early reptiles to colonise drier habitats
- Produced after internal fertilisation
- Fewer eggs produced than amphibians
- Semi-permeable (gas-permeable) outer shell - Permeable for gaseous exchange
- Hard, mineralised outer (tougher) covering but leathery in some lizards, snakes and turtles
- Shell protects internal fluids from evaporation and protects embryo from physical damage
- Amniotic membranes, forming fluid-filled sacs – amnion protects embryo; yolk sac encloses food supply; allantois sequesters wastes (solid uric acid) – all enclosed in chorion
    - Excretion of wastes into allantois

- Embryo develops using nutrients from yolk sack
    - Larger yolk sack - Longer development
    - Constraint how long embryo can develop - Size of allantois dependent
    - Chorion - Allows gaseous exchange
- Oviparous = Egg Laying. Some reptiles became ovoviviparous; retain eggs internally where they hatch; give birth to live young
- Oviparous reptiles lay amniotic eggs (hard shell, special membrane prevent embryo drying out)
- Viviparous - Give birth to live young (live-bearing)
- Allowed reptiles to be more independent of water
- Not tied to wet areas to reproduce
- Higher cost to produce eggs - Fewer young produced compared to amphibians

Physiological Water Retention

- Water loss during excretion minimised by excretion of almost insoluble solid uric acid
- With water reabsorbed from urine and faeces through wall of cloacal chamber
- Excretion of fairly solid uric acid
- Withdraw water from urine and faeces - Retain for physiological processes
- Less water loss through excretion

Adaptations to Ectothermy

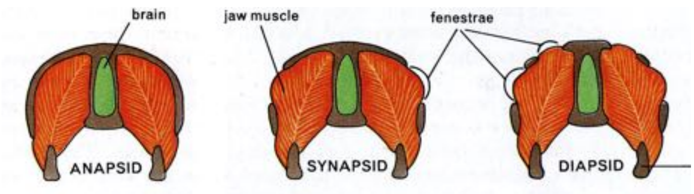
- Behavioural Adaptations – Sun-basking, with orientation varying depending on level of incident radiation
- Some burrow or lie in water to avoid overheating
- Basking or in sheltering in shade

The Evolution of Temporal Fenestra - Skull Openings

Temporal fenestrae evolved in reptiles to allow expansion of jaw muscles to give greater freedom of movement; happened differently along 3 evolutionary lines. Aids recognition of phylogeny in fossil record to current day.

Temporal fenestrae - Large holes in side of skull

- Openings in skull allows greater freedom of movement of jaw
- Increases surface area for muscular attachment
- Bigger more powerful muscles
- More variety in how jaw is used



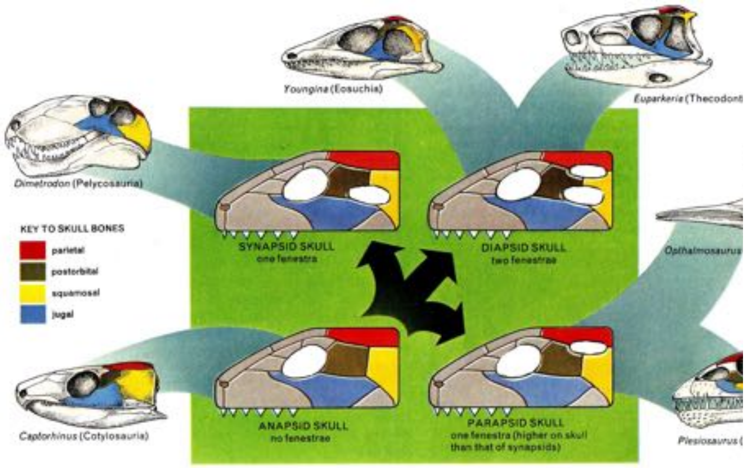
Cross sections through skulls with an increasing number of fenestrae, showing how the jaw muscles are given greater freedom of movement

Anapsid Skull - No fenestrae

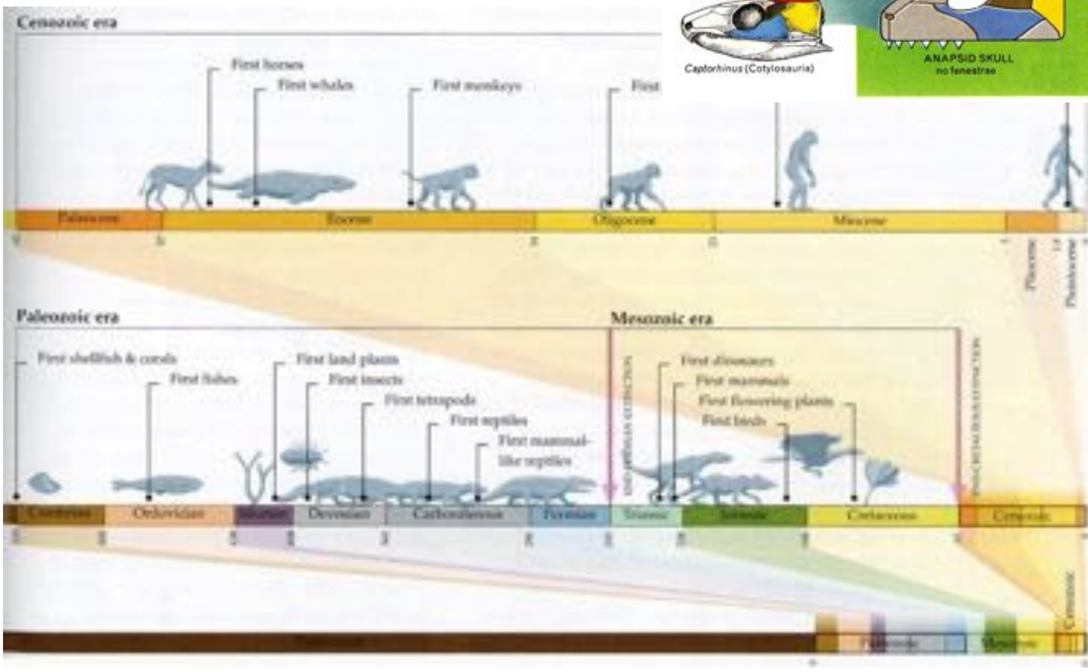
Synapsid Skull - 1 fenestrae

Diapsid Skull - 2 fenestrae

Paraspid Skull - 1 fenestrae (higher on skull than that of synapsids)



Timeline



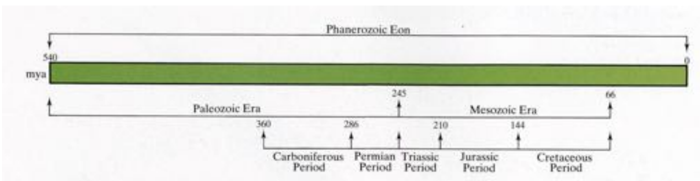
The Reptile Radiations

Radiation - Refers to evolutionary diversification of basic form into spectrum of diff forms adapted to diff habitats/ecological conditions

Each radiation replaced over geo time by subsequent radiation showing more advanced form

Each expansion proliferates and flourishes at particular time, then declines and replaced by a subsequent radiation, with adaptations linked to prevailing ecological circumstances

In reptiles, fossil record is exceptionally complete, allowing reconstruction of these radiations which, in simplified terms, are as follows:



Carboniferous Stem Reptiles

- With a limited radiation
- Declining in Permian
- Replaced by primitive mammal-like pelycosaurs

Pelycosaurs

- Radiated into herbivores, large carnivores, insect-eaters and fish- eaters

- All extinct by mid-Permian, to be replaced by therapsids with more advanced mammal-like features

Therapsids
- Became extinct in late Triassic, when great dinosaur (Archosaur) radiation commenced
- Lasting throughout Jurassic and Cretaceous
- Terminated by great Cretaceous-Tertiary mass extinction event
- Led to demise of dinosaurs and radiation of birds and mammals

Anapsid's

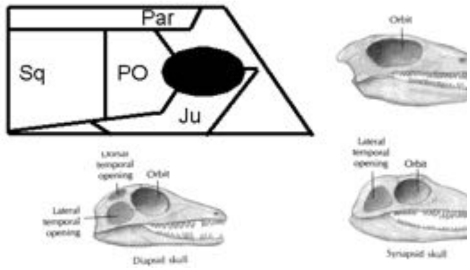
- No fenestra (temporal openings in skull)
- Primitive condition
- Fish, amphibian, stem reptiles and in turtles/tortoises
- May be secondary loss of fenestra (actually parapsids)
- All now extinct except chelonia (turtles and tortoises)
- Protective shell of horny external scales fused to underlying body scales
- Ventral abdominal shield
- Head and legs protrude through holes

Synapsida

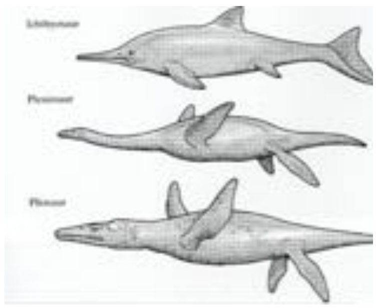
- 1 pair of fenestra, low behind eye socket

- Includes pelycosaurs (e.g Dimetrodon - sail fin to aid ectothermic homeothermy)
- Wide radiation of herbivores and carnivores
- Gave rise to extinct mammal-like reptiles (therapsids)
- Reptilian stance (wide gait) but more mammal-like features

- Pelycosaurs died out in middle permian, after giving rise to therapsids
- Therapsids: Mammal-like reptiles with more powerful jaw muscles, more diverse and advanced dentition, greater agility
- Therapsids dominated later permian and early Triassic
- Were large carnivores and smaller insectivores (e.g megazostrodon)
- Most disappeared by end of triassic
- Cynodont therapsids gave rise to early mammals in triassic
- e.g Thrinaxodon - Dog teeth, bony palate so could simultaneously breathe and chew



Arapsids:



- 1 pair of fenestra (openings) behind eye socket but higher than in synapsids
- (May include turtles - which secondarily lost openings)
- Secondarily adapted to marine envi
- Includes extinct marine reptiles (plesiosaurs and ichthyosaurs)
- Convergent evolution in body form and function of plesiosaurs and ichthyosaurs with modern day cetaceans (dolphins, seals etc)
- Fish and squid eaters in shallow seas - common in Jurassic and Cretaceous -> Then extinct

Diapsids:

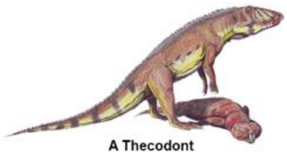
- 2 pairs of fenestrae, one above the other, both behind eye socket
- Includes lizards, snakes, dinosaurs, crocodiles, pterosaurs and birds
- Oldest diapsid groups originate from late carboniferous

2 Main Subgroups:

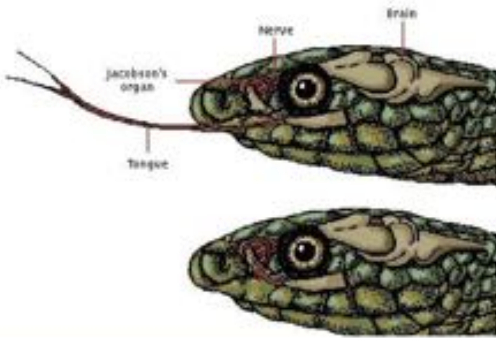
1. Lepidosauria: Tuatara, lizards, snakes, mesosaurs (extinct), plesiosaurs (extinct) etc.

2. Archosauria: Crocodiles, Thecodonts (extinct), pterosaurs (extinct) and dinosaurs

- 2 surviving groups date back to triassic - Tuatara and Crocodiles
  - Tuatara - Living fossil lepidosaur (in NZ)
  - Crocodiles - Tropics worldwide (only extant ancient archosaurs)



- Lizards and snakes (squamata) are of more recent evolutionary origin

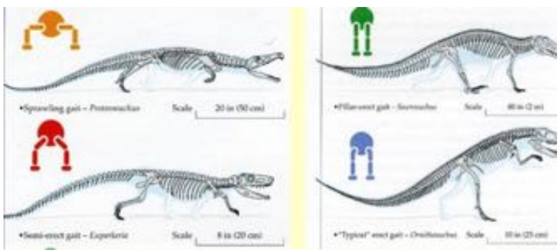


Squamata (Lizards and Snakes):

- More recently derived diapsids
- Basic diapsid skull modified to allow greater movement for feeding adaptions
- Paired copulatory organs
- Jacobson's organ for smelling - Highly mobile and sensitive tongue brings chems to organ, which has specific nervous connection to brain

Lizards
- 4800 species - diverse forms
- Mostly tropical/sub tropical and terrestrial (range of niches)
- Started to radiate in jurassic
- Largest lizard is Komodo dragon (3m long)
- Parthenogenetic (reproduction from ovum without fertilisation)

Snakes:
- 2900 species
- Most diverse in tropics in warm temperate climates
- No external limbs but some with vestigial pelvic girdle
- Eyes protected by transparent covering - no eyelids and no ear drum
- Belly covered in single row of laterally expanded scales
- Snakes evolved from lizard-like group, losing legs and moving via waves of muscular contraction
- Relying on scales to maintain a purchase with substrate
- Skull highly modified - Allows separation of lower jaw hinges to swallow whole large animals, with ventrally unattached ribs to allow prey to travel down distended gut
- Consequent weakening of skull has necessitated methods of subduing prey - posing injected via fangs or crushing using coiled body before swallowing



Archosauria:

- All diapsids
- Teeth set in jaw sockets
- Extremely diverse

- Tendency towards larger, more powerful hind limbs for improved locomotion
- More erect gait allow faster movement (longer strides) - More bipedal
- Euparkeria - Archosaur with bony armour along either side of backbone - Feature of crocodilians

Archosaur Radiation

- Early archosaurs (thecodonts) mostly less than 1m long
- Some were crocodile-like fish eaters
- Gave rise to 4 key groups:

1. Crocodilia: In freshwater and saltwater habitats, present today
2. Pterosauria: Flying reptiles, extinct
3. Dinosaurs: Ornithischia
4. Dinosaurs: Saurishcia

- All archosaur reptiles expect crocodiles were extinct by end of Cretaceous

Pterosauria:

- Adapted to flight
- DID NOT GIVE RISE TO BIRDS
- 4th finger elongated to support membranous wing for gliding
- Weak legs, probably lived on cliff edges and fed on fish
- Jaw with long, slender teeth
- Extinct at end of Cretaceous - Along with dino
- Long tail in some lineages for flight stability

Radiation of Pterosaurs

a) Dimorphodon (jurassic) - Could maybe run as well as fly

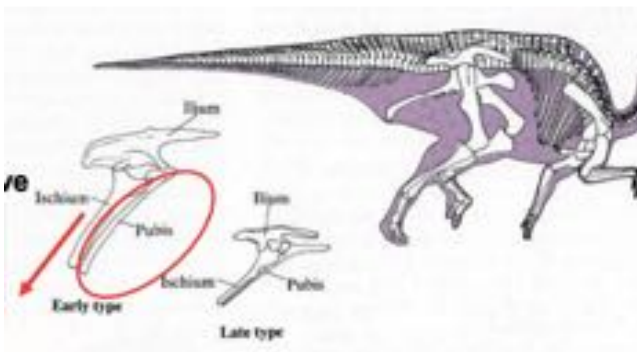
b) Pterodactylus (Jurassic) - Lost long tail of pterosaurs, fed on insects and small fish

c) Eumorphodon (Triassic) - Early pterosaur, with long tail for flight stability

d) Tropeognathus (Cretaceous) - Had keel on jaws, which may have stabilised head whilst foraging

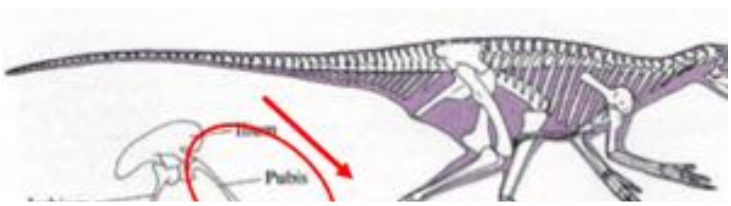
e) Quetzalcoatylus (Cretaceous) - Largest flying animal ever, wingspan of 15m, head crests may have been for courtship or counterbalance of large jaws, would've had aerodynamic consequences

Dinosauria:



- Chicken sized to 100+ tonnes in weight
- Archosaurs evolved in 2 separate lines from small bipedal diapsids
- Mechanical advantages of hip arrangements for upright, efficient locomotion
- Freeing of arms for foraging
- Some secondarily returned to quadrupedal locomotion

2 Lineages:



1. Ornithischian - Had ‘bird hips’ with pubis parallel to ischium, but didn’t evolve to bird

2. Saurischian - ‘Lizard hips’ with pubis in opposite direction to ischium - Gave rise to birds

<u>Ornithischian (bird-hipped):</u>

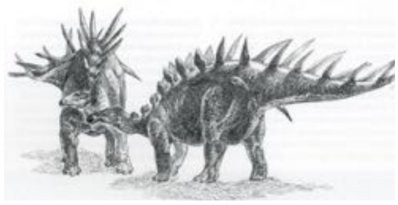
- Dinosaurs with ventral pubis bone extending backwards and downwards
- Hind limbs very large
- All herbivores
- Earliest fossils from late triassic and were bipedal
- Increase in size of largest species as radiation progressed
- Some groups returned to quadrupedal stance
- Pachycephalosaurus: Thick bony crests for head butting contests ?— male/male contests?
- Crest structure on head with cavities

Ornithopod - Group of ornithischian dino, started as small bipedal running grazers, grew in size and become most successful group of herbivores in cretaceous period, progressive development of chewing apparatus, most sophisticated ever developed by non-avian dino rivalling modern mammals (i.e. domestic cow), reached apex in Duck-Bills (hadrosaurs)

<u>Hadrosaurs (Cretaceous)</u>

- Duck-billed with large crests (for display/sound production - alarm calls/communication)
- Parasaurolophus

<u>Quadrupedal Ornithischians</u>



a) Stegosauria: Hard vertical bony plates on backs, for defence or for aiding thermal regulation (heat up or cool down quick), diversity of form of basic body plan, some more spiny, some larger plates, potential signalling (behavioural aspects speculative - how did they mate)

b) Ceratopsia (tricertaops) : Large diversity, Largest heads of any dinosaur known, bony frills - bony plate projecting from back of neck, skull to protect neck, diversity of horns with - Rhino like horns product of sexual selection? (colouration - display for conspecific)

c) Ankylosauria - With thick interlocking body scales

<u>Saurischia (lizard-hipped):</u>

- Diverged early on as upright bipedal reptiles (theropods = wild beast) using forelimbs for grasping and sauropods (lizard-foot) with quadrupedal form
- Plateosaurus: First large dinosaur (6m), plant eating theropod, very abundant in Europe
- Many theropods were predators
- Gave rise to modern day birds

Theropods - Large group of saurischian dino, including largest terrestrial carnivores

<u>Birds:</u>

- Reptile (and especially dinosaur) diversity reached maximum in Cretaceous

- Some theropods were nimble, up-right bipedal lightly boned and bird-like (Jurassic onwards)
- Smaller forms and predatory of large insects
- Compsognathus - Ancestor to modern day birds
- Coelophysis - Many theropods were small, fast moving and bird-like (late Triassic), evolutionary trajectory towards birds
- Erect stance due to changes in pelvic girdle.
- Theropods evolved feathers - Simple fibres for insulation
- Diversity of feather forms from downy to flight feathers

Ordovician Dino —> Lizard-Hipped (Saurischia) —> Allosaurs —> Small agile theropods —> Rise to more bird-like forms

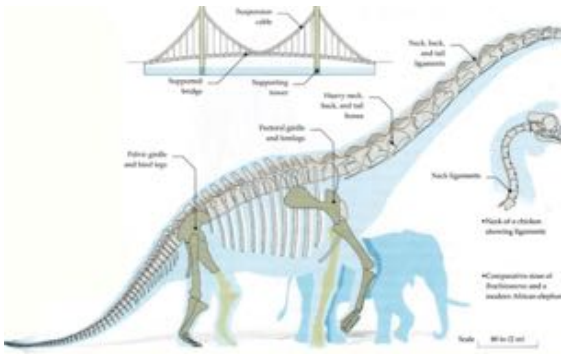
Allosaurus - Large bipedal predator, skull large and equipped with dozens of sharp, serrated teeth, avg. 8.5 m

Hypothesis - Small aboreal theropods, used feathers to slide down from trees to pursue prey - Activating flight

Archaeopteryx - Earliest true flying birds, Theropod genus of bird-like dino, transitional between non-avian feather dino and modern birds

How big did Dinosaurs get?

- Dinosaurs ranged from chicken size to giant sauropods weighing 30 tonnes or more (largest terrestrial animals)
- Necks of sauropods supported by thick ligaments running up tail, back and neck, tensioning neck
- Connective tissue running down spin (like suspension cable of bridge)
- Erect stance facilitated by pelvic levels



- Graph of circumference of leg bones plotted against body weight – can be used to estimate mass of extinct animals
- Maximum theoretical body mass (due to Cope's Law - organisms within radiation get bigger over evolutionary time) is around 140 tonnes, as at this weight legs would touch
- As body volume (+ mass) increases, legs become proportionately broader
- At a body mass of about 140 tonnes the legs would be so wide that they would touch

Dinosaurs Ectothermy or Endothermy?

- Initially were ectothermic but transitioning to endothermic

- In modern animals, metabolic rate proportional to max rate of locomotion - many dinosaurs (i.e. theropods) moved fast and may have been tachymetabolic (endothermic - metabolism at high rate)
  - Spacing of footprints in fossilised mud (up to 23 miles/hour)
  - Due to high rate of locomotion, some dins had high metabolic rate (heat associated movement)

- Todays endotherms usually out compete sympatric ectotherms

- Erect posture - Indicative of endothermy (erect bipedalism?)

- Brain size correlated to endothermy - Theropod and Ornithopod dinosaurs relatively large brains
- Ectotherms not often found at high latitudes, where dinosaurs fossils have been found
- Mammalian predator/prey ratios lower than ectotherm predator/prey ratios - Dinosaur predator/prey ratios were low
- Large, long necked dinosaurs had high hydrostatic blood pressure, requiring 4-chambered heart — characteristic of endotherms
- Dinosaurs are ancestors of birds, birds are endothermic
- Endotherms grow faster than ectotherms, dino must've been endotherms to reach large size
- Dinosaurs bone more similar to endotherm mammal and bird bone (with haversian canals) than typical ectotherm reptile bone
- Thermal inertia when ratio of body mass to body surface area is high allow large living reptiles to retain heat, so dinosaur body temp should increase with body size
  - Relation of body mass - body temp, body mass increases along with body temp
  - Larger body size leads to thermal inertia (heat)
- Oxygen isotope data supports contention that endothermy, with 36-37 body temperatures, is ancestral condition in reptiles and ectothermy is derived condition in modern reptiles
- Dinosaurs were most likely endothermic

Vertebrate Evolution: Mammals

Why Interested?

- Help understand wheres and whys of present day distributions, ecology and life histories

- Help understand ourselves and evolutionary history, interpret behavioural pattern

What is a Mammal?

- Hairy, milk producing, endotherm, gives birth to live young (exceptions to classic characteristics)
- Only approx. "4700" described species of mammals - However greatly distirbuted across earth
- Stepwise transition to full mammalian form

Huge diversity amongst mammals

- Diversity in amount of size (morphology):

    Smallest mammal: Bumble bee bat - 30 mm from nose to tip, weighs 2g

    Largest mammal: Blue whale - 30m in length, weighs 150 tons (body mass supported in water envi)

- Mammals exist at many trophic levels (herbivores, carnivores and omnivores)

- Colonised most of earth, occupy diff habitats: Terrestrial, Aerial (flight) and Aquatic Envi

    Ecological goals - Key ways of thinking about success of mammals
    Extreme of south pole to north pole, cold dessert to dry dessert, to wet envi's
    Occupied marine envi, dive to great depths (except deep ocean trenches)
    Aboreal habitat and underground (burial) habitat
    Wide range of geo colonised during mammalian radiation

- Diversity of behaviours - Wide range of behaviour repertoire

    Mammals exhibit diverse behaviours
    Maternal offspring bonding
    Highly structured cast systems
    Complex social interactions - Including humans
    Emerging properties: Social learning and cultural transition of evolution
    Particularly prevalent in some mammalian species

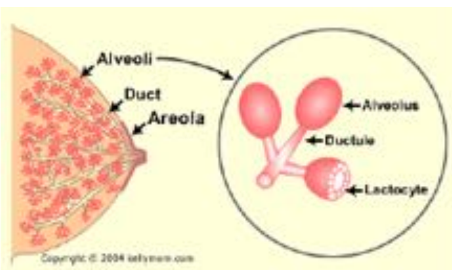
    Behaviours - Adaptive traits
    Helps in survival and reproduction within fluctuating envi
    Mechanism of success of mammals

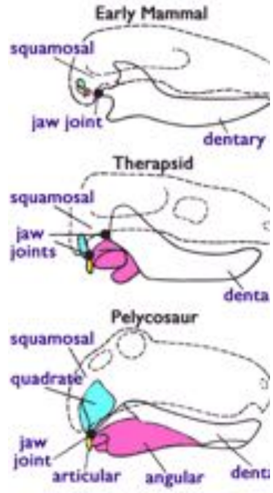
Diagnostic Mammalian Characteristics

Various characteristics and traits - Giving adaptive adv. in mammalian radiation

Key Adaptations and Defining Features:

1. Lactation





- All female mammals possess mammary glands
- Modified apocrine (sweat) glands
- Lactate and produce milk to nourish child/offspring
- Milk rich in nutrients/fats for rapid growth

- Immediate food source
- Buffer - Carry form of nutrition for offspring wherever they go
- Can allow mother-offspring to remain in shelter away from predation

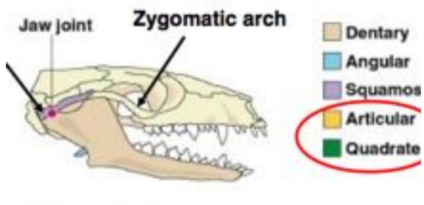
- Primitive form of mammals (Platypus) don't possess mammary glands
  - Have larger sweat glands secrete milk substances, young lap milk from fur

- Only advanced placental mammals processes mammary glands with alveoli containing lactocytes producing milk and milk passes into nipple for provisioning young
- Num of nipples vary based on litter size and life history
- Some have 2 nipples (1 offspring at a time)
- Some have numerous (rodents or dogs with large litter of pups)

Many Specialisations - Advg due to nutrients provided to offspring (high amount of protein/fats)

First phase of milk - High level of cholesterol, passes antibodies and aids immune function in offspring, giving selective adv. in children

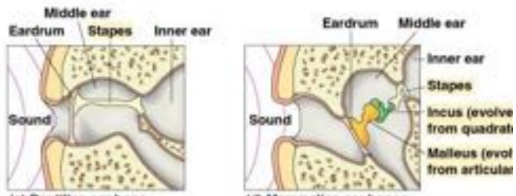
2. *Hair or fur (pelage)*



(b) Mammalian jaw

- Uniquely to mammalian
- Found on all mammals at some phase of lifestyle
- Dead epidermal cells strengthened by keratin
- Providing insulation, sensing and signalling

- Specialised hair - Insulation function (useful in diff envi)
  - Diff layers of hair - Otters have tougher outside rigid guard hair, and inner softer hair providing insulation
- Spiky hair - Defensive purposes (porcupines)
- Other function - Tactile sensory function, whiskers (walrus)
- Or communication through display of crest



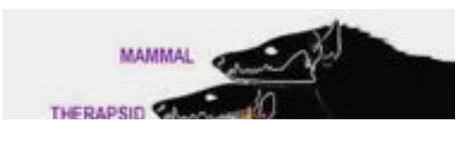
(c) Reptilian ear bone
Dimetrodon (reptile)
(d) Mammalian ear bones
Morganucodon (mammal)

3. *Skull Architecture*

- Particular aspect of skull - Key areas changed in lower jaw bones
- Reptilian jaw - Composed of multiple bones with sutures in between
- Mammalian Jaw - Comprised of 1 bone (simplified form) and no sutures
- Jaw joint between denture and squamosal bone
- Stronger jaw
- Zygomatic arch - Protecting eye
- Articular and quadrate bone no longer present in jaw - Migrated to mammalian ear

3 Middle Ears Bones:
Stapes, Incus (evolved from quadrate) and Malleus (evolved from articular)

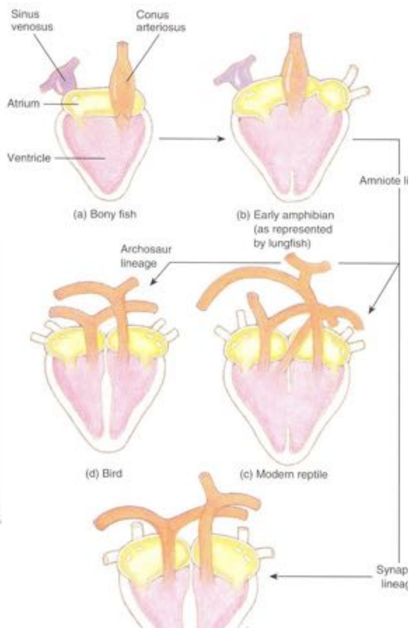
From Lobe Fin Fish —> Amphibian —> Therapsid —> Mammal



Bones derived from gills - Migration of bone shrinking and moving to middle of ear

4. Circulatory System

- 4 chambered heart acting as double pump - Stronger pumping action
- To circulate blood around body - Facilitates more active lifestyle
- Pump to body and lungs
- Biconcave enucleated erythrocytes
- Left aortic arch
- Seen in birds evolved through diff lineages

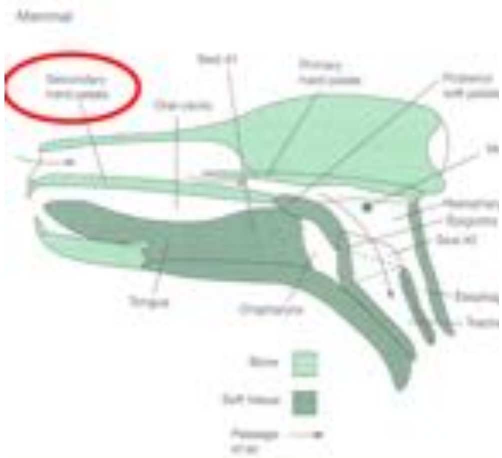


5. Muscular Diaphragm

- Muscular sheet separating thoracic and abdominal cavities
- More active
- Allows greater ventilation of lungs and higher metabolic rate

6. Secondary Palate

- Separates nasal passages from mouth
- Allowing for breathing and eating at same time (unlike reptiles)
- Boney plate separating nostrils from cavity mouth
- Unlike reptiles, mammals can continue to breathe whilst consuming food
- Over top of trachea
- Respiration momentarily blocked when epiglottis falls over trachea to prevent food going down trachea, instead down oesophagus



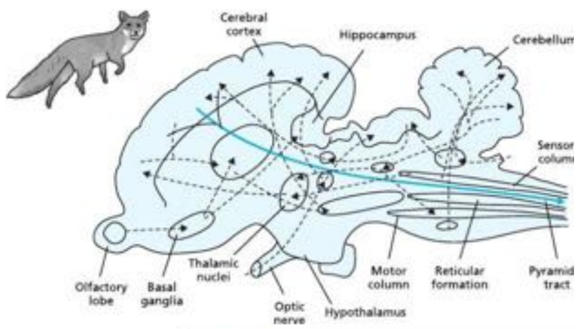
7. Endothermy

- Sustain high levels of activity - Active hunters
- Maintain thermal homeostasis
- Allows huge range of ecological and behavioural adaptations
- High metabolic rate
- Persist in more challenging environments (in cold envis etc.)

<u>Other Mammalian Characteristics - Heterodonty</u>

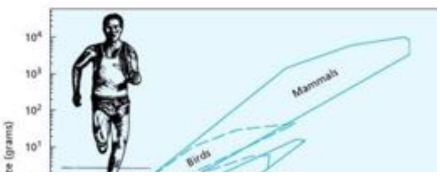
<u>Heterodonty - Specialisation of Teeth</u>

- Similar teeth size throughout entire jaw
- All have diff functions: Molars, canine, premolars and incisors



<u>Large Brains - Infolding of cerebellum; Convolutions</u>

- Increasing centralisation of nervous tissue brain with greater development of neocortex from ancestral forms (amphibians) -



Seen in Chordates

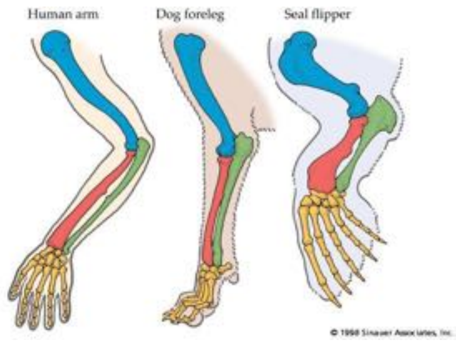
- Elaboration of forebrain - Cerebral hemispheres
    - Consists of new brain tissue - Neocortex (element of forebrain of lower vertebrates remains in form of hippocampus)
    - Forebrain: Major association centres
    - Allow for cognitive capabilities - spatial and social aspects

- Relationship between brain and body (encephalisation quotient - EQ)
- Across range of diff groups (Fish -> Reptile - > Birds -> Mammal) - Increase in body size correlates to brain size
- Step change - Higher line for mammal and birds, Due to evolution and increase in neocortex
- Discontinuity is result of elaboration of forebrain cortex (neocortex) in higher vertebrates

Locomotion - Modification of Limbs and Skeleton

Mammal Forelimbs:

- More upright, less sprawling gait, improved properly erect form
- More diverse forms and agile rapid forms of body movement
- Supporting mass of body above limbs



Ancestral Forms (Reptile Forelimbs):

- Body swung between bent limbs
- Very wide gait

Diverse Structure of Bones:
Human - Arm
Dog - Foreleg
Seal - Flipper

- Limb more flexible (range of forms)
- Proportions, shape and size adapted to diff functions (grasping, flying, walking, swimming etc.)

Modification to Reproductive System

- Internal fertilisation
- Most develop a placenta
- Carry young internally
- Viviparous - Birth to live young (except monotremes - platypus/echidnas)
- Foetus within protected placenta (for provisioning nutrients/oxygen etc. and removal of waste products)
- prolonged periods of development - Bored at advanced stage
- High level of maternal care post birth

Evolution of Mammals

Key remaining Characteristics - Didn't emerge all at same point in evolutionary record - Transitional change

Eras:

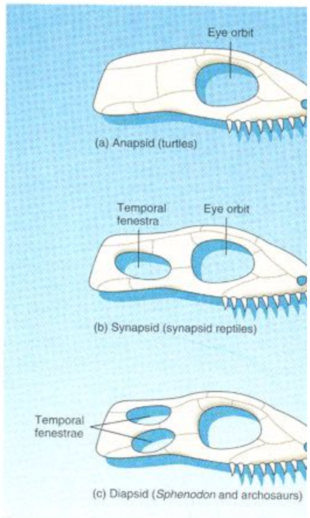
Cenozoic = Age of mammals (dominant)

Mesozoic = Age of reptiles

Paleozoic = Age of fishes

Precambrian = First life (algae, bacteria, worms)

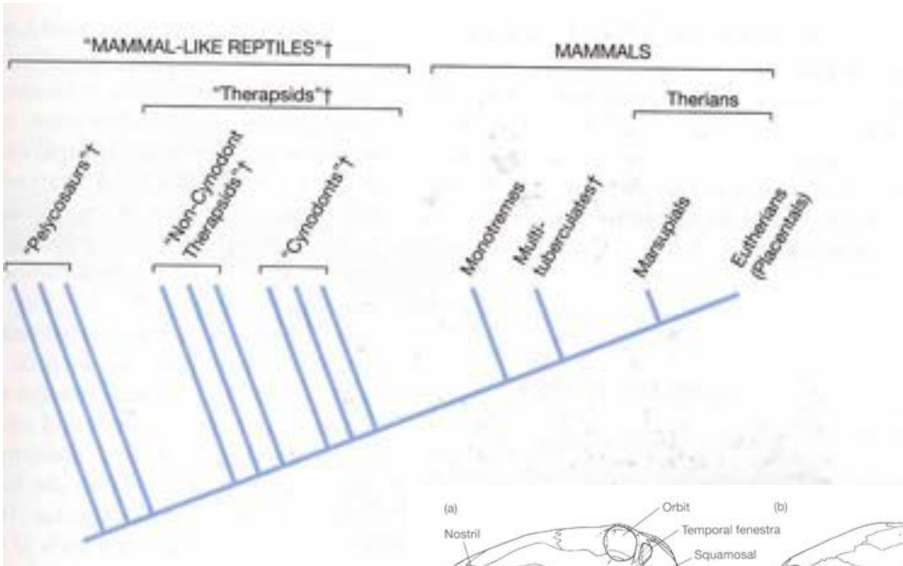
Ancestor of mammals extend very far back to Palaeozoic era



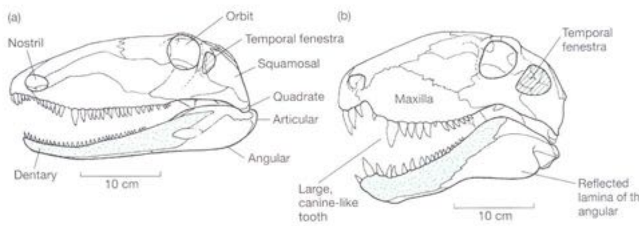
First Mammalian-like Reptiles - Synapsids

- Appeared during Palaeozoic Era - Pennsylvanian period
- Synapsids - Literally Fused Arch
- Characterised by single opening in skull - Temporal fenestra
- Allowing attachment of larger lower jaw muscles
- First amniote to radiate widely into terrestrial habitat
- From aquatic envi to terrestrial habitat
- Successful full terrestrial forms
- Outcompeted by dinosaurs

Mammalian Origins - True Mammals - Mammal like Reptiles



2 Main

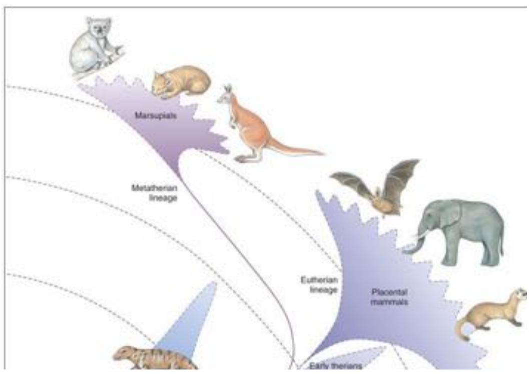


Groups of Synapsids:

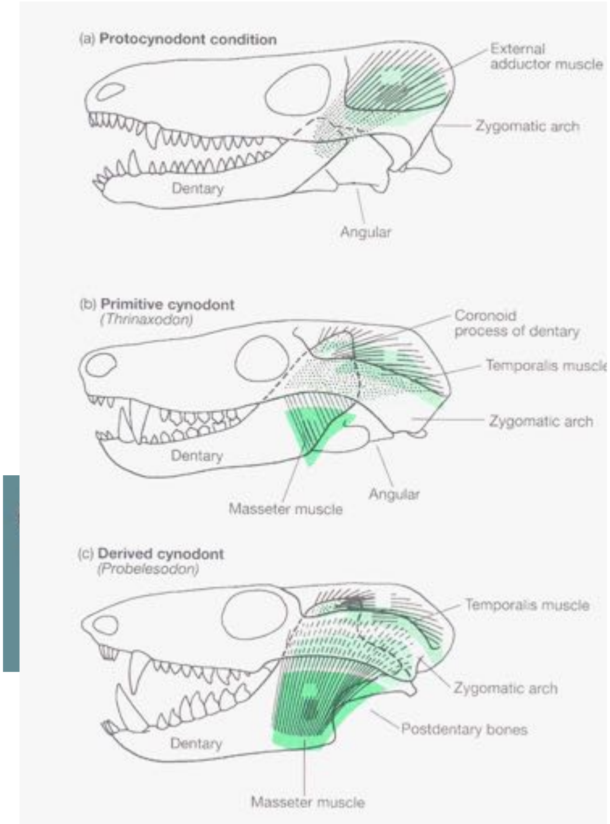
1. Pelycosaurs
2. Non-cynodont "Therapsids"

Order - Pelycosauria
Example - *Dimetrodon*

Mammalian Characteristics:
- Reptiles starting to show mammalian traits
- Basically generalised amniotes (embryo develops in amnion or chorion)
- No increase in metabolic rate, teeth were largely undifferentiated
- Arched palate
- Reflected lamina (important)
- Transition of bones becoming middle ear bones (late evolution)



1 Group of carnivorous Pelycosaurs led to Therapsids



Only synapsid group to survive into the Mesozoic
Limbs positioned under body

<u>Order - Therapsids</u>
Example - *Lycaenops*

- Light, agile skeleton:
  Slender limbs – greater movement in shoulder joint
  Longish legs
  Semi-improved stance
- Limbs supporting body weight
- Evidence of higher metabolic rate
- Larger temporal fenestra
- Differentiation of teeth
- Some may have possessed hair
- Occupied wider range of ecosystems
- Branched off from Pelycosaurs
- Fossil evidence - More mammal like

- Diversified in mid-to-late Permian
- Declined during end of Permian mass extinction, & End of Triassic extinction
- Extinct by early Cretaceous

<u>Infraorder - Cynodontia (Dog-Tooth)</u>

- Most successful and diverse group of therapsids
- Large carnivorous (e.g. Cynognathus) forms
- General trend towards smaller, mammal-like forms (e.g. tritylodontids) during Triassic
- Ancestor of mammals

<u>Advanced Cynodonts</u>

Adaptations to increasing musculature and muscles to attach to powerful jaws

- Jaw articulation and denture
- Enlarged jaw muscles
- Specialisation of dentition
- Extension of secondary palate (improving separation of nasal cavity form pupil cavity)
- Increasing temporal fenestra size
- Limb position - Improving stance
- Loss of cervical and lumbar ribs (change in number of ribs)
- Hair - Thermoregulation

<u>General Trend of Mammal Like Reptiles</u>

Primitive mammal-like reptiles had decidedly reptilian characteristics
- More advanced mammal-like reptiles have sprawling stance
- But very mammal-like in many other skeletal features
- Pits in skulls of some forms even suggest whiskers

Possible First Mammal Appearance - Morganucodon

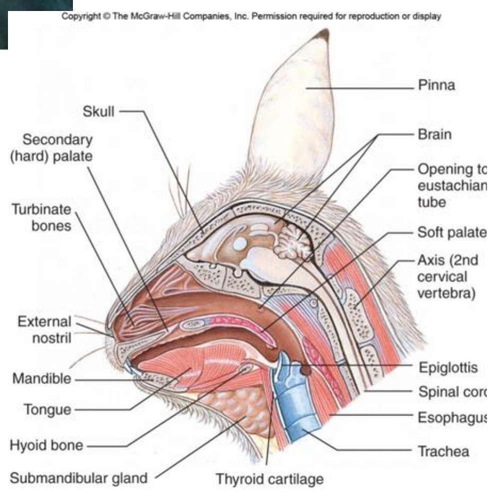
Permian Extinction - Loss of 90~95% species
Mammalian ancestors were those that survived radiation of dino and extinctions

First Mammal - Morganucodon

- Posses all key characteristics
- Difficult to define 'First" mammal
- Probably insectivorous, arboreal and nocturnal
- 245 MYA (late Triassic)
- Dino were diversifying dominating landscape
- Relatively small mammal
- Nocturnal (large eye sockets) - Erect improve stance, small , agile active form

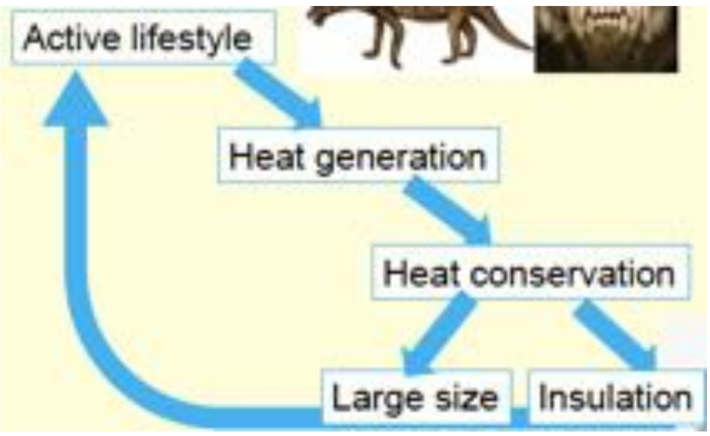
Castorocauda (Early Form) - Jurassic Beaver
- Diversity in mammalian form already
- Adapting to aquatic envi
- Highly specialised semi-aquatic fish-eater
- Approx. 164 mya

Evolution of Endothermy?



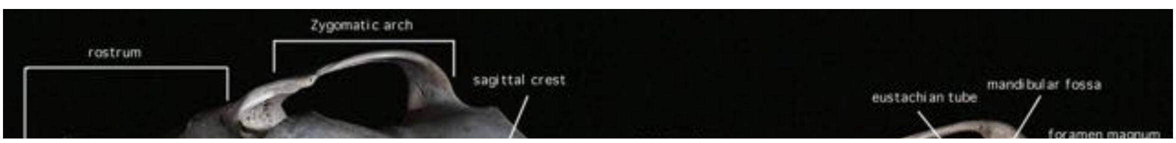
- Speculative - Based on general life-history
- Insulation and heat generation
- Increase in size
- Mammals forced to remain small - To keep out of site from dino
- And improve insulation - Hair
- Large size promoted once dino went extinction
- Feedback
- **Turbinate bones** in nasal cavity - aid in retention of heat
- Evidence of higher metabolic rate

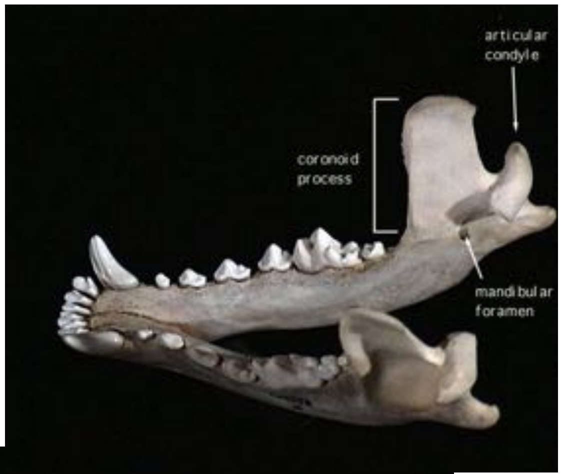
Mammalian Radiation

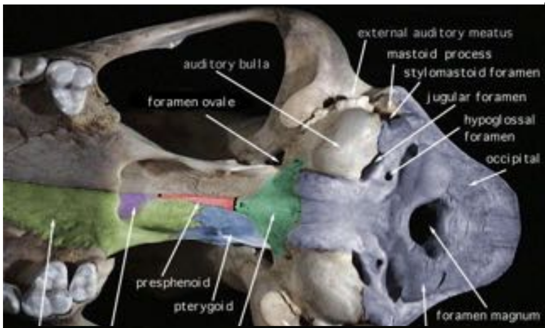


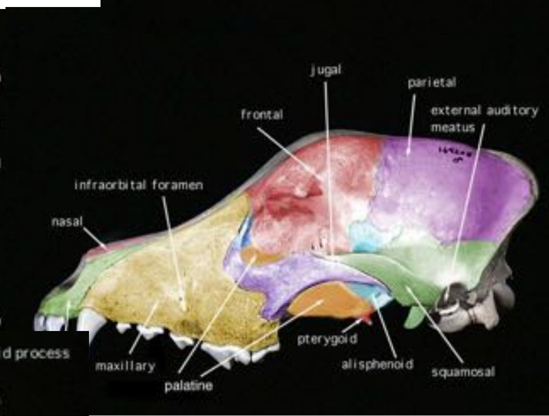
•Living lineages of mammals originated in Jurassic, but didn't undergo significant adaptive radiation until after Cretaceous.

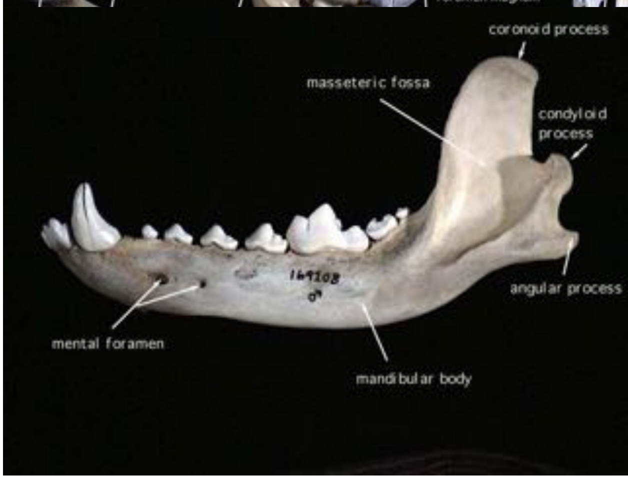
Evolution of Mammal - Anatomy of Mammalian Skull (e.g. Domestic Dog Skull)

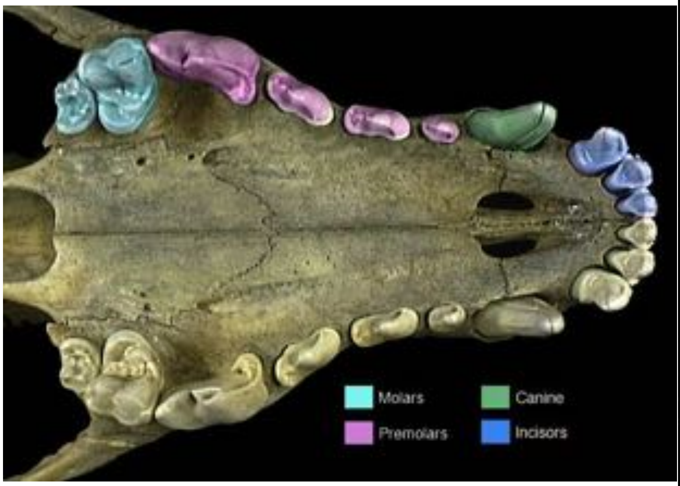


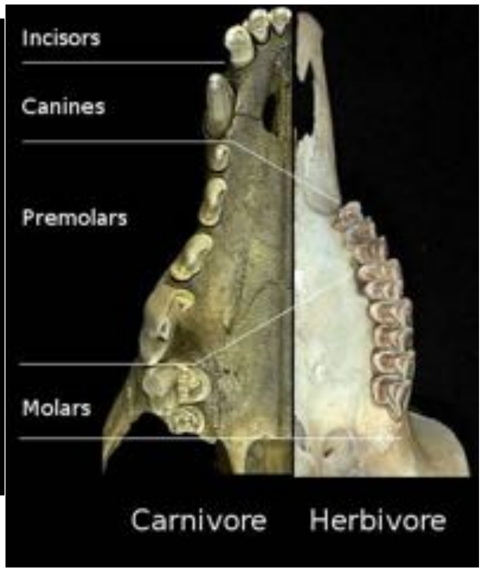

articular condyle
coronoid process
mandibular foramen


external auditory meatus
mastoid process
auditory bulla
stylomastoid foramen
foramen ovale
jugular foramen
hypoglossal foramen
occipital
presphenoid
pterygoid
foramen magnum

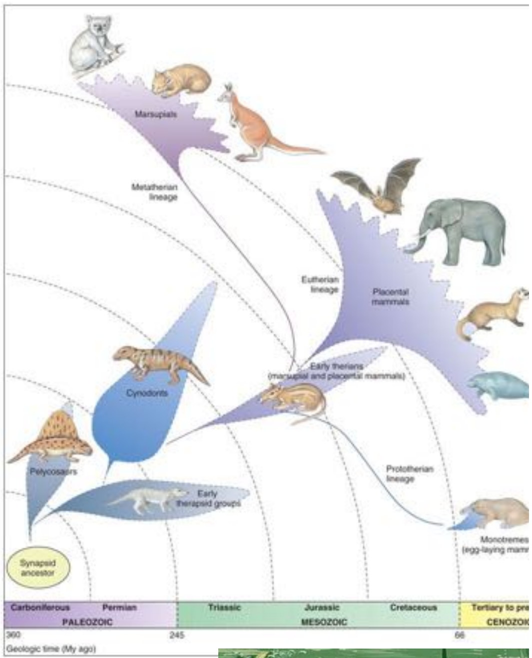

jugal
parietal
frontal
external auditory meatus
infraorbital foramen
nasal
pterygoid
maxillary
alisphenoid
squamosal
palatine


coronoid process
masseteric fossa
condyloid process
angular process
mental foramen
mandibular body


Molars
Canine
Premolars
Incisors


Incisors
Canines
Premolars
Molars
Carnivore
Herbivore

Vertebrate Evolution - Mammals 2



Mammalian Radiation

- Ecological processes led to diversity of mammals
- Patterns and Processes
- Adaptive value of characteristic traits
- Extant mammal groups - Relative success of Monotremes, Marsupials and Placental mammals

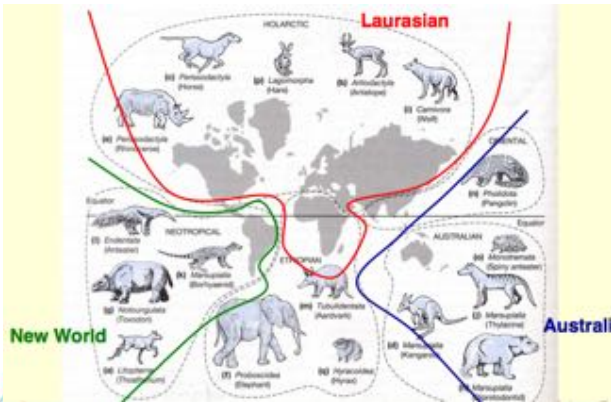
Radiation of Mammals

1. Extinction of Dinosaurs = Removal of comp/predation

- Not entirely - Crocodiles persisted, 1 line evolved into modern day birds
- Mammals cant diversify in ecosystems dominated by dinosaurs

- After mass extinction, certain mammal groups diversified (e.g. Andrewsarchus, sloths and armadillos)
- Freeing up new niches and resources, remove pressure on early mammals

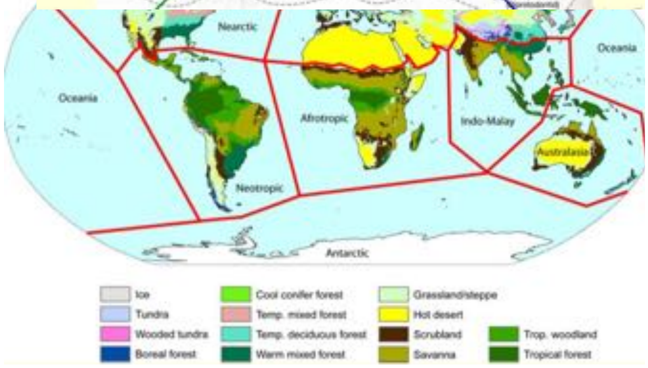
- But many of these species/groups have since died out (e.g. Andrewsarchus) or declined in diversity (e.g. sloths and armadillos) - Thalassocnus natans (semi-aquatic sloth)
- Existing mammals radiated time when sudden increase in temp of plant occurred - around 10MY after extinction of dinosaurs
- Not immediately after mass extinction



Current Patterns of Distribution of Mammals

- Biogeo regions
- Defined/Classified mostly by flora (composition of regions)
- Fauna composition matches closely onto this

Major Biogeographic Regions and Faunal Provinces
- Laurasian, Australian and New World
- Fundamnetal diff in evolutionary lineages with animals there (and similarities)



What Processes lead to these patterns? - Enabling Mammalian Radiation

- Process involved in occupying and utilising new resource/habitat

Migration, Dispersal, Vicariance, and Plate Tectonics and Continental Drift (land bridges)

Migration

- Occurs due to change in resource availability (esp. in seasonal envis)
- Over successive generations envi shifts due to climate change -> migration cycles shift with changing envi
- E.g. Migrating south in northern winter

Autochthonous Faunas: Originated in current area

Allochthonous Faunas: Originated elsewhere, geographically form elsewhere due to migration

Corridors: Pathway of little resistance to migration (suitable envi for spp.)

Filter Routes: Allows passage of pre-adapted species e.g. Beringia (only spp. adapted to cold could migrate)

Sweepstake route: Chance events, few individuals (e.g 1998 hurricane in Caribbean - Iguanas carried on rafts between islands and subsequent colonisation)

Dispersal

- Geo ranges shift over numerous generations -> Envi Changes = Dispersal
- Unidirectional movement

- Tendency to disperse depends on:
    - Comp for resources
    - Spacing of conspecifics (e.g. territoriality - alpha individuals monopolise reproductive opps, beta individuals must disperse and find own territory to reproduce)
    - Comp between non-specifics also drives dispersal
    - Pop Expansion -> Colonise unoccupied suitable areas

- More widespread species = More resilient to local mortality
- Ability to cope with envi change, adaptability,
- Selection “favours” species with broad distributions, high dispersal ability

- Ability to Disperse:
    - Innate dispersal ability (e.g. fliers more adv. than burrowers who rely on established dens)
    - Generalist vs. Specialist (generalists diet is favoured, specialists more constrainted in dispersal routes)
    - Social system (dominant individuals monopolise and dominate resources - favoured)

- Physical and Ecological barriers (i.e. mountains and rivers etc.)

Vicariance

Vicariance - Geo separation of pop, typically by physical barrier (i.e. mountain range or river) resulting in pair of closely related species

- On an evolutionary time scale:
- Barriers Emerge (e.g. rivers, sea, mountains) - Orogenesis (mountain building), Land masses converging or diverging
- Changing landscape of which species are dispersed upon
- Successive generations encounter different migratory pathways

- Can split pop and species, restricting gene flow
- Divergent evolution occurs
- Allopatric speciation of each group occurs

- Adapts to their local envi (different niches/climatic conditions, temp, selection pressures etc)
- Passive separation of pops and their consequent evolutionary trajectories

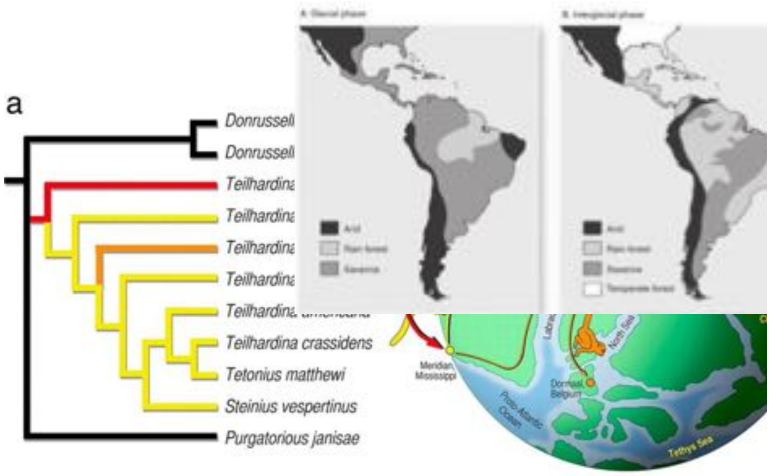
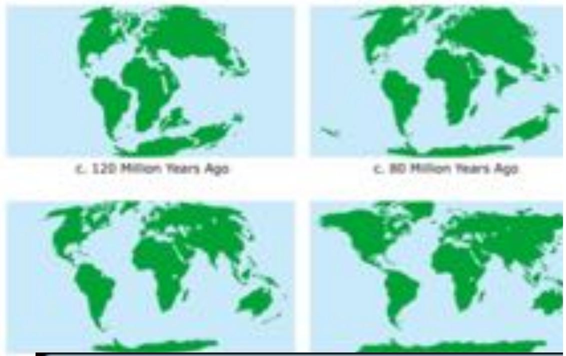


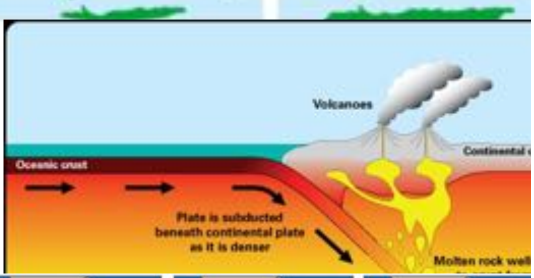
Plate Tectonics and Continental Drift

- When mammals arose, continents were in close proximity - Super continent = Pangea
- Continental drift over time caused geo isolation of pops
- Period of very rapid mammalian evolution
- Groups evolved under diff conditions (diff selection pressures) - VICARIANCE



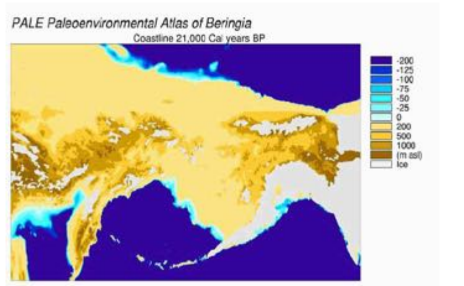
- Topographical changes (e.g volcanic activity generating new mountain ranges), plates sliding past, submerging or diverging
- Changing envi locally and globally

- Consequences for ocean and atmospheric circulation -> Knock on effect on climate -> Change ecosystems
- Ecosystem changes due to changing plant communities and subsequently higher up food chain, during key mammalian radiation
- Generating regional and local specific envi
- E.g. Prior to N America and S America being joint, ocean current could flow between, however once joined divergence of currents occurs in Atlantic generating gulf stream creating trade winds altering temp and humidity



Examples

Beringia - Land Bridge

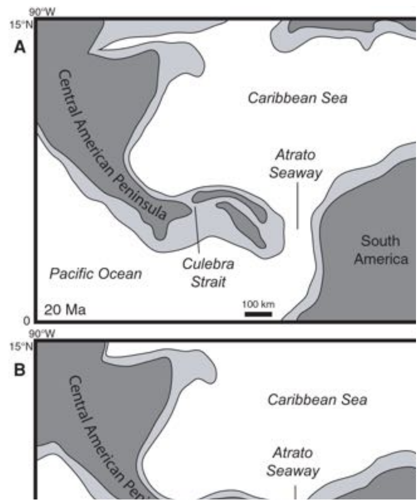


- Connected North American and Asian continental plates
- Allowed movement of animals
- Very high latitude - Cold envi thus only adapted **species** could utilise this land bridge and colonise new habitats

- *Teilhardina* - Early marmoset-like primate
- Originated in Asia used land bridge colonise America
- Rapid diversification in new envi (due to change in habitat)
- Dispersal and colonisation of humans across ice bridge - native american indians)
- Pops spread along coast and through northern ice sheets (eskimos)
- Gradual separation of North American and Asian plates, sea levels rose

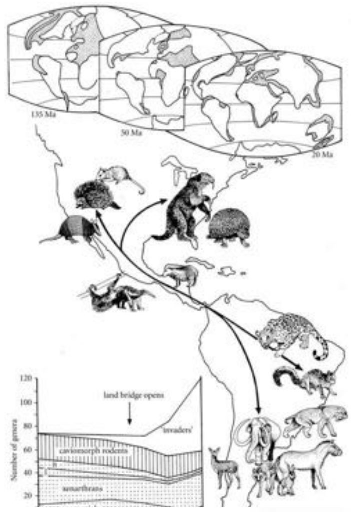
Great American Biotic Interchange (GABI - 20 ~ 15 MYA)

- Convergence of Central American Peninsula and South America allowed distribution of mammals across Atrato seaway
- Animal communities from S into N and vice versa
- Species evolved separately on diff continents -> Then interchanged



- Colonisation of new envi with new selection pressures
- Some sp had selective adv over others
- Native vs. Alien sp.
- Initial exchange sp. in equal proportions, diverse fauna in each continent

<u>Late Miocene/Early Pliocene "Waif" Migrants</u>



• South —> North
  - Megalonychidae (giant sloths)
  - Mylodontidae (extinct - ground sloths)

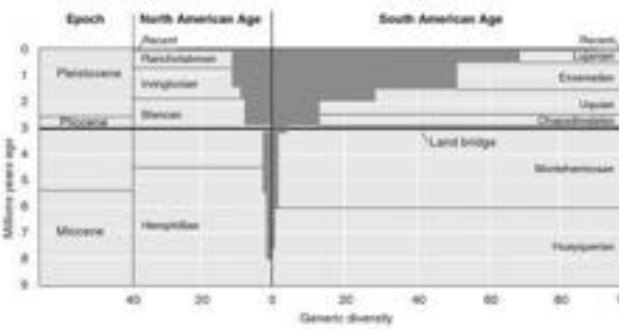
•North —> South
  - Procyonidae (new world family of carnivora - racoons, monkeys)
  - Cricetidae (rodent like)

South American Taxa Diversified little in North America

Northern American taxa radiated exponentially in South America in Pleistocene

<u>Why did northern sp. diversify more??</u>

- Better Competitors: better adapted to long immigrations (movement across berginia)
- Late cenozoic mountain building (Northern Andes) altered atmospheric circulation and climate
- Glaciations pushed spp. south and altered climate, forming narrow corridors for movement and dispersal (savannah - corridor eventually sealed off by development of rainforest)



<u>Radiation of the Mammals</u>

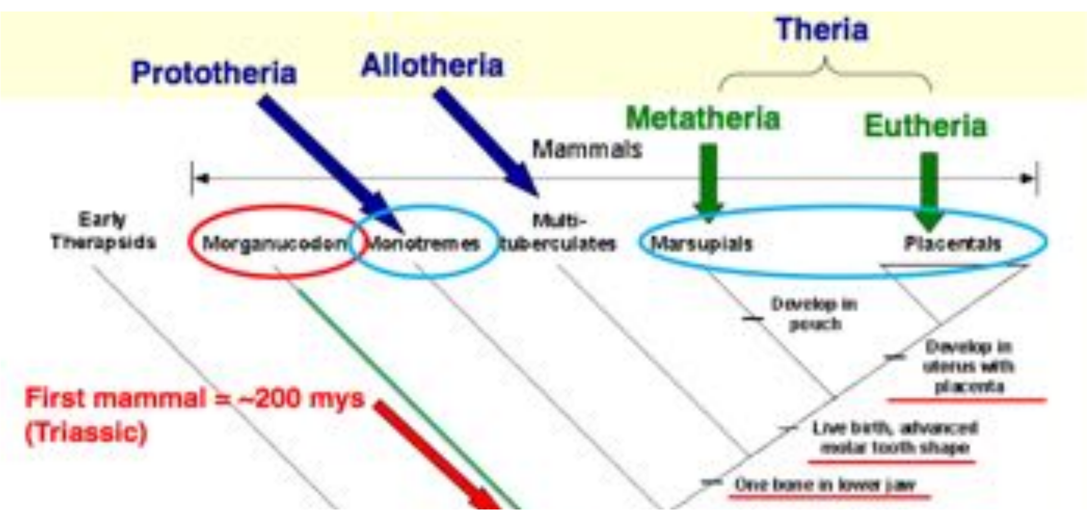
<u>Summary:</u>

- Range of processes
- Complex interactions

- Mammalian adaptations allow various faunas to capitalise on opportunities

- Focus here = terrestrial (various mammalian group also adapted secondarily to marine envis)

<u>Mammalian Phylogeny</u>



Extant = Monotremes, Marsupials and Placentals

- First mammals arrived 200MYA in Triassic
- Monotremes: Mammary glands, hair, ear bones on skull
- Multi-tuberculate: 1 bone in lower jaw
- Marsupials: Live birth, advanced molar tooth shape, develop in pouch
- Placentals: Develop in uterus with placenta

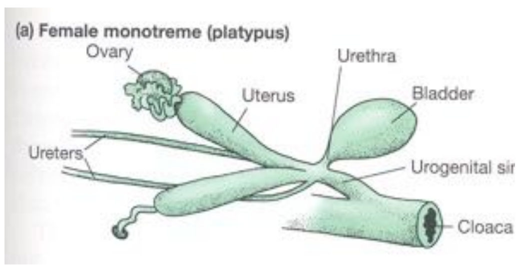
Allotheria (superorder) - Multi-tuberculates

- Relatively recently derived
- Means other beats or multi cusps
- Extinct brach of successful mesozoic mammals
- Characteristic - Presence of lower molariform teeth with 2 longitudinal rows of cusps
- Around for long time - 100 my
- Primarily from Northern Hemisphere
- Multi-cusped molars and pre-molars (gap between molars and incisor)
- Range of habitats and life histories: Burrowers, climbers etc.
- Narrow pelvis - live young, but at very early developmental age?
- Flexible ankle joint to allow gripping onto trees
- Small in size

- Form similar to modern-day rodents
- Comprised 50% of mammalian community

Prototheria - Monotremes

- Both primitive and derived traits
- Exact phylogeny unclear
- Diverged from rest of mammals (190 MYA - Cretaceous)
- Subclass contains 1 order
- Monotremata - Only 3 species today:
    - Duck-billed platypus, long-beaked Echidna, short-beaked Echidna

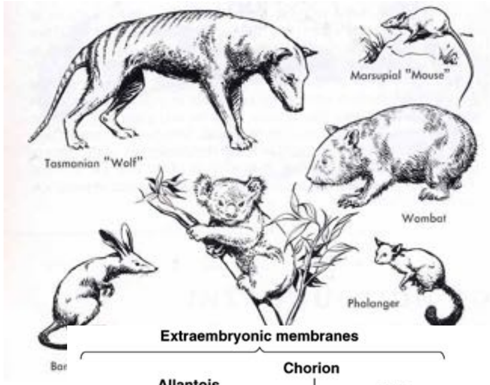


Primitive Characteristic: 1 hole retaining a cloaca (1 hole), reproductive/excretory system (like amphibians/reptiles), single opening for urogenital and rectum, only 1 ovary is active and other is regressive

Reproductive System
- Oviparous (lay eggs) - Leathery shell
- Young hatch at almost embryonic stage - nursing by mother continues for 16 weeks

- Milk produced by mother but from underdeveloped mammary glands (seepage of milk)
- Eggs hatch 10 days after laying
- 4 - 6 weeks of nursing with young being retained with mother or in pouch

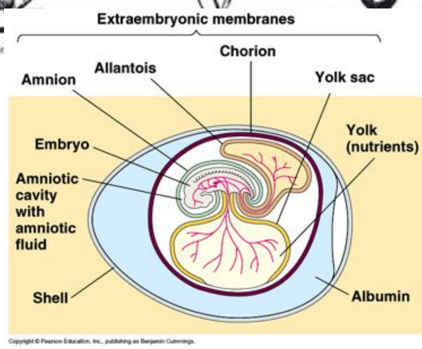
Metatheria - Marsupials



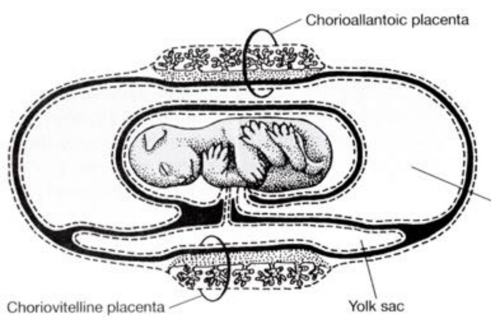
2 Superorders: Ameridelphia (2 orders) and Australidelphia (5 orders)

- 2 Major adaptive radiations occurred in South America and Australia
- Approx 272 specie sin total
- Arose alongside Eutherians at end of the Mesozoic (65MYA)
- Origin in North America

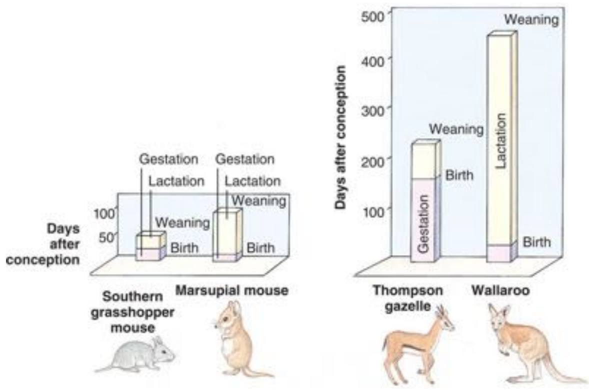
Ecology
- Wide range of niches (habitats and trophic levels)
- Arid desert to moist tropical wet rainforests
- Trophic levels:
    - Omnivores - Tree Wallaby
    - Herbivores - Wombat
    - Carnivores - Tasmanian devil



Reproductive System:
- More advanced than monotremes
- Viviparous - Give birth to live young
- Females DO have placenta but only initial chorio-vitelline placenta (not fully formed)
- Membrane (vitaline) containing yolk (yolk-sac membrane)
- Associated with gas exchange
- Allantois membrane (for wastage) not involved
- Doesn't collect waste products - Limit on gestation length
- Waste stored in membrane thus
- Young born not fully developed - Early stage (8~43 days)



Reproductive System (genitals):
- Double reproductive tract in females (left and right vaginae and uteri fused at ends)
- Uterine horns unfused
- Separate exit for urogenital sinus and rectum - very close though
- Male pensi is doubled (bifid)
- Pouch (or marsupium) enables growth of relatively undeveloped offspring till they reach reasonable size - Within pouch are nipples (underdeveloped young feed off nipples within pouch)
- Short period of gestation - offspring with strong short limbs crawl to pouch
- Majority of development occurs in pouch



Eutheria - Placental Mammals (us)

Reproductive System:
- Viviparous - Give birth to live young
- Develop Chorioallantoic placenta - Collects wastes (allows extended gestation and development)

- Allantois membrane (wastage) - Excreted by mother, waste material of foetus metabolism passes into mothers blood stream via chorioallantoic placenta
- Chorion (gaseous exchange)

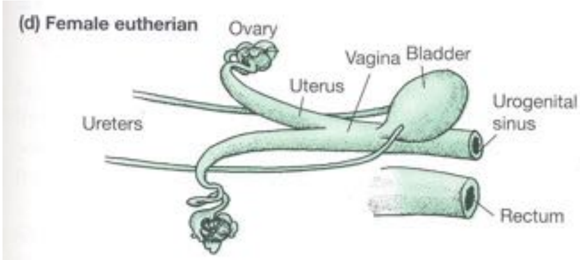
- Physiological adaptation prevents female immune response

- Examples of:

  - Altricial (poorly developed young) - Prolonged period of nursing, high litter size, shelter/burrowing for protection

  - Precocial (highly developed young) - can stand & run (to maintain proximity to mother), tends to be species where young born to risky envi (little shelter, many predators), small litter size

- Left and Right Vaginae are fused
  - Each uterine hole leads to ovaries
  - No cloaca - Spatially separate anus



Comparisons:
- Eutherians have longer period of pregnancy
- Longer gestation in larger mammals
- Longer gestation correlated with shorter lactation- More development in womb, requiring less provisioning
- Length of time until independence shorter in placental mammals compared to marsupials

Eutheria vs Metatheria – More advanced?

- One is not more advanced than the other
  - Some eutherians produce very altricial young
  - Some marsupials possess chorioallantoic placenta

- Diff but equivalent reproductive strategies

- KEY DIFFERENCES:
  - Marsupials invest more energy in lactation
  - Eutherians invest more energy in intrauterine development (internal - gestation)

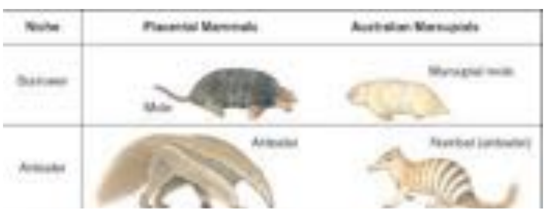
- BUT 2 METATHERIAN DISADVANTAGES:
  1. No aquatic marsupials (nursing difficult in aquatic envi, and born young so vulnerable, long period of lactation difficult)
  2. Higher reproductive rate in eutherians (can wean and reproduce again)

Major selective adv..

Allotheria (died out) vs. Eutheria (replaced)

Due to reproductive strategies
Allotheria - Live young born, however lower reproductive rate - Disadvg to placental form/rodents

Convergent Evolution Occurred:



- Simialr niches and functional roles filled by both marsupial and placental mammals
- Both groups undergone similar radiations
- Diversity of radiations

Many Examples:

Mammalian Diversity - Ability for mammalian template to adapt to diff morphologies in response to selective pressure

Strange relationships:
- Subungulates - May all have descended from common stock
- Close relationship between rock hyrax, elephant and sea cow
- Close relationship between towheaded whale and giraffe
- Shows mammals adapt to diff morphologies under different selective pressures

Marine Mammal Evolution

Diversity and Distribution - Intro to Species classified as marine mammals

Evolution: Cetaceans, Pinnipeds, Sirenians, Carnivores

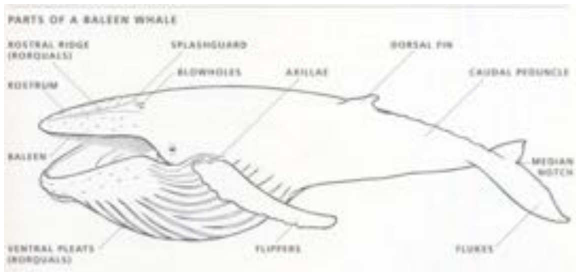
<u>Marine Mammal</u>

- Collection of various mammals that secondarily adapted to marine envi
- Adaptation enables them to utilise and be successful in marine Envi
- Mammals utilised marine envi again - Using pre-existing mammalian body plan
- Machinery available to them - Adapted and miffed by natural selection
- As they reoccupy old niches
- Those morphologies, body forms under selective pressures etc.

<u>Diversity Of Marine Mammals</u>

Whales, dolphins, polar bears, sea otter (not river/lake) and manatees - All marine mammals

<u>Cetaceans (Order)</u>:



(Whale, Dolphin and Porpoise)

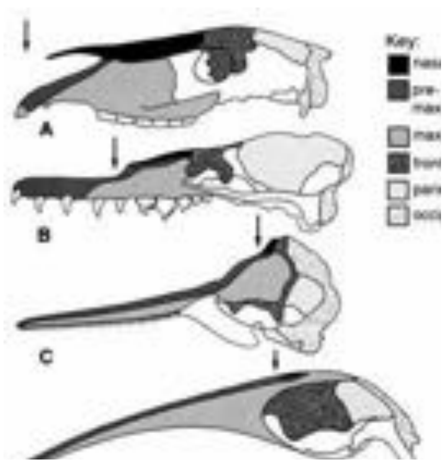
2 Main Groupings: Mysticete's and Odontocetes
Fully aquatic and obligate ocean dwellers

<u>Mysticete's (Baleen Whale):</u>

- Whales with baleen (whalebone)
- Baleen whales split from toothed whales (Odontocetes) 34 MY ago by losing teeth
- Sexually dimorphic
- Filter feeding mechanism - Baleen plates to filter out food from water either lunge-feeding or gulp-feeding
- Symmetrical cranial bones
- Strong jaws (large arching upper mandibles) to support these plates
- Throat grooves (folds of skin on throat) - Allows expansion to swallow large amounts of water

Example: Blue Whale (Largest Mammal - 30meters), Grey and Humpback whales (15 diff species)

<u>Odontocetes:</u>



- Teeth (homodont - teeth all of same type)
- Anterior position and asymmetry of nasal bones
- Naries - Bones protecting nostrils reduce in size and migrate to top of skull (blow hole)
- Lipid filled cavity in front of frontal bones and above rostrum called Melon - For diving
- Secondarily adapted to marine envi then colonised freshwater envis
- Forming long upper jaws (rostrum elongation)

e.g. Sperm whale, Dolphin, Porpoise, Amazonian River Dolphins, Killer Whale

<u>Pinnipeds (Clade)</u>

- Commonly known as seals
- Widely distributed and diverse clade of carnivorous, fin-footed, semi-aquatic marine mammals
- 33 extant species
- Split into 3 main groups (families)
- Semi-aquatic

<u>Otariids</u>
Sea lions, fur seals

- Eared seals (small external ear lobes - pinna)
- Large fore flippers and pectoral muscles
- Can rotate hind limbs
- Manoeuvrable on land
- Less adapted to aquatic life

<u>Phocids</u>
Elephant seals, ribbon seal, monk seals, grey seals, leopard seals (veracious predator)

- Earless seals (lacking external ear)
- True seals
- Vary in body size
- Confined to polar, sub-polar and temperate climates (except tropical monk seals)
- Sleek, streamlined bodies
- Fore flippers for steering, hind flippers for momentum
- Awkward movement on land

<u>Odobenids</u>
Walruses (only living member)

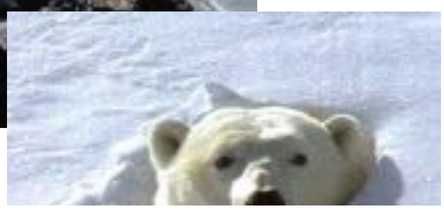
- Long tusks
- Atlantic and pacific species (regarded as 2 species)

<u>Sirenians (Order)</u>

- Fully aquatic, herbivorous (eat sea grass) mammals
- Inhabit calm waters, estuary type areas swamps, rivers, estuaries, marine wetlands, coastal marine waters
- Tropical and subtropical regions
- Slow moving

- 4 Species living (2 families)
- Dugongs (1 species) - Triangular tail flute
- Manatees (3 species) - Flatter, fan like tail

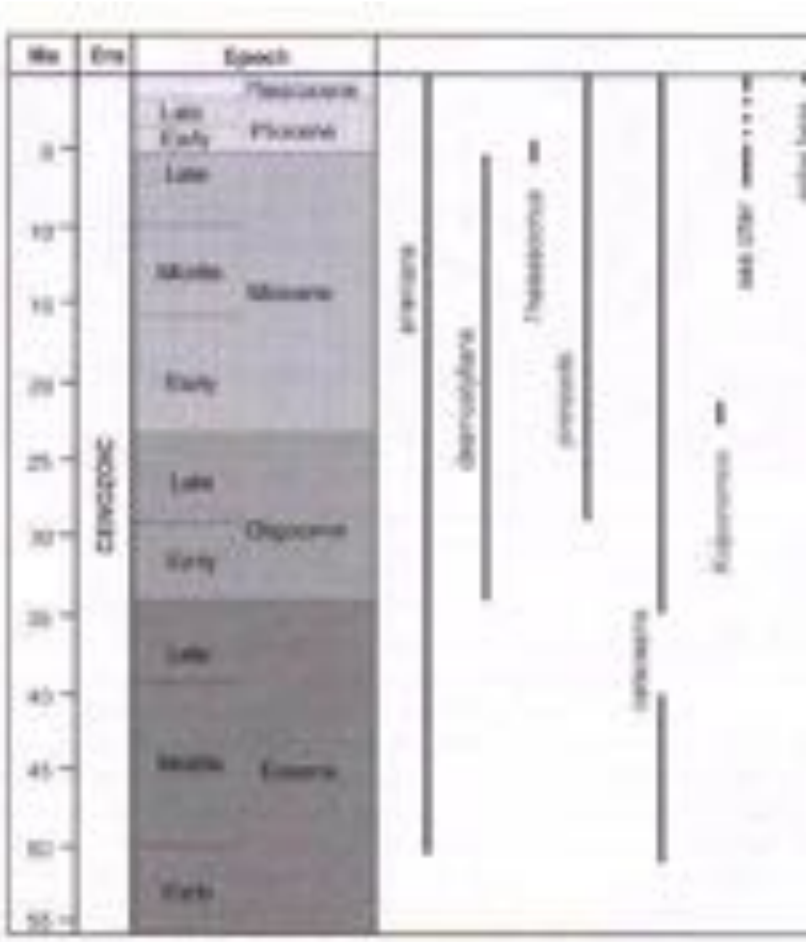
- Stellar sea cow - Inhabited cold water (now extinct)



Carnivora (group)

Polar bear and sea otter (2 species)
With separate digits
Much less adapted to aquatic living

Evolution of Marine Mammals



Diverse groups - Multiple origins
All adapted to marine envi

- Recolonisation of marine envi

- Sirenians and Cetaceans evolved first (fully adapted to marine envi - can't survive on land)

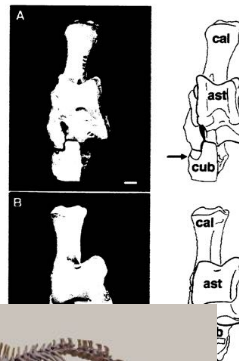
- Followed by pinnipeds (Sea lions, fur seals - Come onto land to give birth to pup)

- Lastly sea otters and polar bears (very recent)

Evolution of Cetaceans from Ungulates

- Evolution of Cetacea from Ungulates: Diff Theories

1. Common Ancestor - Shared ancestor with Artiodactyls and Perissodactyls (molecular evidence)
2. Shared ancestor with Perissodactyls (morphological data - weak)
3. Shared ancestor with Artiodactyls (morphological data - stronger)



Ungulate-Like Ancestors

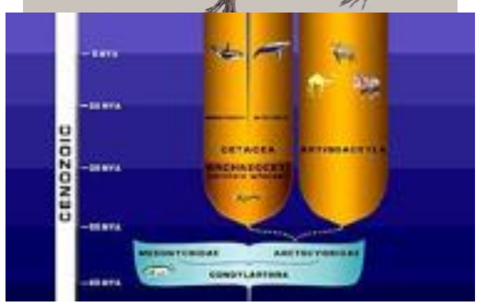
Artiodactyls - Even-toed ungulates, Bisson, warthog, hippo etc.
Perissodactyls - Odd-toed ungulates, herbivores, horses, donkeys, zebras, rhinos

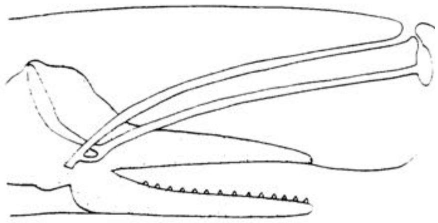
Within Artiodactyls, cetaceans are closest to hippos (molecular data - best) sharing common ancestors

Evidence?

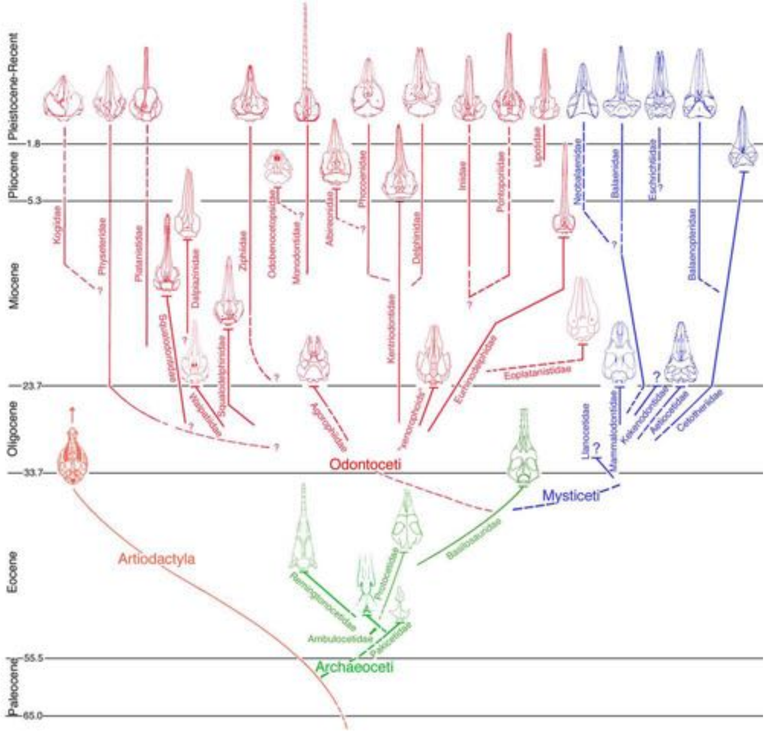
- Discovery of *Pakicetus attocki* - Direct link to Artiodactyls
- Most important aspect = Ankle Bones
- Supported on 4 toes (even-toed ungulate)
- Terrestrial mammal (more homodont teeth)

Earliest Cetaceans - Now extinct Archaeocetes:





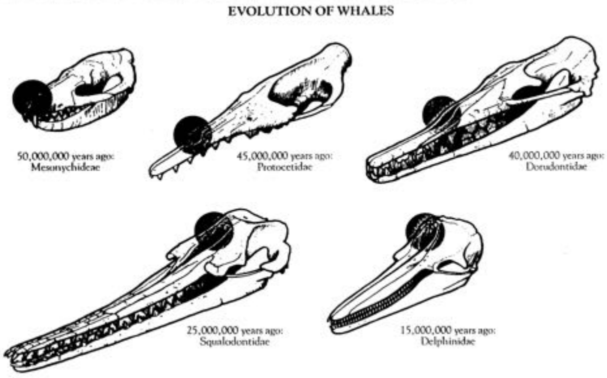
- Linked from Arctocyonidae
- Division between Odontoctetms and Mysticeti
- Late radiations in Oligocene - Miocene



Adaptive Radiation

Archaeoceti: Split into Artiodactyls and fully aquatic forms (Mysticeti and Odontoceti)

Adaptations - Evolution of Skeletal



Morphology

1. Position of Blowhole:

- From typical terrestrial mammalian ancestors
- Position of blowhole moved backwards and towards tip of skull
- From bones of upper jaw around nostrils
- Adaptive as allows breathing by lifting tip of head to surface
- Advg. to exhale and inhale
- Esp. in Toothed whales (Narwhal, pygymy sperm whale)
- Sperm whale - Unusual, development of huge spermaceti organ (nostrils open at anterior edge)


2. Dentition:

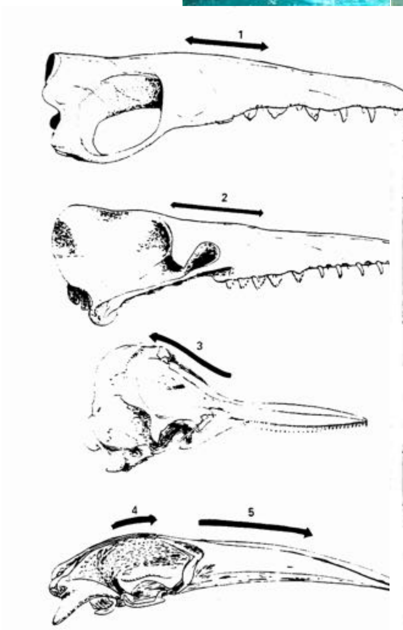
- Drastic modification
- Fit more teeth
- Adv. if marine envi based on cephalopods and fish
- Increase number of teeth -> Can grab hold of slippery fish (peg-like)

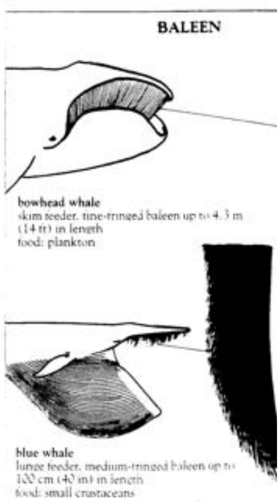
*Overtime increase in number of teeth -> Transition towards Homodonty

Protocetus: Typical creodont pattern (to shear fish), ancestral mammalian form (semi-aquatic), degree of heterodonty (terrestrial adaptation)

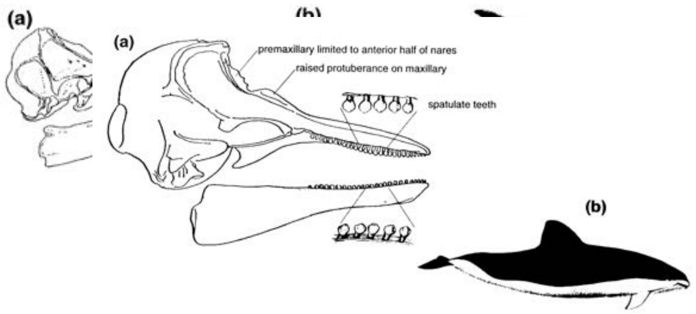
Prosqualodon: Transitional

Tursiops: Fully homodont, modern delphinoid odontocete





Balaenoptera: Teeth replaced by baleen (modern mysticete whales), toothless, use tongue to force water out through baleen (sieve-like) collect food particles



Bowhead whale: Baleen up to 4.3m in length, eats plankton (krill), take in large vol of water

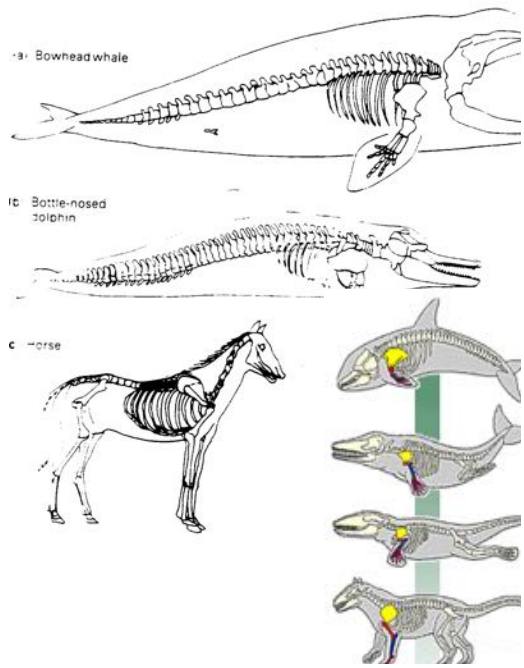
Blue whale: Baleen up to 1m, eats small crustaceans, shoals of fish

Grey whale: Baleen up to 50cm, bottom feeder, silt from ocean sediments (orgs - shellfish etc.)

<u>Modern Homodont Dentition</u>

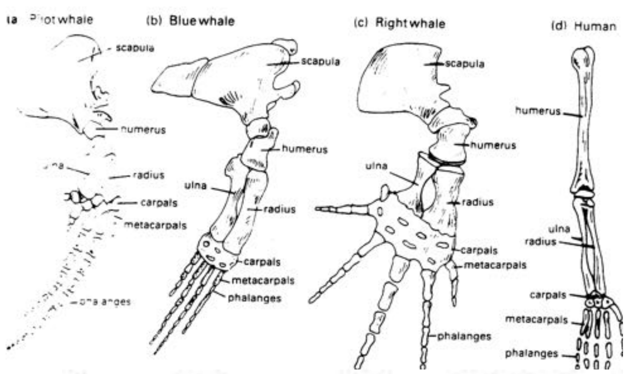
- Toothed whales: Variation between species
- Bottle nose dolphins (homodont) and other dolphin species (spatulate teeth)

3. <u>Evolution of Jaws</u>



- From Horse -> Odontocetes -> Mysticete's (Baleen whales)
- Same layout of limb (same num of bones)
- Change in limb structure, shape and conformation -> Adapted to form paddle like fins (flippers)
- Hind limbs mostly lost (some residual bones in some sp.)
- Shortening of neck vertebrate - More robust neck to support larger head
- Tail vertebrae more robust and pronounced in horse
- Fluke is boneless (fleshy muscular fluke) to power animal through water
- Metacarpals and carpels fuse to give rigidity

4. <u>Evolution of Flippers</u>



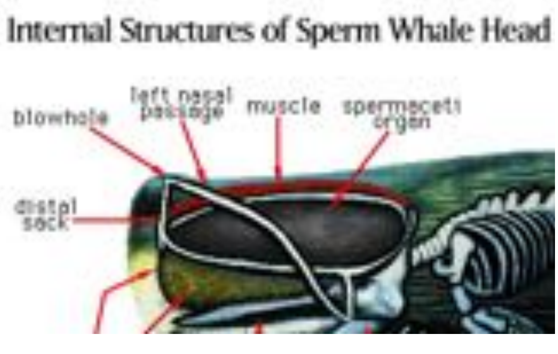
- Hind limbs and pelvic girdle lost or rudimentary
- Metacarpals and carpals fuse into rigid form of flipper
- Fore limbs reduced to form flippers

<u>Placement of Sperm Whale - Mysticete or Odontocete?</u>

- Like Mysticete's: Paired nostrils, large body size
- But toothed

Molecular Data suggests Mysticete's

Spermaceti Organ
- Oily, wax-filled cavity
- Enhancing diving capacity (deepest diving)



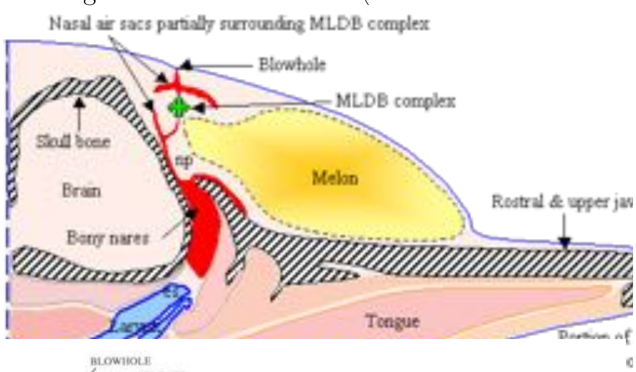
- Fluid (oily) liquid at about 30 degrees
- Maintain buoyancy at surface
- When drops to 1 degree, oil starts to form into wax, pulling animal down to depth (diving weight)
- To forage in deeper water
- Actively can control and regulate this organ
- Cooled by taking in cold sea water via nasal passages going around organ (right -> left)
- Warmed by pumping more blood near organ

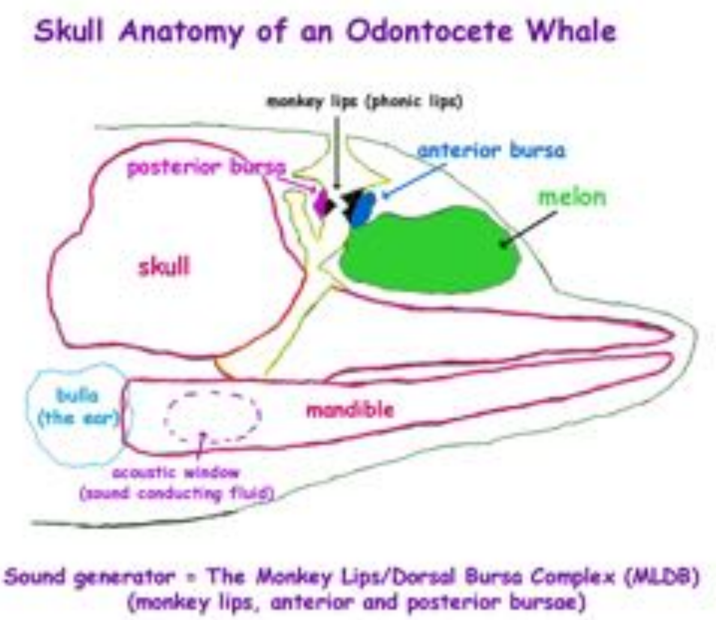
<u>Cetaceans Sound Production and Vocal Behaviour:</u>

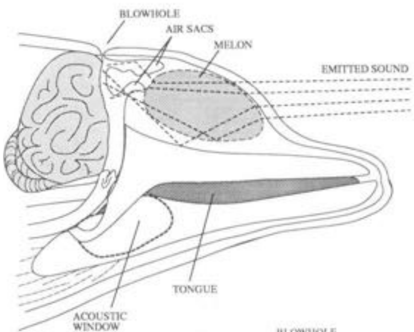
Anatomical specialisation for sound production and reception:

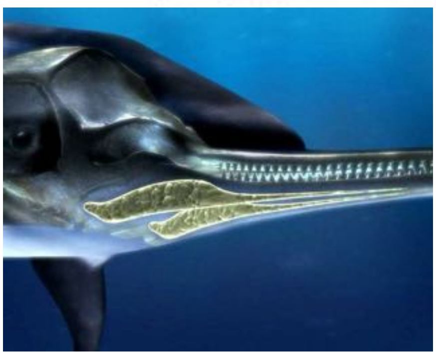
- Produced at larynx
- **Odontocetes**, also have fleshy plugs at top of bony nares (nostrils)
- Sound focused through lipid-filled cavity "Melon"
- Echo - Production of sound
- Air passes through blood hole and through larynx into skull
- Passes MLDB complex (controlled by muscle movement)
- Flow of air produces sound
- Expulsion of air from lungs towards blowhole produces sound
- Air sacs surrounding MLB allows diversion of air and recycling for continued sound production
- Melon focusses sound into narrow beam which can be projected forward

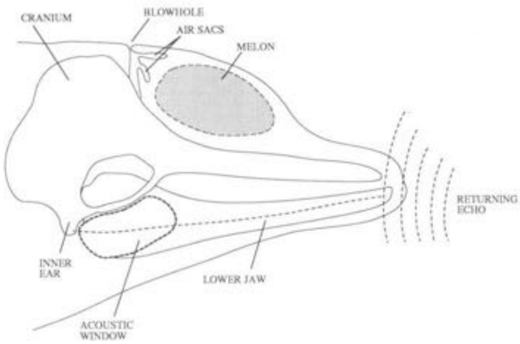
- Acoustic windows (sound-conducting fluids) in lower mandible allowing echoes to be detected (sound reception)
- Transmitted to inner ear (bulla)
- Production of sound from monkey lips (phonic lips)











Acoustic Communication

Vocal behaviour used in conflict, mating displays, signature sounds, searching for food etc.

Mysticete's: Mating display signals (humpback whale song), typically quite elaborate, signature sounds?

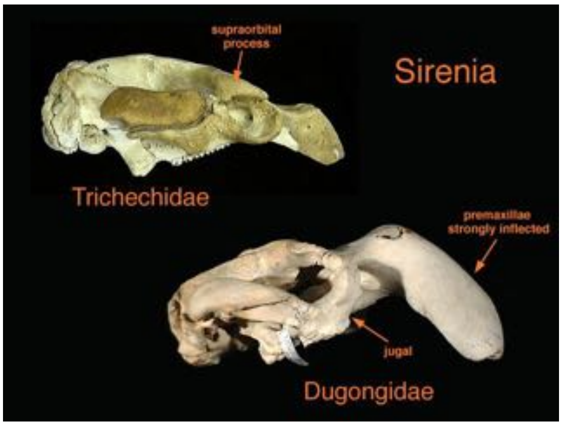
Odontocete Cetaceans: Signature whistles, Echolocations: use broad-band, high freq. pulses of sounds used to image envi by interpreting echoes

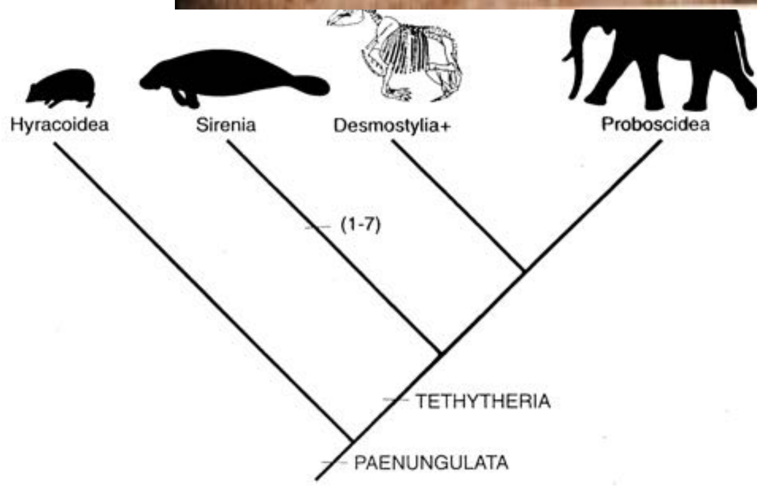
Evolution of Sirenians

- Fully adapted to aquatic envi
- 4 Families, 2 extinct in Eocene
- Extant Families:
- Trichechidae (manatees) and Dugongidae (dugongs)
- Far less diverse than Cetaceans
- Both only have teeth at back of jaw

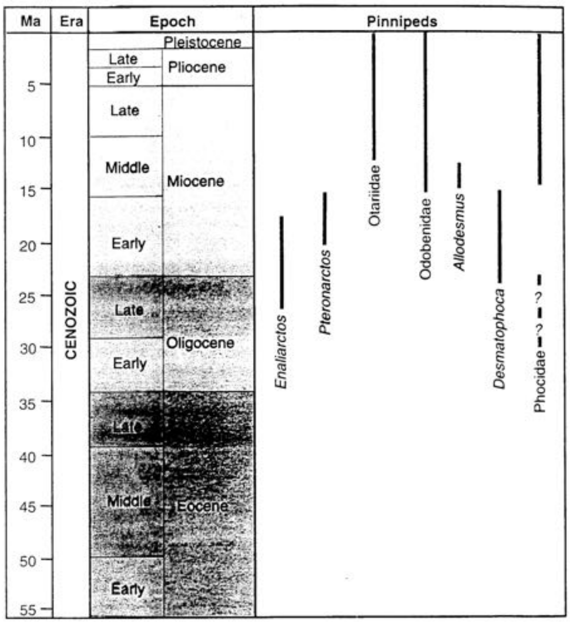
- Main diffs between both is tail fluke structure and also diff in skull structure (more pronounced curvature)
- Manatee - Supraorbital process
- Dugong - Jugal (bony arch of cheek) and pre-maxillae strongly pronounced, angle of snout more pronounced, short pair of tusks (pojecting incisor teeth)

- Desmostylia (within Elephant lineage) - Possible sis clade to sirenians





Evolution of Pinnipeds



Earliest radiation of Pinnipeds in Oligocene

Eared and True Seals (walruses)

Phocids (true seals) - More ancestral and adapted to marine envi

Otatrids (eared seals) - Recently derived

Phocidae (True Seals)

General Characteristics:

- Generally larger than otariids
- Exists in diversity of sizes
- Possess ear canals but lack external ears "earless seals"
- More streamline, complete movement towards aquatic lifestyle
- Short fore flippers - Used for fine tuning manoeuvring (steering)
- Hind flippers longer - Bulk of power comes from them - digits long and strong
- All flippers are clawed
- Swimming: Scull hind quarters and hind flippers
- Flipper webs are spread out into broad paddle - Sculling
- Better at diving - More adapted to deeper waters, for longer time
- Less adapted to land - Cannot lift torso, more awkward, undulation and dragging, unable to rotate hindlimb forward to lift body off ground

Species:

- Bical seal
- Grey seal
- Hawaiian monk seal
- Southern elephant seal

Reproductive Behaviour

- Sexual Dimorphism - Varies within species
- Southern elephant seal - 400-200kg female, 2000-5000kg in males
- Whilst other species are monomorphic

- Generally polygynous (1 male numerous females) but varies
- Varies on degree of aggregation on breeding colony
- Highly aggregated - Extreme polygyny
- Less aggregated where envi less constraining - Less potential for polygyny
- Alpha, dominant, territory holding, or sneaky males, opportunistic, subordinate
- Range of male strategies (territories, maritories, dominance hierarchies),

Mode of Reproduction

- Placental mammals
- Need to give birth and care on land
- Energetic investment differs

- Capital Breeders:
  - Most of year spent at sea to stock up on food reserves, build up thick layer of blubber used for provisioning themselves and pups on land/ice
  - Don't forage during raising and lactation (condensed period)

- Hooded seals - Birth to weaning 4 days due to fat rich milk (45%)
- Grey seals - Birth to weaning 18 days

<u>Condense rearing into short period and wean - (adaptive to short intense period of provisioning and growth)</u>

+ Get back to sea for feeding
+ More vulnerable on land or unstable pack ice
+ Don't need to be close to good foraging grounds
+ More flexibility in breeding ground
+ Will mate again at end of lactation period

- Not good for individual recognition - Less selection for enhanced recognition capabilities

<u>Otariidae (Eared Seals):</u>

<u>General Characteristics:</u>

- Longer fore flippers
- Twisting body action
- Hind flippers act as rudders
- Claws lost on outer two digits - Small nails away from flipper edge
- Swim - Breast stroke action, hind flippers used as stabilisers, head and neck for steering
- Limited to depth of dive
- Land - Can rotate hind flippers forward to walk, allowing lifting of bodies on land
- Allows faster movement

<u>Species:</u>

- Antarctic fur seal
- Stella sea lion
- Southern sea lion

<u>Reproductive Behaviour:</u>

- Highly polygynous, males very territorial
- Pronounced sexual dimorphism (male 2-4 times larger than females)
- Pregnant females haul out onto male's territory, give birth soon after arriving, mate few days after parturition

- Females alternate periods feeding at sea for several days with shorter bouts of nursing pup on land
- 4~6 days forage and come back to pup
- Pups left unattended, recognition system required, auditory signature cals and olfaction
- Income breeding
- Period of foraging and nursing
- Must be geographically close to food source
- Longer pups nursing period - Several months
- Milk (30% fat) - Less than phocidae

Odobenidae:

General Characteristics:

- Both Phocid and Otariid characteristics
- No external ears
- Can use both fore and hind flippers
- Hind flippers for locomotion on land - Cannot lift due to large mass
- Swimming - Use mix of both, sculling and breast stroke (phocid and otariid techniques)
- Only living member - Walrus

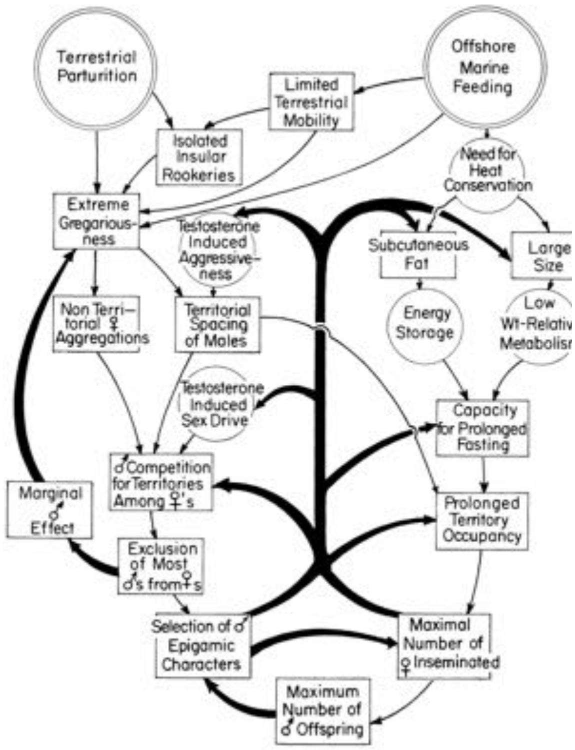
Tusks - Unique

- Lacking in fossil odobenids
- Recent in evolution

Reproductive Behaviour:

- Income breeding strategy
- Highly polygynous
- Longest pup nursing and dependency
- Prolonged periods of lactation - 2 years
- Lowest fat content (fat 20-25%) of milk

Once thought more closely related to otariids, now closer to phocids



Schematic Model for Evolution of Pinniped = Polygyny

2 Key Pinniped Traits:

1. Terrestrial Parturition (giving birth)

    - Coastal envi, offshore islands
    - Large aggregations of females
    - Sexual selection - For larger meals
    - Compete for access to females

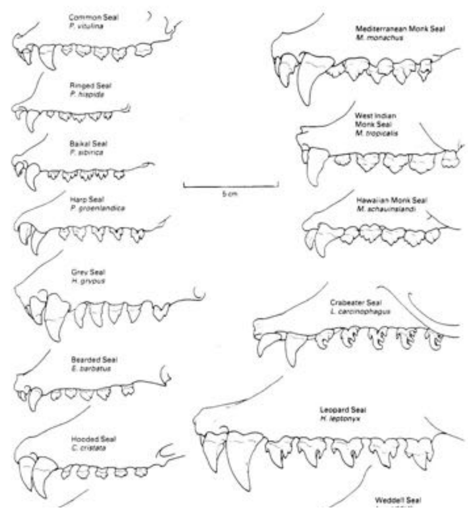
2. Offshore Marine Feeding

    - Larger males stay ashore and fast longer to allow more mating
    - Feedback and dries evolution of polygyny

Fur vs. Fat For Insulation:

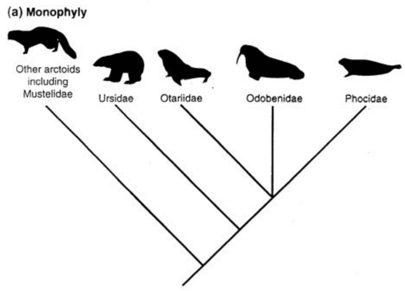
Phocids - Rely on fat for insulation and fast for longer periods, but fur for streamlining

Evolution of Pinniped = Dentition



- Important for classification
- Large canines
- Some variation across diff species

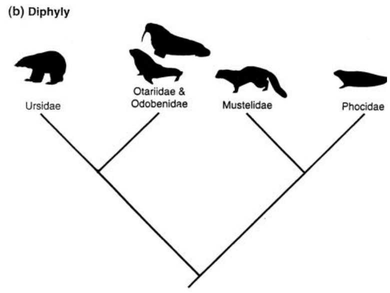
- Leopard Seal: Large slicing pre-molars and molars
- Crab-Eater Seal: similar form but more cusps. eats Krill, will sieve out



Evolution of Pinniped = Monophyletic or Diphyletic

2 branches - Monophyly vs. Diphyly
Monophyly:

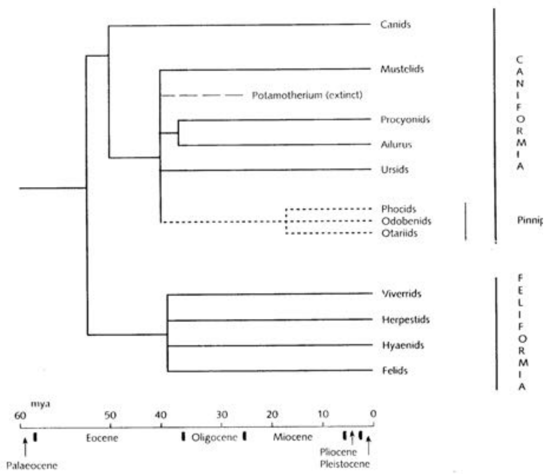
- Common ancestor of pinnipeds includes: Bears, Otters
- 1 Branch



Diphyly:

- Split into 2 major groups
- Otariidae and Odobenidae splits off with bears
- Phocidae splits off with otters

Modern Genetic Tests: Phocids and Otariids resemble each other more closely than any other carnivores - Monophyletic view



<u>Monophyly vs. Diphyly: Molecular Phylogeny of Carnivore Evolution</u>

Caniformia

Feliformia

Potamotherium - Fossil evidence for mustelid-phocid sis relationship

Rapid radiation of both Feloids and Canoids at same time

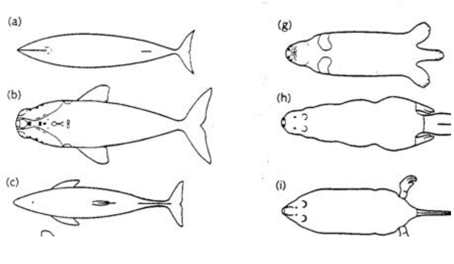
<u>Evolution of Pinnipeds</u>

- *Puijila darwini*: 24-20 MYA
- Walking seal, semi-aquatic, upright stance
- Limbs powerful - For digging or swimming
- Movement across land bridge
- Diversification into modern pinnipeds
- Phocids lineage along east coast
- Otariids lineage along west coast
- Hawaiian monk seal and Northern fur seal - Equatorial regions

Marine Mammal Adaptations:

a) Anatomical and Physiological Adaptations

Swimming:

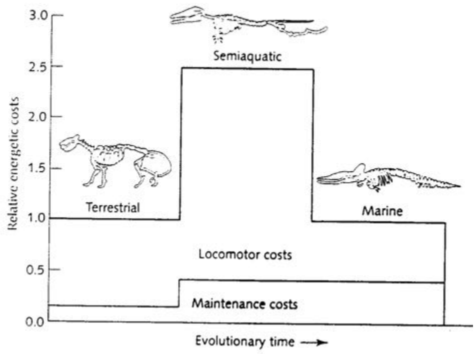


- Streamlining body - Reduce cost of movement in aquatic medium, bladder aids this generating smoother body shape, skeletal system

- Modified appendages - Aquatic vs. Amphibious species

- Marine mammals - Whale, manatee, seal, sea lion, sea otter
- Semi-aquatic mammals - beaver, muskrat, mink, platypus, human

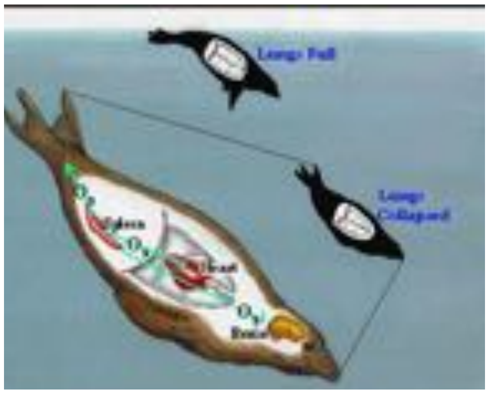
  - Costs of semiaquatic compared to exclusivity
  - Land - High locomotion costs, low maintenance costs (esp. if warm envi)
  - Aquatic - High maintenance (cooling of water), lower locomotion costs (mass supported by water)
  - Semi-aquatic - Suffer higher costs
  - Need to keep warm but also high locomotive costs - Not fully streamline, but this would constrain ability to move on land



- Change in locomotor & basal maintenance costs with evolution of marine mammals
- Similar total costs for terrestrial & marine specialists
- But change in relative contribution of locomotor & maintenance costs.

<u>Dive Physiology</u>

- Dive response - Adaptations to permit prolonged, deep dives
- More efficient utilisation of oxygen stores - higher oxygen stores

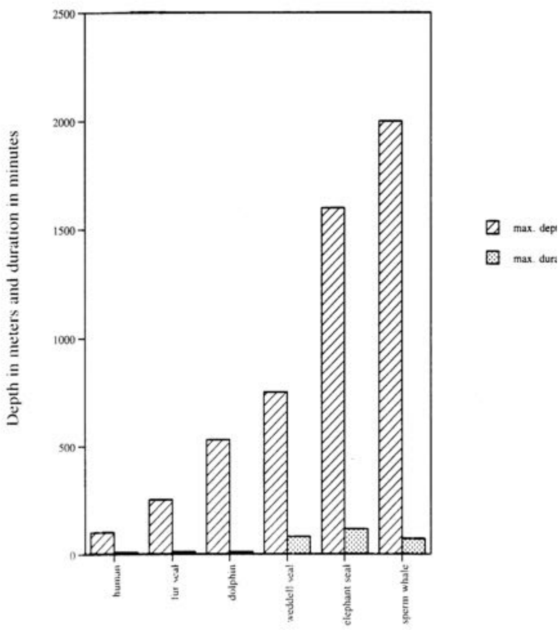


- Minimising risk of nitrogen toxicity (bends)
- At 30m lungs collapse - Flexible lungs allows this
- Reduce nitrogen when coming back to surface

- Force oxygen into muscles and myoglobin
- Oxygen delivered to key organs
- Lungs expand on coming to surface - Thick coating mucus, prevents lung surfaces sticking together and hindering re-inflation
- Much higher oxygen storage in muscle

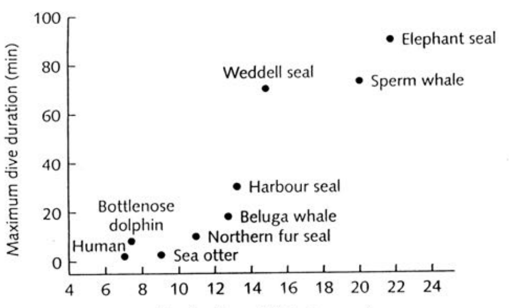
Elephant Seal (Phocids) - Up to 1 hour, dive down to 1600m depth

Fur Seal (Otariids) - Short dive, up to 200m dives



<u>Diving Physiology:</u>

- 3~10x more myoglobin in muscles than terrestrial vertebrates
- Greater affinity for oxygen
- Haemoglobin has saturation curve to right of myoglobin
- Blood vol of marine mammals as % of body mass vs. max. dive duration
- Blood vol is higher relative to body mass
- Correlation with maximum dive duration



Thermal Regulation:

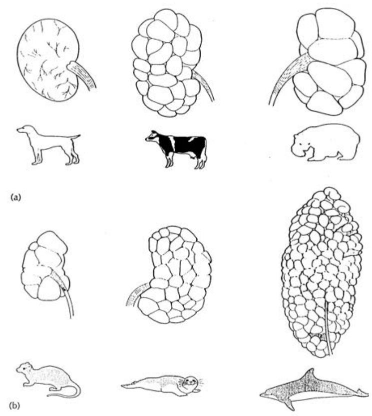
a). Pelage (fur)
- Dense, oily fur of sea otter and otariids
- “blow” air in for added insulation - fluff up on land for air trapping
- Useful for shadow dives - Pressure at depth expels this air limiting dive depth

b). Subcutaneous Fat (blubber)
- Blubber very thick
- Energy stores and insulation

c). Behavioural Thermoregulation
- Behavioural adaptation on land
- At risk of overheating so need to cool down
- Wet sand or bathing
- Clustering caused by need to be close to pools or shady areas

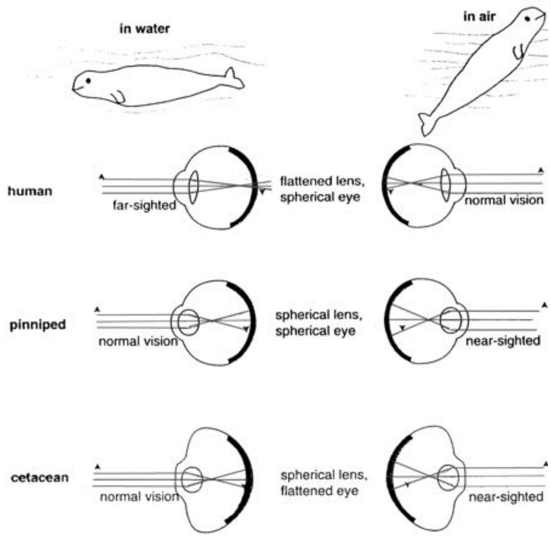
Digestion

- High salt intake due to foraging at sea
- Regulating salt - Specially adapted kidneys increased num of lobes (reniculi)
- Indicates greater efficiency at removing salt
- Mariposa - Ability to drink sea water and excrete salt, non-reliant on fresh water source



Neural Physiology:

- Visual adaptations
- Rounded lens to match refractive properties of water
- Except in river dolphins
- Fatter lens, greater bending allowing focus in water
- Near-sighted on land
- Humans - Far sighted in water
- Cetacean (dolphin/whale) - More adapted, flattening of eyeball, more rods, low-light sensitivity and great vision in poor light conditions
- Large pupil when dividing deep
- Reflective cells at back of retina reflect light back to retina and ensure maximum absorption
- Mucous to keep moist (particularly on land)



Olfactory Sense:
- Mostly lost in cetaceans — Olfactory lobes and nerves absent in toothed whales
- Sense of smell limited in marine environment
- Pinnipeds - Well developed (as good as terrestrial mammals)

- And also well developed Gustatory sense

Tactile Sense:
- Used for mother-pup recognition - Tactile Sense
- Facial enervation and foraging behaviour
- Used to sense envi
- Via whiskers (bearded seals)
- Enable sensing envi through tactile sensory modalities in zero light conditions
- Pinniped vibrissae - Mechanoreceptors

Modes of Sensation and Communication Underwater
- Tactile sensation is similar in air and water
- Other modes of sensation/communication differ
- Acoustic/Hearing - Doesn't change air or water
- Vision, olfaction, electrical sense - Differs in water or air

Cetacean Brain
- Largest brains on earth - Sperm Whale
- Size does not indicate cognitive capabilities
- Well developed (cerebrum)
- Relative size of brain is low in sperm whale
- Greatest cognitive capability is harbour porpoise (Cetacean - Phocena)
- Relatively larger than most vertebrates (except humans)

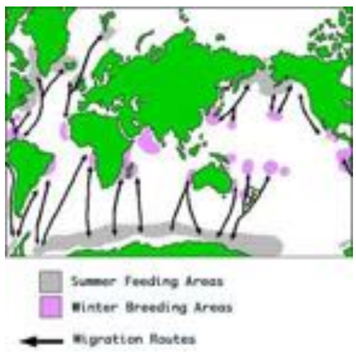
Brain/Body Weight Ratios (EQ):

Mysticete (whales) - Greatest ratio diff in Blue Whale

Odontocetes - Greatest cognitive capability is harbour porpoise, but large ratio in sperm whale

Pinnipeds - Similar to primates (1:110 - common seal) ~ (1:592 walrus)

Primates - 1:50 human ~ 1:509 gorillas



b) *Behavioural Adaptations*

Migration and Dispersion:

- Example - Baleen whale species
- Seasonality in marine envi
- Grey Whale - Bering Sea (Alaska) to Mexico (12000km) twice a year
  - South birthing grounds and North breeding grounds

Humpback whales:
- Feeding in higher latitude nutrient-rich waters in Summer and breeding at lower latitudes in tropical waters in Winter

Seal Species:
- Foraging trips between annual breeding seasons
- Delayed implantation: extends 6-8 month gestation period to allow for annual cycle
- Migration route and breeding area of ringed seals (orange)
- Feeding and Breeding areas of bearded seals (yellow)

- Females - Coastal
- Males - Foraging in deeper water, better diving capability
- Movement with annual cycle of ice edge
- Access to food and water and substrate for hauling out

Marine Mammal Evolution: Summary

1. Diverse groups classed as marine mammals have multiple origins, united by adaptations to marine envi

2. Earliest cetaceans evolved in early Eocene (approx. 50 MYA) - Archaeocetes (extinct), Most modern spp evolved 10 MYA in middle Miocene & divided into mysticetes & odontocetes

Mysticete's - Baleen whales: Blue, Right, Bowhead Whales
Odontocetes - Toothed whales: Sperm whale, Orca, Dolphins etc.

3. Discovery of *Pakicetus attocki,* spp with traits of both Archaeocetes & Mesonychids, showed direct link with Artiodactyls

4. Earliest radiations of pinnipeds 25-30 MYA in Oligocene, 3 extant lineages: Phocids (earless seals), Otariids (eared seals) and Odobenids (walrus)

5. Sirenians evolved in Eocene & most closely related to elephants (Proboscidae). There are two extant groups, the dugongs (Dugongidae) & the manatees (Trichechidae).

Sirenians (Order) - Fully aquatic, herbivorous mammals inhabit swamps, rivers, estuaries, marine wetlands, and coastal marine waters. 4 species living, in 2 families and genera = dugong and manatees

6. Marine carnivores evolved much later in Pleistocene (within last 2 million years)

Macroevolutionary Process 1

Aims

Evolution of Vertebrates from Invertebrate Chordates

Chordata (phylum): Vertebrates, sea squirts and lancets

• Evolution of jawed vertebrates
• Evolution of land-dwelling, four-limbed (tetrapod) vertebrates
• Evolution of reptiles and birds

Macroevolutionary Processes

- Introduce you to fossil record and other evidence of evolution
- Introduce you to macroevolutionary processes,
  - Radiations
  - Extinctions
  - Gradual change vs punctuated equilibrium
  - Co-option of existing evolutionary features for new purposes

Macroevolutionary Processes

Fossils and the Cambrian explosion

- How to examine macroevolutionary processes
- Cambrian Explosion - Rapid diversification of taxonomic grops

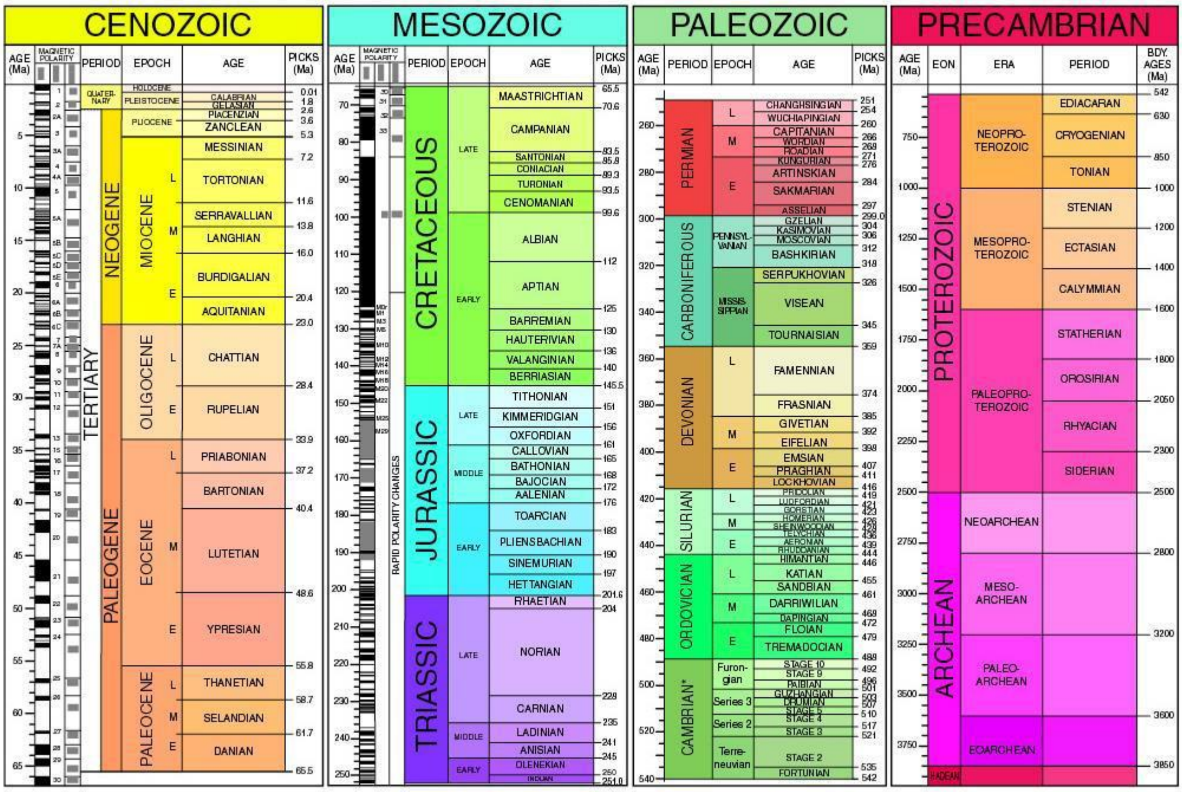
Key Processes on Earth and Evolution of Life: Past to Present

22.1 *Earth's Geological History*

ERA	PERIOD	ONSET	MAJOR PHYSICAL CHANGES ON EARTH	MAJOR EVENTS IN THE HISTORY OF LIFE
Cenozoic	Quaternary	1.8 mya[a]	Cold/dry climate; repeated glaciations	Humans evolve; many large mammals become extinct
	Tertiary	65 mya	Continents near current positions; climate cools	Diversification of birds, mammals, flowering plants, and insects
Mesozoic	Cretaceous	144 mya	Northern continents attached; Gondwana begins to drift apart; meteorite strikes Yucatán Peninsula	Dinosaurs continue to diversify; flowering plants and mammals diversify. **Mass Extinction** at end of period (≈76% of species disappear)
	Jurassic	206 mya	Two large continents form: Laurasia (north) and Gondwana (south); climate warm	Diverse dinosaurs; radiation of ray-finned fishes
	Triassic	248 mya	Pangaea slowly begins to drift apart; hot/humid climate	Early dinosaurs; first mammals; marine invertebrates diversify; first flowering plants; **Mass Extinction** at end of period (≈65% of species disappear)
Paleozoic	Permian	290 mya	Continents aggregate into Pangaea; large glaciers form; dry climates form in interior of Pangaea	Reptiles diversify; amphibians decline; **Mass Extinction** at end of period (≈96% of species disappear)
	Carboniferous	354 mya	Climate cools; marked latitudinal climate gradients	Extensive "fern" forests; first reptiles; insects diversify
	Devonian	417 mya	Continents collide at end of period; asteroid probably collides with Earth	Fishes diversify; first insects and amphibians. **Mass Extinction** at end of period (≈75% of species disappear)
	Silurian	443 mya	Sea levels rise; two large continents form; hot/humid climate	Jawless fishes diversify; first ray-finned fishes; plants and animals colonize land
	Ordovician	490 mya	Gondwana moves over South Pole; massive glaciation, sea level drops 50 m	**Mass Extinction** at end of period (≈75% of species disappear)
	Cambrian	543 mya	O_2 levels approach current levels	Most animal phyla present; diverse algae
Precambrian		600 mya	O_2 level at >5% of current level	Ediacaran fauna
		1.5 bya[a]	O_2 level at >1% of current level	Eukaryotes evolve; several animal phyla appear
		3.8 bya	O_2 first appears in atmosphere	Origin of life; prokaryotes flourish
		4.5 bya		

- Summary of many changes in global geo and envi
- From Precambrian into Quaternary (modern day)
- Major physical change: Structure of Continents - Drifting and colliding (plate tectonic processes)

Eras - Cenozoic, Mesozoic, Palaeozoic, and Precambrian



*International ages have not been fully established. These are current names as reported by the International Commission on Stratigraphy.

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Walker, J.D., and Geissman, J.W., compilers, 2009, Geologic Time Scale: Geological Society of America, doi: 10.1130/2009.CTS004R2C. ©2009 The Geological Society of America.

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Era -> Period -> Epoch -> Age

Geo Time Scale

Order of Periods:

Cambrian
Ordovician
Silurian
Devonian
Carboniferous
permian
Triassic
Jurassic
Cretaceous
Tertiary
Quaternary

Eon	Era	Period		Epoch	Time Began (Million Years)
Phanerozoic	Cenozoic	Quaternary		Holocene	0.01
				Pleistocene	1.8
		Tertiary	Neogene	Pliocene	5.3
				Miocene	23.0
			Paleogene	Oligocene	33.9
				Eocene	55.8
				Paleocene	65.5
	Mesozoic	Cretaceous			146
		Jurassic			200
		Triassic			251
	Paleozoic	Permian			299
		Carboniferous	Pennsylvanian		318
			Mississippian		359
		Devonian			416
		Silurian			444
		Ordovician			488
		Cambrian			542
Proterozoic					2500
Archean					4000
Hadean					4560

Rocks and Fossils

Fossils - Relates to something found in ground, obtained by digging, preserved remains or traces of orgs from remote past

- Evidence for macroevolutionary processes comes from fossil material
- Entities buried in ground

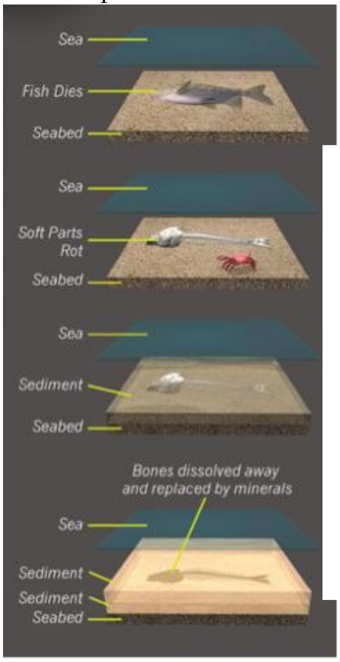
- Particular fossil types were associated with certain rock strata gave rise to idea of a geo timescale

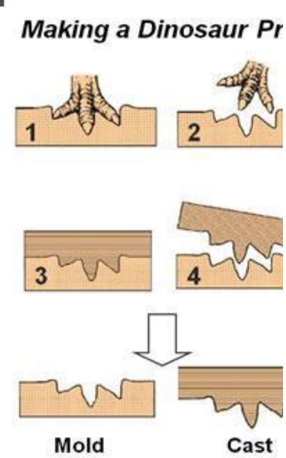
- Fossil Record: Overall combo of fossils over known-aged multiple strata - possible to infer change over time
  - Chronological sequence on how orgs changed

<u>Fossil Formation</u>

- Very specific conditions required

1. Orgs live or die in wet and shallow areas
2. End up on sea bed
3. Flesh (soft material) rots or scavenged
4. Leave bones behind - Silt covers this
5. Slow flowing water required for silt to settle and build up on top of bones
6. Over time, pressure builds, bones turn into rock via compression
7. Bones replaced by minerals seeping in from rock forming around skeleton
8. Skeleton replaced by minerals
9. Diff composition to surrounding sediments





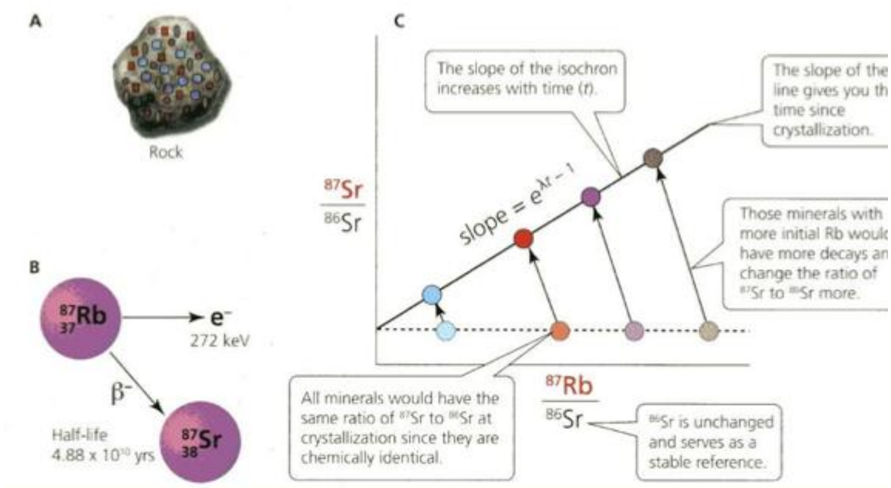
<u>Radiometric Dating of Rocks</u>

- Became possible in early 1900s
- Rate of decay (half life) of radioactive elements provides clock to age rocks and sediments
- Elements used are chosen to match timescale of interest
- Example elements: 14C, 40K, 87Rb, Radioactive element

- 87Rb (Rubidium) forms 87Sr (Strontium) half life 48.8 Billion years

- Sr also present as 86Sr (stable isotope, form doesn't change over time)

- Ratio of 2 isotopes used to estimate age of rock - chronology of fossils



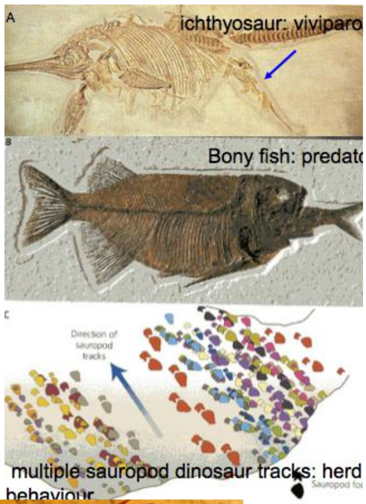
<u>Dating Fossils</u>

- Fossils generally dated from rock layer from which they are taken

- Esp. easy in rocks which form distinct bands (sedimentary rocks) and which haven't been widely perturbed
- Aid in dating of fossils
- Bands can be counted and depths measured to estimate periods over which they were laid down (stratigraphy) as well as specific bands being dated
- Extrapolating data from successive key points and specific features to allow interpreting of dates of fossils
- Oldest fossil of Homo sapiens in Ethiopia dated using volcanic ash from distinct eruptions - Radiometric techniques used (from volcanic ash)

<u>Info From Individual Fossils</u>

- Mainly: Anatomy of an org
  - Example: Imprints in soft muds that have then formed rocks
    - i.e. mineralised tissues (usually only hard tissues - even more specific conditions required for soft tissued orgs)



However mineralised tissues rarely provide full picture

Beyond basic morphology, sometimes provide life-history or even behaviour etc.

<u>Example:</u>

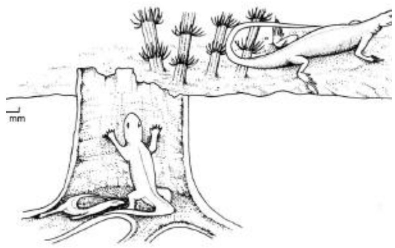
A - Ichthyosaur: Viviparous - Live birth
B - Bony Fish: Predator (fish prey in mouth)
C - Multiple Sauropod Dino Tracks: Herd Behaviour

<u>Info from More Intact Orgs</u>

Amber (preserved plant resin):
- Allowing fossilisation of whole orgs (including soft tissue)
- Fossilisation of organic debris and (usually) insects in amber
- Encapsulated in lobs of tree sap
- Also for small reptiles and arthropods

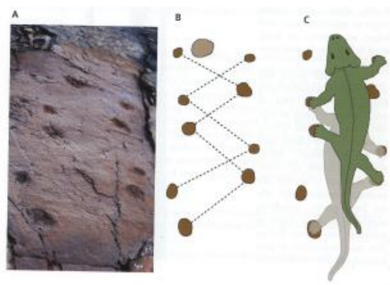
Largely preserved ant from 50 MYA

<u>Info on Community and Ecosystem-level Info:</u>



- Give info on ecosystem dynamics
- Fossil of *Paleothyris* (Reptile from carboniferous period)
- Found within a fossilised stump of tree fern
- Determines what kind of vegetation that was around during time of this reptile

<u>Info from Fossils on Behaviour</u>



aka - Behaviour

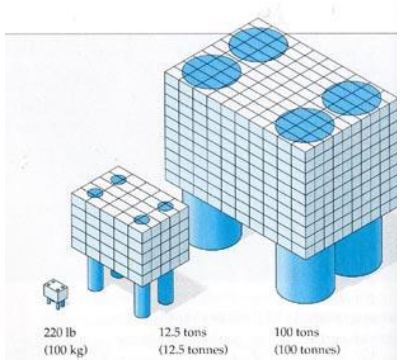
Earliest reported trackways from soft sediment marshy habitat - 390 MYA
- Created by an early tetrapod (4-limbed terrestrial vertebrate)
- No just behaviour, can also estimate size and mass of animal
- Tracks can also show modes of locomotion

<u>Info from Fossils on Animal Mechanics</u>

Animal Mechanics: Models and Mechanics from anatomical info

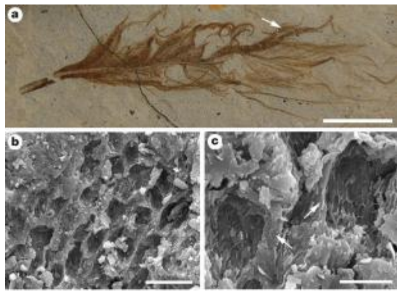
- As body vol (weight) increases legs become proportionally broader to accommodate
- So can backtrack size of feet in fossils to body size and weight of organism
- Providing body mass size of extinct species though modes of locomotion

Potential limit - At body weight of about 140 tonnes legs would be so wide they would touch



Info from Individual Fossils - Microscopic Info (More Recently)

- Discovery of fossilised melanosomes (cells containing pigmentation) from feathers of fossil birds and in integumentary filaments of dinosaur ancestors
- Evidence for banding and pigmentation/colour patterns of early feathers
- Cant tell what color they were however can tell distinct patterns (bands, stripes etc.)
- Can postulate function: mate attraction, camouflage, displays?



Faeces can also show life history/foot items consumed

Problems with Fossil Evidence

1. ***Most orgs don't fossilise when they die***
   - Most are eaten/decompose
   - Conditions for fossilisation in rock very specialised
   - Requiring settlement of fine sediment over hard structures, and infiltration into pores

2. ***Soft tissues rarely mineralise***
   - Fossilisation of soft tissue (e.g. muscle) requires anoxic muds
   - Prevent rapid decomposition and enable preservation of fine tissues
   - These sites are rare – Lagerstätten - Sedimentary deposit exhibits extraordinary fossils with exceptional preservation, sometimes including preserved soft tissues
   - Conditions must be precise - Habitat and envi wet medium, fine sediments settles on hard structure

3. ***Most rock is inaccessible***
   - To Palaeontologists (high up in mountains, cant reach these fossils, or buried under top rock)
   - Most study occurs in 'hotspots'

4. ***Gaps*** - Often appear in fossil record, giving discontinuous info on evolutionary patterns (conditions not right in producing fossils)

5. ***Interpretation*** of fossils can be contentious; gathering evidence by independent methods is difficult. Estimate time of divergence of taxa from calibrated molecular clocks (rate of BP substitutions) to compare with extant groups bio, Interpretations tend to change over time

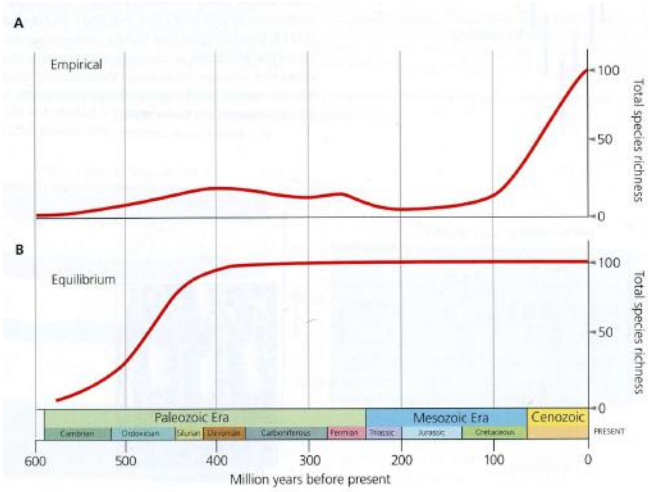
6. ***Dating*** can be tricky (rocks/sediments can be churned by geo processes)

7. ***Different rock types*** (and geo periods) vary in their suitability for fossilisation, affects fossil availability

8. ***Availability of Rock Outcrops*** of diff geo ages cause bias that requires correction

9. Difficulty in ***distinguishing species*** from limited anatomical detail; bio species concept cant be invoked

Gap in fossil record - How significant that can be shown in graph



Unadjusted (A) and adjusted (B) marine invertebrate richness index

(B) is modified to take into account bias in fossil preservation and rock outcrop availability

Empirical - Actual measurements based on fossil record, low diversity till very end (mesozoic era)

Equilibrium - Scientists best estimate on what diversity was like (modified)

Integrating Methods to Undrestand Events In Macroevolution

- Range of techniques are integrated
- Stratigraphy and radiometric dating, including geo techniques such as imaging of rock surfaces
- Usually estimates of diversity are adjusted from fossil record to give better representation

Example - Fossil evidence with chemistry, geological imaging for mass extinction event at end of Cretaceous period, 65 MYA; 76% of spp. estimated extinct, wiped out dinosaurs, postulated to be asteroid impact < 2.5 MY.

Cambrian Explosion (488~542 MYA)

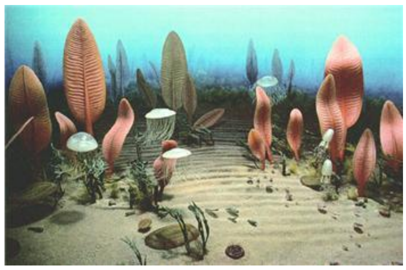
Before Cambrian Period

Metazoan Life Started before Cambrian

Metazoa - Kingdom Animalia

- Increased oxygen in envi
- P/S marine Eukaryotes (plankton and benthic biofilms)

Pre-Cambrian - Late Proterozoic Eon



- Evidence of substantial diversity of complex multicellular marine animals
- Soft bodied org, becoming more complex, origins may have bee earlier but not preserved in fossil record

Cambrian Period

- O2 conc. approaching current levels
- Influenced species diversity
- Rapid diversification of animal groups
- Greater increase in **community complexity** and ecological roles
- Increase range of orgs using sub-surface habitat and diversity on surface - those who can swim around in shallow marine envi

Rapidly Diversifying Fauna:

- Most of which live in modern day originated in Cambrian - Including sponges, cnidarians, worms, molluscs, and arthropods
- But many Cambrian major taxa have since become extinct (e.g. lobopoda)

Key Fossil Beds e.g. Burgess Shale (BC) and Chengjian (China):

- Burgess shale - yielded over 65,000 specimens of 93 mostly soft bodied marine animals
- Provide good quality fossils with details - Good preservation
    - Including some soft-bodied taxa (e.g. Cnidaria)

- Reconstruction of shallow marine envi->

- First evidence of primitive vertebrates at end of Cambrian
- Great increase in community complexity and ecological roles
- New life forms created ecological niches for new life forms

- Added selection pressures
- Evolution of Predators —> evolutionary arms race e.g. Protective hard coverings

Burgess Shale - Experiments in Macroevolution

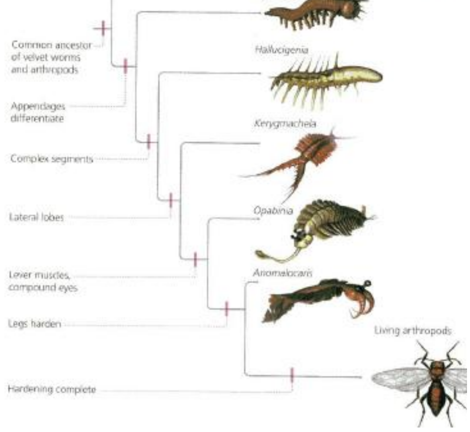
- Key Lagerstatt of Cambrian age
- Yielded over 65,000 specimens
- More than 93 soft bodied marine animals
- Includes sponges, lobopods, arthropods, chordates, polychaete annelids and priapulids as well as other unclassified orgs
- Included fossils of part of org with shrimp-like abdomen
- Prime fossil beds - Yield highly detailed and resolution fossils

Reconstruction of some orgs identified from Burgess shale

Anomalacaris - A Cambrian Puzzle

- Abundant fossils in Burgess shale shows parts of this beast
- Difficult to interpret - Many not ascribed to Anomlaocaris
- Fossils of part of an org with shrimp-like abdomens (with long arm)
- New interpretations from full fossils, 'shrimp-like abdomens' were found to be paired, anterior grasping appendages, then further refinement – a large ventral mouth, with grasping/piecing plates
- A relatively large (*ca.* 0.6 m) mobile predator with large eyes. No longer an anomaly!
- Large ventral mouth used for grasping prey items

Cambrian Origins of some of todays animal groups



Many precursors originated much earlier in pre-cambrian

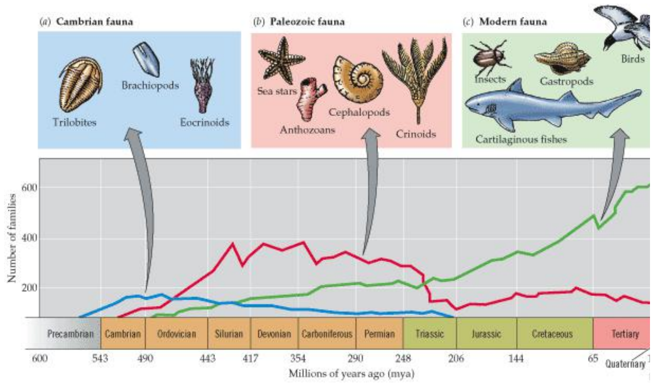
Processes evident in Burgess shale record of evolution of key anatomical traits evident in living arthropods e.g Trend towards increased armament leading to fully hardened exoskeleton seen in modern arthropods

The Burgess Shale Experiments in Macroevolution

Burgess Shale - Contains numerous taxa with body plans that don't occur in later rocks (nothing like them living today - e.g. wiwaxia and hallucinigenia)

Lagerstatten like burgess shale indicates world we live in today is result of chance evolutionary trajectories

Multiple alternatives of biota might have been possible, if failed experiments of evolution had perpetuated



The Great Radiations

Based on marine fossils (orgs)

- Evolutionary lineages diversified and in many cases become extinct
- Chance event: Species suited to changing envi or not
- Various points where taxonomic diversity is removed, then recovery and radiations occurs

- Radiations increased diversity
- 3 great radiations of animals:

1. Cambrian - Trilobites, brachiopods and eocrinoids (marine)

2. Palaeozoic - Sea stars, anthozoans, cephalopods and crinoids (marine)

3. Modern - insects, gastropods, reptiles, birds and cartilaginous fishes (marine and terrestrial)

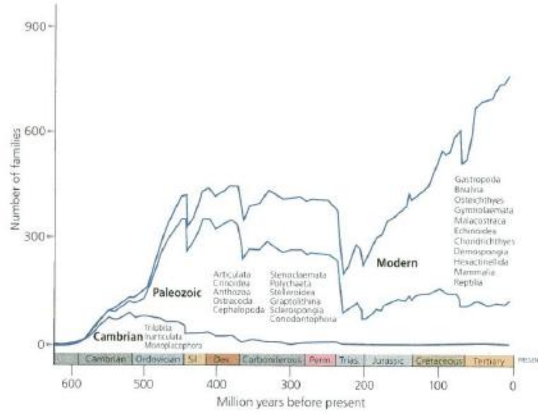
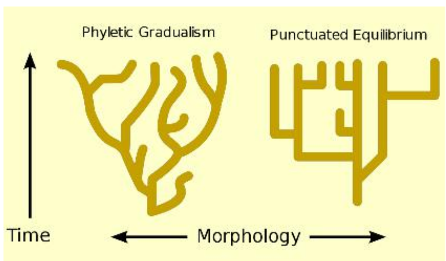


Diagram - Right
- Same but original data based on marine fossil record - More specific and finer temporal resolution
- Shows more clearly reductions at mass extinction events

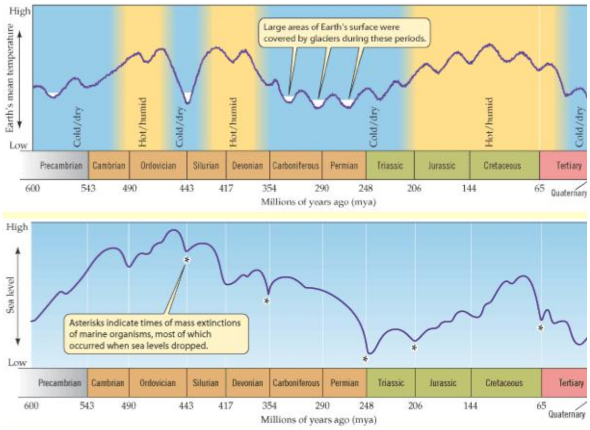


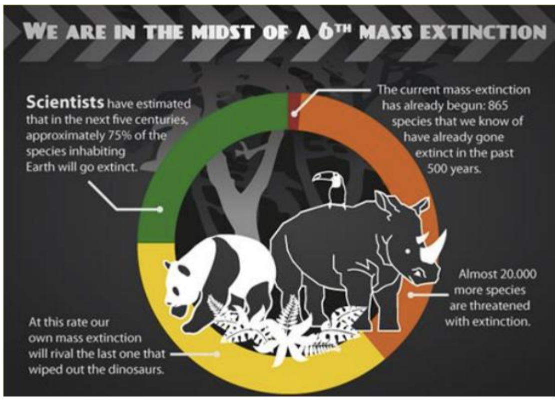
Gradualism vs. Punctuated Equilibrium

Punctuated Equilibrium
- Abrupt changes, long periods of stasis (equilibrium), punctuated by periods of rapid evolutionary change and speciation
- Conditions where most ecological niches are already occupied, may be little evolutionary pressure, or opportunity for change
- Over time some taxa diversify and flourish, as other diminish
- Certain periods of rapid diversification and radiations
- Palaeontologists found number of patterns in fossil record that best fit punctuated equilibria model

Gradualism
- Often orgs in fossil record appear to change through series of intermediate stages gradually

- Slow, steady, directional change (surprisingly rare in fossil lineages)
- Reasons triggering this: Long-Term changes in Earths Climate and Envi
  - Reflected in strong changes in evolution of life in diff envis
  - Change in avg. temp of earth and sea levels
  - Diff phases of cold dry and hot humid envi
  - E.g. Ice age - Extended glaciation, rapid drop in sea level during time of mass extinction





- Global envi changing, some species persist and do well and others do poorly (extinction)

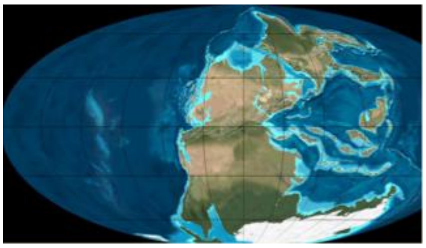
Mass Extinctions within Fossil Record

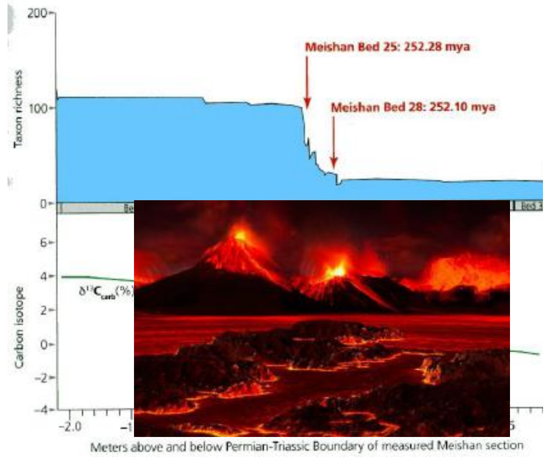
Event	Ended	Duration	Genera lost	spp lost	Factors?
Ordovician	443 MYA	3.3-1.9 MY	57%	**86%**	Raising & lowering of sea level from glacial cycles, changes in sea chemistry.
Devonian	359 MYA	29-2 MY	35%	**75%**	Global cooling, warming; widespread marine anoxia; meteorites(?).
Permian	252 MYA	2.8 MY - 160 KY	56%	**96%**	Widespread volcanism, global warming, widespread marine anoxia, high CO_2 & low O_2.
Triassic	200 MYA	8.3MY - 600KY	47%	**80%**	Marine volcanic activity elevated CO2, global warming, caused calcification crisis in oceans.
Cretaceous	65 MYA	2.5 MYA - **< 1 year !!!!**	40%	**76%**	Meteorite (Yucatan peninsula, Mexico) - caused global cataclysm & rapid cooling. Preceding impact biota already declining (volcanism, CO2 increase, global warming, ocean anoxia episodes).

- Mass loss of species - Permian (one of the most dramatic)
- Cretaceous (only under 1 year) - Where dinosaurs went extinct
- Proposed triggering by meteorite impact - Evidence things were changing prior, decline in diversity (increased anoxia in ocean envi)
- Factors trigger events:
  - Sea level (increase anoxic conditions esp. in early periods due to high marine orgs)
  - Global temp changes (warming-cold cycles)
  - Geo activity - Volcanism (triggered by plate tectonics)

<u>6th Mass Extinction?</u>

- Postulated we are experiencing 6th mass extinction
- Due to human exploitation
- Current extinction rates are approaching equivalent magnitude and speed to past mass extinctions
- In next 5 centuries, approx. 75% of species will go extinct
- 865 species have already gone extinct in past 500 years
- Almost 20,000 more species are threatened with extinction

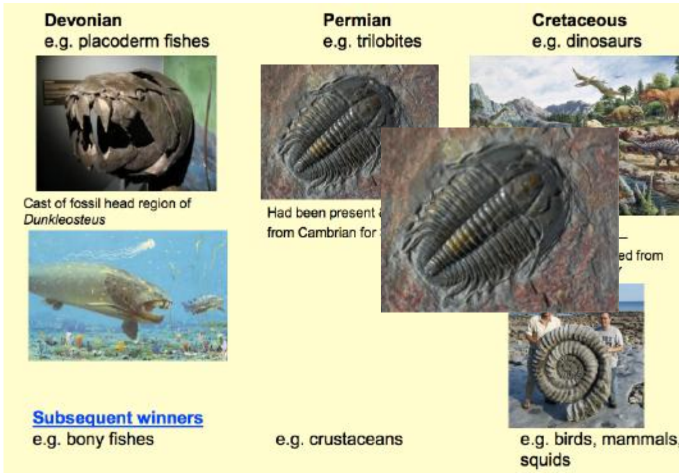




Permian Mass Extinction

- Most dramatic mass extinction event in Earth's history in all envis
- Perhaps 96% of species were lost
- Mass drop in species richness occurred across all envis
- Northern and southern continents collided forming Pangaea
- Conditions for life deteriorated towards end of Permian
- Due to shifting of plate tectonics - Triggering geo activity (EQ and volcanism) - Further deterioration of envi
- Massive, widespread volcanic activity caused ash to block sunlight and dramatic cooling of climate
- Largest glaciers recorded formed
- Atmospheric oxygen declined from 30% to 12% making all but lowest land uninhabitable for many terrestrial animals (inhabitable only for low elevation animals)
- Permian-Triassic Boundary - Huge drop in species richness
- Figures on right - Representation of permian marine community

Losers In Mass Extinctions:



Devonian: Placoderm fishes

Permian: Arthropods e.g. Trilobites (replaced by modern crustaceans)

Cretaceous: Dino and ammonites (replaced by birds, mammals and squids)

Winners (Succesful)

- Bony fishes
- Crustaceans
- Birds, mammals , squids

In Cretaceous Extinction:

- Loss sig community of ammonites (cephalopods)
- Available habitat were colonised by birds, mammals and squids radiation - Ecological niches were replaced by winners

Macroevolutionary Processes 2

(Big and bad: phylogenetic constraints and evolution of large, predatory animals)

Phylogenetic Constraints in Evolution

- Evolution can only work with genetic material provided, whether through directional selection or drift

- Outcomes of macroevolution dictated by **phylogeny**
  - Hence may be diff opportunities/outcomes for diff taxonomic groups
  - Phylogeny - Evolutionary development and diversification of a species or group of orgs or of particular feature of an org

- Machinery changes in evolution -> Lead to Radiations

Example:
- Notable almost all of todays largest predators (>99%) are vertebrates (exceptions - giant squid, giant octopus)
- Wasn't case in the past
- Major predators were vertebrates
- Large orthocones (mollusca), placoderms (chordata) and dragonflies (insects) wingspan over 40cm

- What phylogenetic characteristics and evolutionary processes led to this?

Geo Timescale

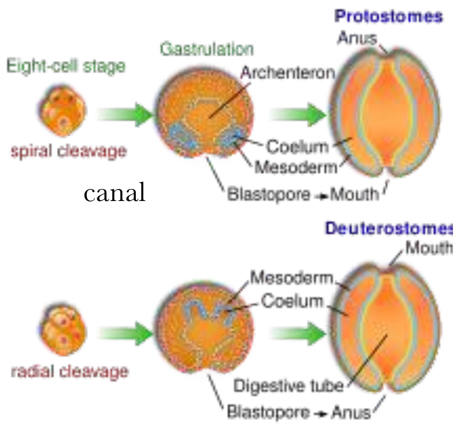
Eon	Era	Period		Epoch	Time Began (Million Years)
Phanerozoic	Cenozoic	Quaternary		Holocene	0.01
				Pleistocene	1.8
		Tertiary	Neogene	Pliocene	5.3
				Miocene	23.0
			Paleogene	Oligocene	33.9
				Eocene	55.8
				Paleocene	65.5
	Mesozoic	Cretaceous			146
		Jurassic			200
		Triassic			251
	Paleozoic	Permian			299
		Carboniferous	Pennsylvanian		318
			Mississippian		359
		Devonian			416
		Silurian			444
		Ordovician			488
		Cambrian			542
Proterozoic					2500
Archean					4000
Hadean					4560

Macroevolutionary changes occurred in Cambrian and so on

Cambrian Explosion

- Oxygen conc. approaching current levels
- Rapid diversification of animal groups
- Most living today originated in Cambrian - Including chordates
- Great increase in community complexity and opening of available ecological roles/niches
- First chordates started to evolve from more sedentary existence towards a mobile, active foraging lifestyle
- Shallow marine envi
- Species evolve and adapt to utilise new resources

Simplified Animal Kindgom Phylogeny



Coelomates: Principal body cavity in most animals, located between intestinal canal and the body wall

Protostomes - Blastopore becomes mouth first
- Ecdysozoans, Platyzoans, and Lophotrochozoans

Deuterostomes - Blastopore becomes anus

- Hemichordates, echinoderms, and chordates

Ancestral Protozoa —> Coelomates

Protozoa - Phylum or grouping of phyla, comprises single-celled microscopic animals (include amoebas, flagellates, ciliates, sporozoans, and many other forms)

Evolution of chordates and major taxonomic groupings in fish, amphibia, reptiles, birds etc.

Echinoderms - Non-chordates, however closely related

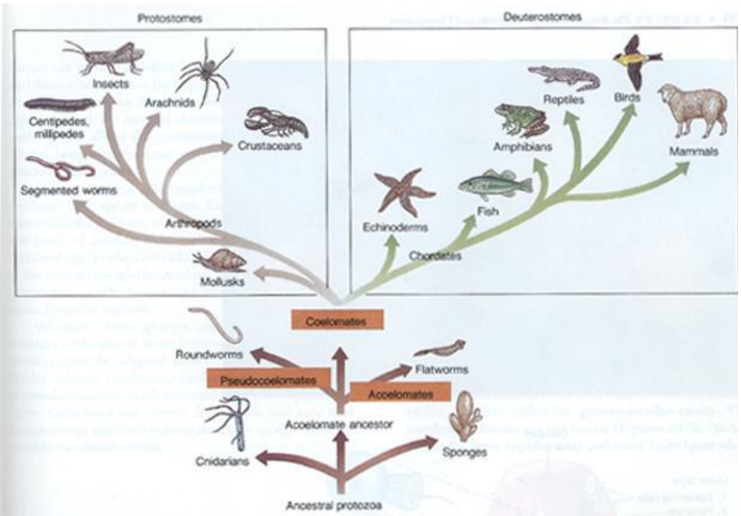
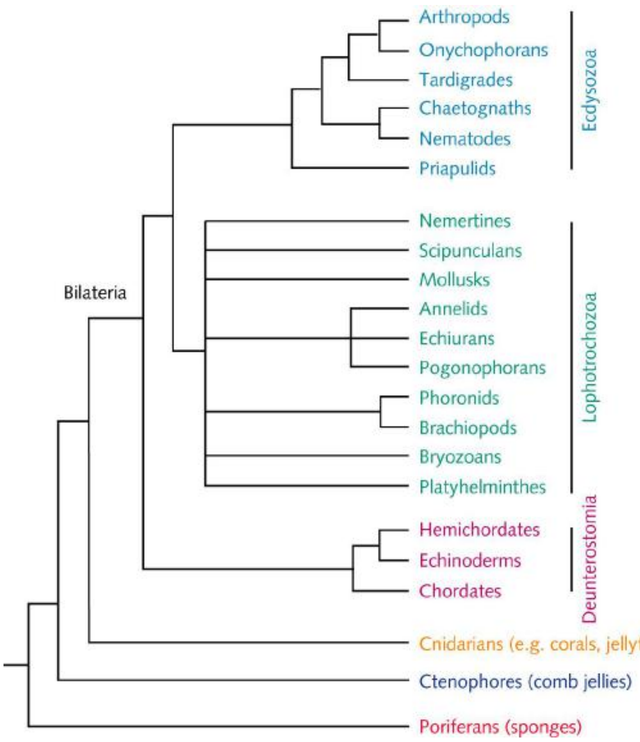
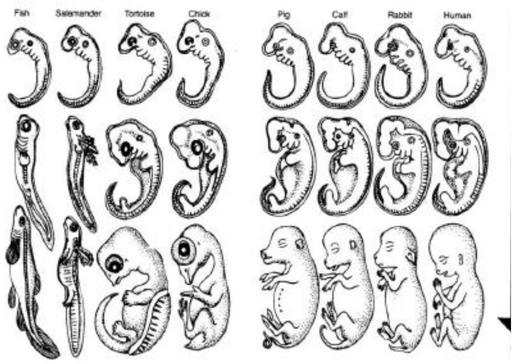


FIGURE 39-5 **An overview of the phylogenetic relations among the major groups of animals.** The sponges, cnidarians, flatworms, and roundworms are referred to as "lower metazoans," indicating their simpler body structure and the fact these were the first types of animals to evolve. Pseudocoelomates and coelomates have a body cavity that is separate from the digestive tract, while acoelomate animals do not. Two major evolutionary lines emerged from the lower metazoa: the protostomes and the deuterostomes.



<u>What is a Chordate? (phylum = Chordata)</u>



Subphyla: Craniata (vertebrata), Urochordata (sea squirts), Cephalochordata (lancelets)

<u>Features of Chordates</u>

- Pharyngeal slits - Oxygen exchange and foraging, gland is located on ventral surface of pharyngeal region

- Notochord - Relatively firm, elastic chord, lies along anteroposterior (head->tail) axis, closer to dorsal portion of body

- Muscular post-anal tail

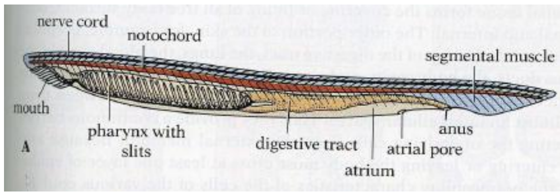
- Endostyle/homologous structure - Longitudinal ciliated groove on ventral wall of pharynx which produces mucous, secretes for trapping food and collecting food molecules passed into gut

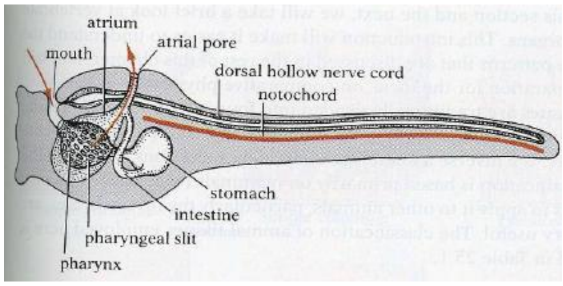
- Dorsal hollow nerve chord

- Dilated anterior end of CNS -> Only present in early embryonic development

<u>Notochord</u>

- Cartilaginous skeletal rod supporting body in all embryonic and some adult chordate animals
- Fibrous rod, runs longitudinal through dorm
- Fairly rigid structure
- Present in all chordates
- Present in embryonic stages - Replaced by vertebral column with cartilaginous or bony vertebrate
- Flexible supportive rod formed of collagen
- Move away from soft bodied orgs
- Ventral to nerve chord





Pharyngeal Slits

- Slits in pharynx
- Origins with feeding (filter function)
- Not always associated with gills for respiration (sometimes called gill slits)
- Present in some fossil echinoderms and chordate ancestors
- Only present in embryonic stage in higher vertebrates
- Runs down from notochord - Muscular segments (myomeres) act with notochord to aid locomotion

Subphylum in Chordates

Urochordata (= Tunicata)

About 2000 marine species

2 Phases in Lifestyle: Larvae -> Adults

1. **Larvae**

   - Free swimming - Mobile
   - Similar body plan to general chordate
   - Anterior end
   - Notochord
   - Dorsal hollow nerve chord
   - After minutes-few days they metamorphose into adult form
   - Pharyngeal gill slits
   - Muscular post-anal tail - Used for dispersal

2. **Adults**

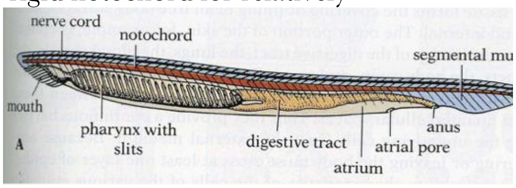
   - Metamorphose into sessile adult form (tunicate)
   - Not like cephalochordates or vertebrates
   - Have pharyngeal slits - But largely no notochord
   - Usually sessile filter feeders (except Larvacea - Free swimming group)
   - Inhalant and exhalent siphons - Spews water out
   - Largely no notochord
   - Tunicate - Marine invertebrate of group which includes sea squirts and salps, have rubbery or hard outer coat and 2 siphons to draw water into and out of body

Cephalochordata

- 22 marine species
- Superficially fish like
- Widely distributed in shallow water
- Usually burrowing, sedentary adults
- Gill slits - Used for food filtering, but also gas exchange, uses pharyngeal apparatus to supply oxygen to gills as well as for feeding
- Looks like primitive vertebrae, but have been evolving separately from vertebrates for 500 million years
- Regarded as a sister group to vertebrates (not direct ancestor to chordates)
- Slight evidence of cephalisation, even though notochord almost extends to front of animal
- Example: Lancelet - live in soft sediments

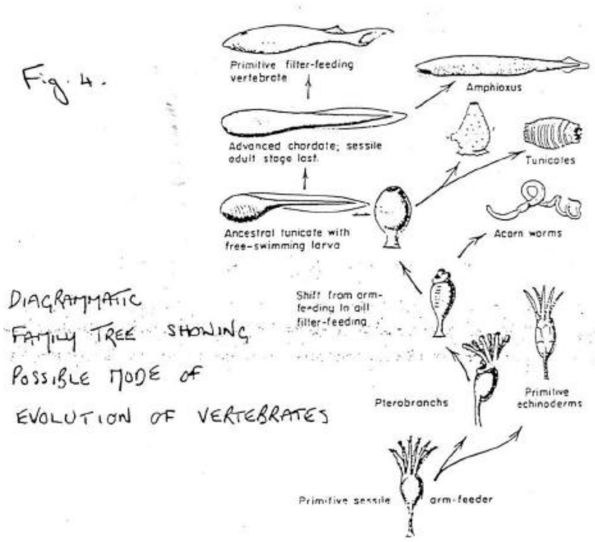
Myotomes:

- Distinct myotomes (= myomere - muscle blocks) supported by elastic semi-rigid notochord for relatively effective swimming
- Blocks of striated muscle fibres on side of body
- Separated by sheets of connective tissue
- Also found in vertebrates
- Homologous to muscle bands in tunicate larvae tails
- Contract in sequence (anterior > posterior)
- Bends body to give waves of undulation (wave like motion) in forward direction
- Wave-like muscular contractions - Propels animal through water
- At any one point, one side of body is contracted whilst other is relaxed
- Notochord - Incompressible elastic rod of collagen, provides supporting rod for translation of muscle force



Possible Schemes of Vertebrates (Craniate - Skull Possession) Origins

- Echinoderm-type ancestor with small planktonic but mobile larva and sedentary filter feeding adult
- To active, bilaterally symmetrical form with a distinct head, diversity of vertebrates seen today



Major Mechanism Involved:

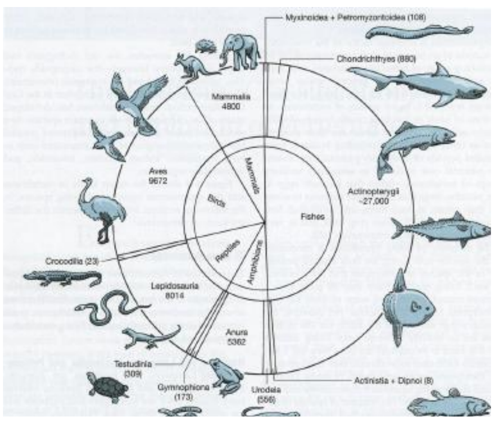
- Heterochrony (change in time schedule of development - Possible developmental pathway via increase in larval form and pedomorphosis:

  - Neoteny - Elongation of larval form, increase in size, with no adult form (larvae in later forms can reproduce)

  - Extension of juvenile phase (morphological characteristics/function)

  - Pedomorphosis - Retention of juvenile morphology into adult form, progenesis (reproduction even before adult morphology - larval forms reproducing)

Example - Tunicates retain more larval like form into developmental stages, juvenile morphology into adult

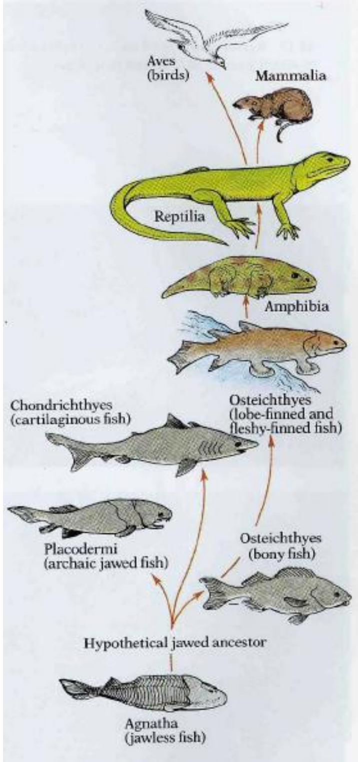


Vertebrates - Craniates

Key characteristics - Distinct Enlarged Anterior Head:

- Protected by cranium - Cartilage or bone
- Enlarge tripartite brain
- Specialised sense organs
- Unique neural crest cells form any derived characters of vertebrates - Leads to neural tube and advanced nervous system
- Most have vertebras

Diagram



- Within chordates
- About half of all extant species are "fish"
- 60% of chordates living today are fish

Evolution of Vertebrates

Simple pictorial scheme of relationships of some key vertebrate groups - Changes in diversity and composition of vertebrate fauna since Cambrian

1. Jawless Fish
2. Hypothetical Jawed Ancestors (archaic jawed fish, cartilaginous fish and bony fish)
3. Bony fish >Lobe-finned and fleshy finned fish
4. Amphibia
5. Reptilia
6. Mammalia and birds

Mobile Cambrian Chordates with Distinct Heads

- Pikaia small (2cm) fossil from burgers shale (preserve good details of soft tissue)
- Show evidence of myotome (muscular segmentation)
- Simple notochord
- Head with tentacles (tentacles are unusual in normal chordates))
- Suggesting marine orgs
- Gill slits not evident
- Swimming, microphagous early chordate
- Early form of chordate but not a vertebrate
- Feeding on very small particles in water

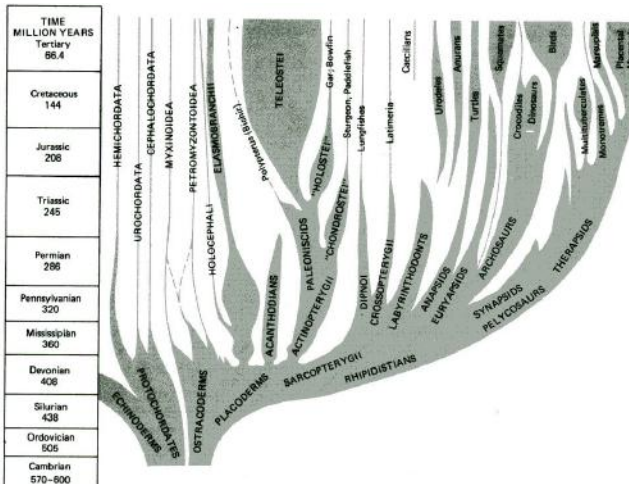
Earliest Vertebrates - Agnatha (Class - "Without Jaws - Jawless Vertebrate")

Evolutionary Step from Pikaia

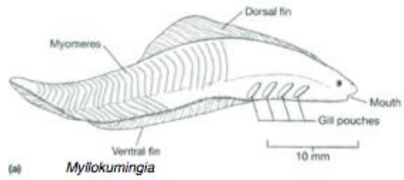
- Evolved in Cambrian from chordate ancestors (similar to but not cephalochordates)
- *Cephalochordates - Group of marine invertebrates orgs (lancelets)*

Recent finds - Of soft bodied vertebrates 540 million years,

Later groups - Bone fragments of dermal armour of Ostracoderms in Ordovician

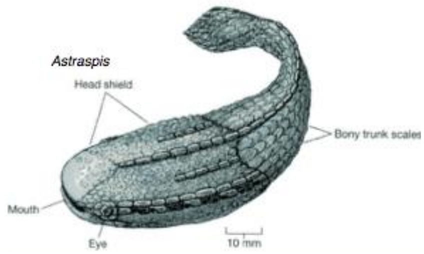


- Class of Agnatha - Early jawless fossil fish of Cambrian to Devonian periods, heavily armoured body

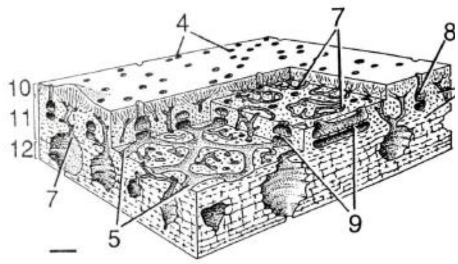


Agnatha - Characteristics

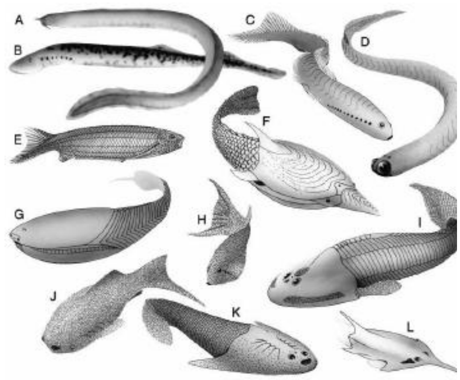
- Originated in shallow seas
- Half living vertebrate species from aquatic lineages



Early Groups
- Early groups show vertebrates characteristics but without backbone or jaws
- Probably detritus (debris) feeders on sea bed and incidental occurrence of small worms - Low energy diet so slow movement
- Evolution of larger pharyngeal gills with supporting gill arches for gaseous exchange allowed greater potential for more activity and faster movement
- Free swimming animal
- Classic features: Notochord, Myotome, Anterior head end, Gill slits
- Example - Myllokuminigia, Haikouichthys



Mineralised tissue in Ostracoderms
- Later forms had harder external armour
- Mineralised tissue - Calcium phosphate (mineral - hydroxyapatite e.g. bone, dentine, enameloid)
- Only in skin in earliest vertebrates - Type of exoskeleton
- Function: Protection or electrical insulation for electroreceptors for sensory cells
- Likely, internal cartilaginous skeleton (collagen and proteoglycan matrix from chondrocyte cells) in more derived, larger ostracoderms
- Protective armour - Calcium phosphate



Agnathan Vertebrates - "Ostracoderms" and Relatives (E - L)

- Up to 50cm long
- Diversity of forms
- Present in Ordovician, Silurian, Devonian (period after Cambrian explosion)

Mouth - Moveable plates around a circular mouth, range of foraging strategies from macrophages to significant predators

Respiration - Pharyngeal gill pouches, Muscle for ventilating gills

Non-vertebrates chordates use ciliary pumps for ventilation
However muscle is more forceful allowing more activity
Led to evolution of larger more active vertebrates in period after Cambrian explosion

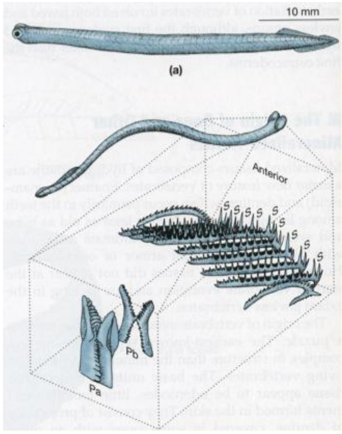
Contrasts in Morphology and Function of Shared Chordate features

Non-vertebrates vs. Vertebrates

Vertebrates: Stronger ventilation, much larger and more robust,

	Vertebrates	Invertebrate chordates
Pharyngeal skeleton	Cartilaginous	Collagenous
Water movement in pharynx	Muscular pumping	Cilia
Aortic arch primary function	Ventilation (gill supports)	Filter feeding
Movement of	Muscular	Cilia propelling

Earliest Vertebrates - Riddle of Conodonts



Conodont - Fossil marine animal of Cambrian to Triassic periods, having long worm-like body, numerous small teeth, and pair of eyes

- Evolutionary riddle
- Large structure
- Small comb-like structures found in fossil record (Cambrian to Triassic)
  - Thought to be from invertebrates or even diatoms (because soft-bodied animals to which they belonged didn't fossilise well)
  - Lagerstatten; With some whole specimens up to 40 cm long [*Promissum*](most whole specimens found = 1~4 cm), with conodont elements *in situ* and distinct myotomes & notochord + distinct 'head' with eyes in some cases

- Composed of hydroxyapatite (mineral)
  - Conodont elements in pharyngeal area - Potential feeding function
  - Experiment in toothlike development?
  - Some evidence of grinding / shearing wear in some fossils
  - Possible teeth-like structure

Vertebrates

Table of vertebrate characteristics

	Jaws	Endoskeleton	Locomotory Appendages	Resp-iratory Surface	Extra-Embryonic Membranes	Body Temp. Energetics	Integument	
AGNATHA	AGNATHA	CARTILAGE	FINS (Pisces)	GILLS	ANAMNIOTA (Yolk sac and chorion)	ECTOTHERMAL	GLANDULAR (Mucous secretions)	Naked
CHONDRICHTHYES	GNATHOSTOMATA							Placoid Scales
OSTEICHTHYES		BONE		Note 1				Dermal Scales
AMPHIBIA			LIMBS (Tetrapoda)	Note 2				Naked
REPTILIA				LUNGS	AMNIOTA (Yolk sac, chorion, allantois and amnion)		AGLANDULAR (Dry)	Epidermal Scales
AVES						ENDOTHERMAL		Feathers and Epidermal Scales
MAMMALIA							SECONDARILY GLANDULAR (Oily and watery secretions)	Hair

- Key changes/stages in morphology are required to transition from early marine orgs to terrestrial tetrapods

Living Jawless Vertebrates/Craniates

Class: Agnatha - Hagfishes

Ecology:

- All marine, worldwide distribution
- Less than 40 species
- Cranium consists of fibrous sheath only
- Live in mud burrows, eat worms and scavenge
- Pair of keratinous plates on eversible pharynx

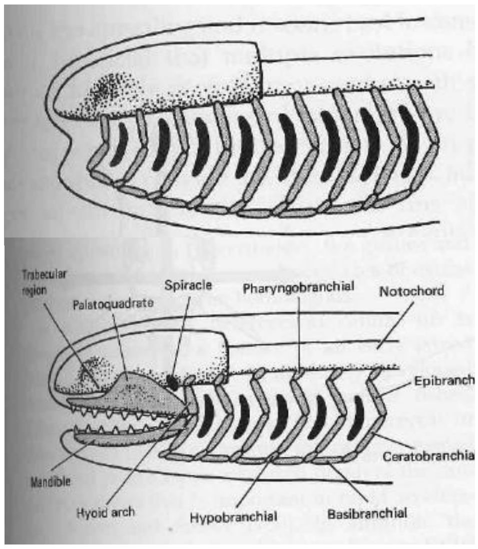
Mucus deterrent to predators:
- Large mucus glands - Secrete lots of distasteful mucus and proteinaceous (nitrogenous) thread

- When danger is gone body is tied in a knot to scrape off mucus

Class: Agnatha - Lampreys

- Cranium consists of cartilaginous case
- All spawn in rivers (freshwater or anadromous - migrating)
- 40 species with anti-tropical distribution
- Larvae are filter feeders, superficially somewhat similar to amphioxus form and nutrition type
- Migrate to oceans where they spend adult hood
- Operation of branchial (gills) basket to facilitate filtering and gas exchange
- Developmental similarities to amphioxus (small lancelet)
- Undergo metamorphosis to highly modified form with sucker mouth and functional gills
- Many adult forms are ectoparasites
- Rasp hole through integument and feed on tissue fluids of host
- Some species are invasive pests but most are threatened due habitat loss and damming of rivers. Free swimming, parasitic lifecycle, many are ectoparasites

Jawed Vertebrates - Gnathostomata



Gnathostomes (jawed fish):

Gnath = Jaws

Stome = Mouth

Early Silurian - First certain record

Evolution of Jaws

- Derived from branchial arches involved in filter feeding
- Co-evolved for gas exchange too
- Likely as body size increased
- Initial enlargement of mandibular arch
    - Improved gill ventilation

Gnathostomes pump water more powerfully
- Internal branchial muscles -> Push and suck (exhalation and inhalation)
- Mandibular arch + Adductor muscle - Allows rapid closing and opening of pharynx (trapping prey)
- Pushing and sucking exhalation and inhalation rather than relying on simple flow of water through gills

Whats Important about Jaws? - Adaptive Benefits

Exaptation: Cooption of phenotypic trait evolved for one purpose to another use
Use - Macrophage using jaws originally likely evolved for improved ventilatory efficiency

New Behaviour: “Macrophagy” is difficult to impossible with chordate body plan, without evolution of some kind of jaw apparatus (but see conodont)

Jaws with muscles allows gripping of objects (initially weakly hinged jaws - but strong muscles)

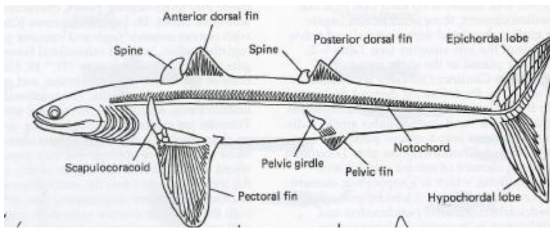
Addition of teeth allows surer grip and tearing of food (more energy rich food sources) and also used for defence

Feeding and Defence:

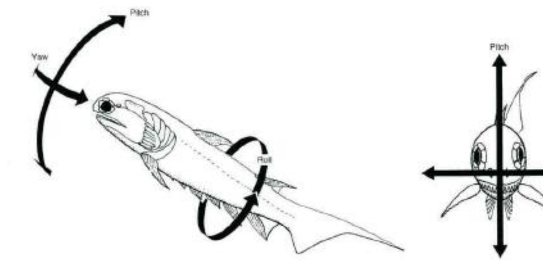
- Capture of food items as large as jaw gape will allow
- Grinding of hard food, biting and tearing chunks of soft tissue
    - Many gnathostomes became bigger than other contemporary vertebrates - due to enhanced energy capture associated with carnivory (BIG AND BAD)
    - Replaced many lineages of jawless vertebrates and eventually outcompeted many other invertebrate top predators

<u>Co-Evolution:</u>

- No single feature evolved in advance of others; a combination co-evolved (evident from fossil record) increasing effectiveness of macrophagy
- Change in 1 aspect of morphology leads to diff changes of morphology
- Head with paired sense organs for prey detection, balance, brain for sensory integration and motor coordination (shift towards distinct head)
- Efficient gills and circulatory system for oxygen extraction and delivery
- Notochord evolved into vertebral column
- Vertebral column (cartilage or bone) with distinct vertebrae, ribs and muscle blocks (myotomes) allowing effective locomotion for prey capture (efficient movement)
- Use jaws for live prey capture and manipulation
- Improved rate of energy delivery for high metabolism from carnivory



<u>Body Control</u>



- Jaws only adv. if there's good body control for prey capture
- Difficult to guide a body in 3D space

    - Yaw - Swinging left/right
    - pitch - Tilting up/down
    - Roll - Rotation around the body axis

- Multiple balance organs (esp. inner ears) and fins required to assist with stability in 3-D
- Contraction of myotomes along body pushes water aside to allow forward movement and dynamic lift
- If prey moves quickly must make quick adjustments

<u>Devonian Seas - Age of Fishes</u>

- Many entire fossils (400 MY before present)
- Agnathan diversity decreases and by triassic just few jawless specialist sp. remained (hagfish, lampreys)
- Jawed fish became increasingly dominant predators
- Some jawed fish became massive top predators
- 4 Main Devonian Gnathostomes Fish (distinctive classes):

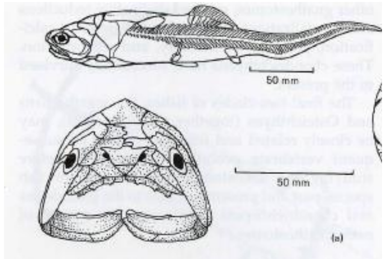
1. Placodermi (now extinct)
2. Chondricthyes - Cartilaginous fish (sharks, fish)
3. Acanthodii (now extinct)
4. Osteichthyes



Earliest Jawed Fish

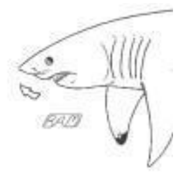
1. **Placodermi (extinct)**

    - Dominant in Devonian
    - Strong jaw muscles and connections to cranium (unique)
    - Heavy apatite-based dermal armour and cartilaginous skeleton (so slow, lumbering) armour plating
    - Slow predating animals
    - No true teeth - Sharp dermal plates
    - Anatomy of paired fins diff
    - No modern descendants



2. **Chondrichthyes (Sharks, Rays and Rabbit Fishes) Cartilaginous Fish**

- Rays for benthic life (dorsoventrally flattened with enlarged pectoral fins)
- Cartilaginous body and cranium
- Reduced scales - Coevolved w reduction of external armour
- Lighter body and increased manoeuvrability
- Evolution of teeth - From placoid scales (dermal denticles)
    - Originally 3 cusped little root development
    - Dentine with enameloid coat (likely replacement of teeth)
- Adv. over Placoderms = Teeth and lighter body -> More mobile than placoderms
- Larger more agile predators



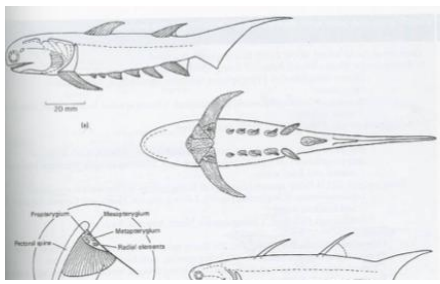
Shark Jaws and Feeding:
- Shark jaws: Relatively simple hinged arrangement
- When jaws are fully extended teeth protrude
    - Can pick up small food from bottom
    - Can bite orgs larger than self

- Modern top predator sharks: sink jaws into prey, undulate their body whilst shaking violently shaking head to allow serrated teeth in upper jaw to act as a saw

Main group is Elasmobranchii (sharks and rays more than 900 sp.) - Rays tend to be dorsoventrally flattened with enlarged pectoral fins, adapted for benthic life

Features
1) Cartilaginous skeleton (no bone in endoskeleton)
2) Cranium formed from one piece of cartilage
3) Almost exclusively marine
4) Spiral valve in intestine
5) Unusually high urea content- increased plasma osmolarity
6) Dermal denticles (placoid scales) = reduced dermal armour
7) Teeth on jaws formed from dermal denticles (or vice versa?)
8) Relatively simple hinged jaws – carnivorous (*Megalodon* was 20+ m long)
9) Internal fertilisation, live young or large eggs
10) K–strategists (slow growing, slow to mature, large ultimate size, few young)

3. **Acanthodii (acanthodians) - Extinct**

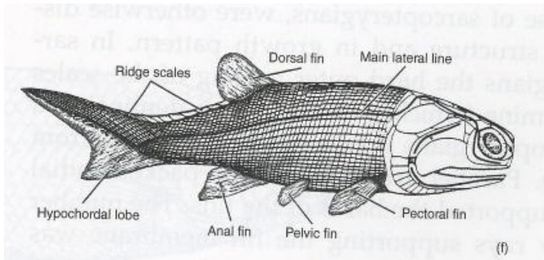


- Mostly < 0.2m some more than 2m
- Brain in cartilaginous box (cranium)

- Marine and freshwater species
- Teeth with no enamel, teeth not replaced
- Several variations of body form, generally multiple paired ventral fins
- Diff feeding specialisations
- Diverse and important in Devonian
- Disappeared from fossil record in early permian (280 MYA - outcompeted by bony fish)
- Like sharks

4. Osteichthyes (bony fish)

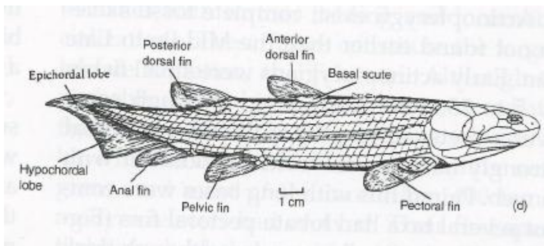
- Probably had common ancestor with Acanthodians
- Complete fossils present in mid Devonian
- Some lineages evolved into tetrapods (land vertebrates)
- 27,000 species of bony fishes
- Having bone is not a unifying characteristic - Also present in other fish groups
- Osteichthhans have endochondral bone which replaces cartilage ontogenetically



2 Groups of Bony Fish:

1. Actinopterygii - Stout ray (ray-finned)

2. Sarcopterygii - Fleshy finned, scaled bony central axis, ancestral to tetrapods (lobe-finned)



Sarcopterygii - Lobe Finned

- Fleshy, scaled central axis
- 2 dorsal fins
- Ancestral to tetrapods
- Jaw muscles massive
- Dermal coated with layer of cosmine (dentine-like)
- Abundant in Devonian
- Dwindled in late palaeozoic and mesozoic

4 Living Non-Tetrapod Genera

Dipnoi (lungfish) - Freshwater, simple lungs, highly vascularised invaginations from oesophagus, enhance gaseous exchange (protopterus, lepidosiren, neoceratodus)

Actinistia (Coelocanth)

Actinopterygii - Ray Finned

- 27,000 living species
- Aquatic habitat comprise 73% of planet (chondrichthyans and sarcopterygian fishes relatively species poor)
- High rates of speciation
  - Particularly in isolated lakes (e.g African rift valley) and high versatility in body plan for aquatic life

- Genera - chondrostei, holostei and teleostei (makes up 99% of Actinopterygii)

- Most species are neutrally buoyant due to swim bladders
- Ray-finned - Make use of neutral buoyancy
- High manoeuvrability
- Jaw versatility allows feeding versatility
- Colour vision
- Radiation in a wide range of habitats, esp. spatially complex habitats (e.g tropical reefs)

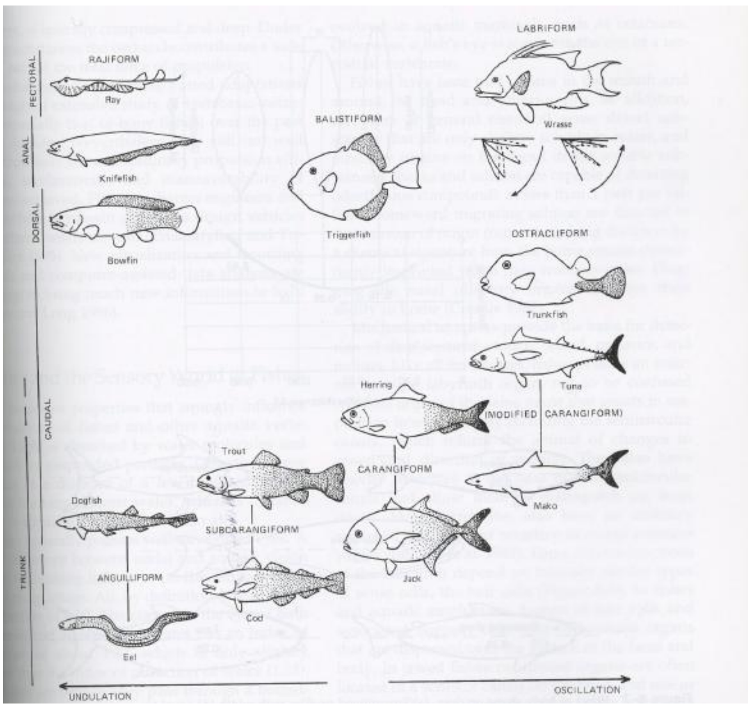
<u>Early Osteichthyes - Oxygen:</u>

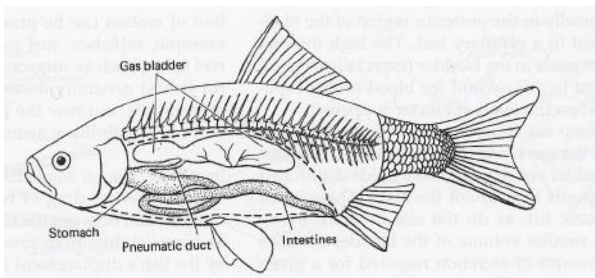
- Most fishes use highly vascularised gills and buccal pumping or ram ventilation to extract enough oxygen for metabolism
- Early osteichthyes evolved in brackish (salty)water
- Devonian and carboniferous: long periods with warm shallow brackish seas and swamps - much organic material deposited in shallow areas
- Low oxygen availability in warm water but higher metabolism by fish demanding more oxygen
- Even less availability in swamps because of decomposition by bacteria (like tropical mangrove swamps)
- Must swim near surface (would have local elevated oxygen due to atmosphere and phytoplankton)
- Gulp air and exchange over moist and vascularised surface in mouth or gill cavity
- Gulp air and exchange over surfaces of gut but feeding may interfere with gas exchange
- Vascularised pockets off gut wall (pouches, invaginations of gut) - simple lungs
- Air breathing originates in this group

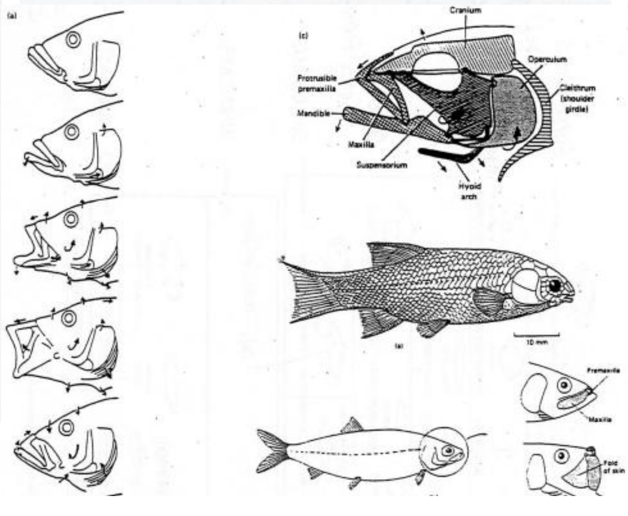
<u>Early Osteichythes - Neutral Buoyancy and Manoeuvrability:</u>

- Gas bladders brought additional adv:
  - Of static lift to offset weight
  - In oxygen rich envi (re-invasion of marine envis) hypothesised gas pouches were retained, no longer for gas exchange but for adv they gave (neutral buoyancy and freeing of paired fins from creating dynamic lift)
  - Swim bladder or gas bladder - Characteristic of most actinopterygians
- Exaptation (co-option) of lung outgrowths modified for use in buoyancy reg = no longer lungs as not used for respiration
- Paired fins (Chondrichthyes) used for fine-tuning of positioning and braking, esp in complex habitats

Wide Variety of Swimming Modes in Fishes







Evolution of Ray-Finned Fish:

- Evolved complex jaws which give enhanced flexibility of feeding types
- Many bones and muscles, together with flexible skin, enables protrusible jaws
- Large gape possible and suction current for small food

Actinopterygii Evolution

- Combination of high manoeuvrability from neutral buoyancy and complex jaws give enhanced flexibility of feeding types
- Successful general body plan enabled wide species radiation and niche filling in wide range of habitats, esp. spatially complex habitats (e.g tropical reefs)
- e.g Cichlids, a perciform with highly adaptable body plan, for which massive species flocks have evolved in the East African rift valley lakes

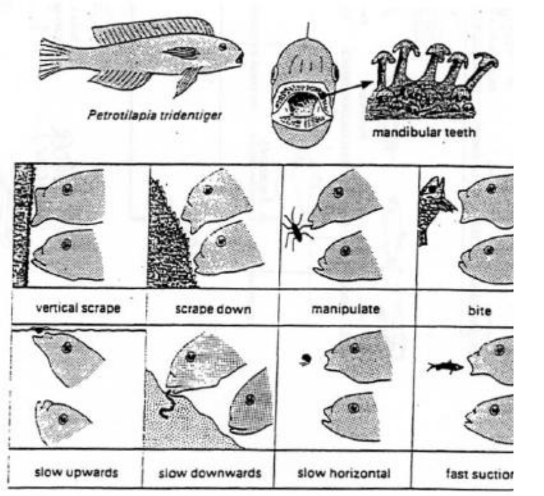


Figure 7.1 Versatile feeding methods of the cichlid *Petrotilapia*. The 3 slow techn... involve slow controlled suction. After Liem (1980).

Fish Classification and Diversity

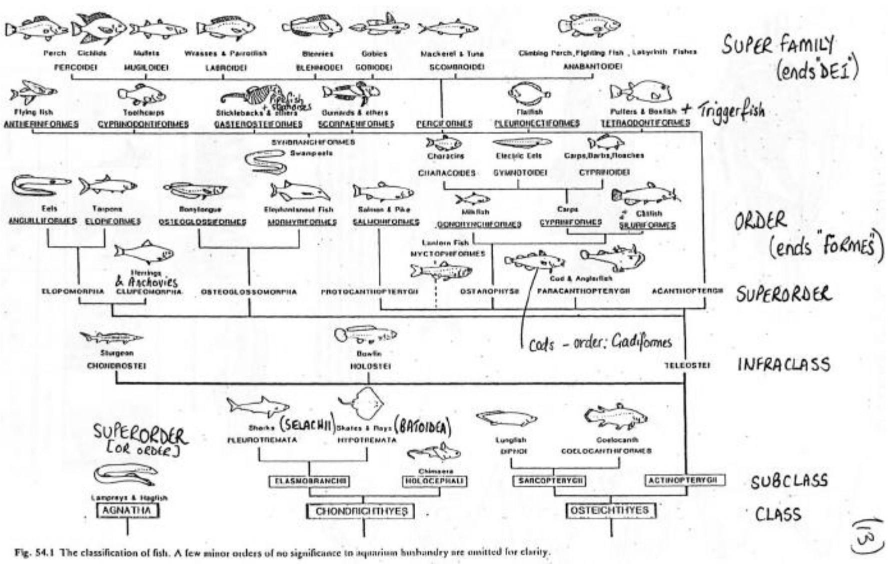
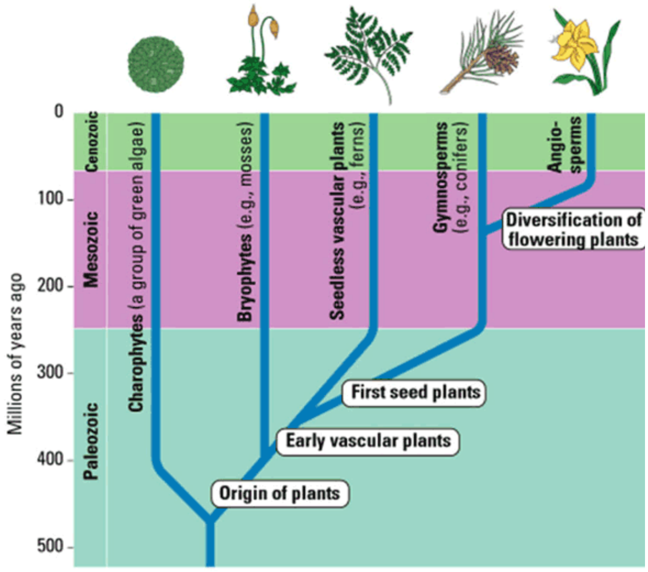


Fig. 54.1 The classification of fish. A few minor orders of no significance to aquarium husbandry are omitted for clarity.

Evolution of Biosphere

Adaptive radiation following key events

1. Chlorophytes
2. Charophytes
3. Bryophytes
4. Ferns
5. Gymnosperms
6. Angiosperms



What drives these adaptive radiation -> Innovations

4 Key Innovations - At Base of Division

1. Development of the Cuticle (waterproof protection/surface)
2. Development of vascular system
3. Development of seeds
4. Development of flowers and fruits

Innovations allow for large advantage over successors -> Leading to adaptive radiation
Synapomorphies: Roots of Branches

Hadean Period

- Moon ripped off the earth (4.6)
- Earth is 4.8 billion years old
- Early earth quite like rockall (large piece of granite, unweathered) = Largely Granitic
- Within largely fresh water => As salts in seas come from weathering of rocks
- Atmosphere - Low in oxygen, CO2 and methane

Early Evidence of Life - 3.8 billion years

- Rocks from Isua in Greenstone
- Living things take up isotopes at diff ratios
- If isotope ratios are diff from inorganic material then they are organic
- Peculiar isotope ratios found in Isua Greenstone = Evidence signifying characteristic of life
- Early life evidence - Peculiar isotope ratios, not fossil evidence

Delta 13C and Delta 18O - Diff in carbon ratios

Archaean (Methanogen Era) Evolution of Life - 3.8~3.6 billion years ago

- Since beginning of life, has shaped earths geo-form
- Life breaks down gases allowing molecules to be available
- First Orgs - Methanogens = Converted CO2 —> Methane (CH4)

- Made atmosphere more reducing allowing earth to warm up

Half of Worlds History - Found in precisely 3 rock formations

Oxygen Photosynthesis (2.8 MYA)

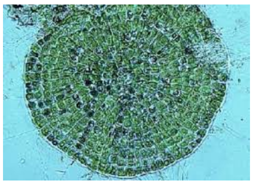
- Take Reducing Atmo —> + Water —> Oxidised into Oxygen
- Oxidised Methane to Oxygen using water
- Oxygenic photosynthesis introduced
- Evidence found in fossil reefs
- Oxygen (gas) bubbled in water - Mats of things formed in euphotic zone due to oxygen
- Forming Stromatolites = Structures of successful layers formed by p/s bacteria
- Each lump is a layer cake of bacteria (microbial) - p/s bacteria build up
- From reducing atmosphere —> Switch to Oxygen filled atmosphere (oxygenising atmosphere)
- Early photosynthetic community

Multicellularity (Green Algae)

- Great Oxygenation Event - Oxidising atmosphere produced
- Endosymbiosis - Gave rise to eukaryotes
- Allowed for evolution of multicellular orgs
- Unicellular to Multicellular (all aquatic)
- During mitosis -> Daughter products didn't split not releasing mitotic product
- Formed filaments
- 1D multicellular into 2D and 3D multicellular orgs
- Ending up with film = Gave rise to filamentous eukaryotic algae

Multicellular Green Algae

Mesotigma (unicell to 1D multicell) —> Klebsormidium (1D multicell to 2D~3D multicell) —> Coleochaeta



Coleochaeta
- Same size in all direction
- Mutation to keep track of how large it gets - Isomorphic growth
- 3D requires more innovation as more complex

Fossils of earlier multicellular orgs - Body plans established

Plants Invasion of Land - 500~600 MYA

Complex Charophyte Algae

- Reproducing in water as easier to travel in
- Released from plant and swim (motile sperm) through water to reproduce
- Green algae could absorb nutrients from all surface and enter body was photosynthetic
- Algae are Thallus - Undifferentiated tissue

Algae began washing up on shore and found on beach a lot

Selective advg. to stay on land:

1. No predators - Plants eaten by predators within sea thus high risk of predation
2. Plentiful nutrients (light, CO2 - diffuses quicker in air than water)

** Requires adaptation to become land plants

Adaptations - Issue to Overcome

1. Waterproofing - Cuticle (avoid potential desiccation)
2. Reproduction (?)

Water proof everything - Reproductive cells and rest of body = Waxy cuticle formed

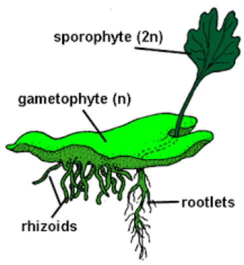
Trilete spores covered by Sporopollenin
- Tetrad spore formation - Trilete Spores
- 1 cell divides twice -> 4 cells (tetrahedra)
- Each cell is in contact with the 3 others (Y shape comes from)

First evidence of plant invasion of land - Rhynie Chert
- Geo formation from 420 MYA
- A lot of fossil evidence comes form here
- Evidence of cuticle formation in spores (thickening of outer wall - outer epidermal waterproofing)
- Spores covered by Sporopollenin (complex polymer waterproofed)

Cooksonia
- Extinct grouping of primitive land plants
- Only has sporophyte phase
- Spores carried by organs for extra waterproofing and protection
- Evolution of organs to protect spores in plants from dehydration
- Waterproof coating of spore and organ developed to carry spore

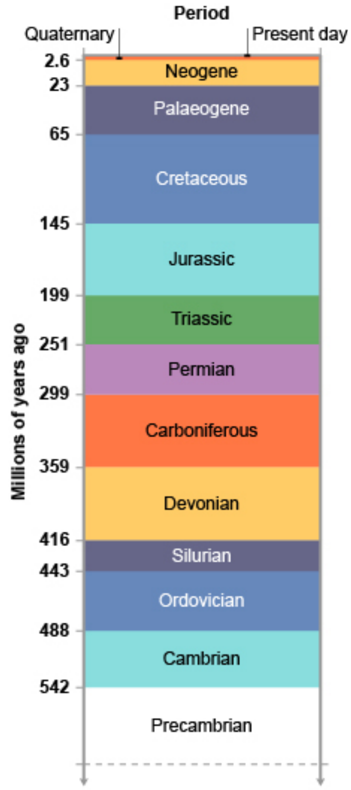
Moses - Reduced Sporophytes (400MYA)

- Alternation of life cycle generations: Sporophyte and Gametophyte generation
- Similar structures to early land plant forms
- Haploid gametophyte generation (visible)
- Waterproofing of cuticle gave rise to bryophyte



Ferns - Reduced Gametophyte

- Increased vascularisation
- Vascular tissues developed = Similar to ferns
- Vascularisation and reduced gametophyte
- As plants moved further onto land -> More adapted to life outside water
- Mosses - Grow in wet areas and close to land (not well adapted from coping away from water)



- Ferns - Larger plants, further away from water
- Protection by reducing of gametophyte
- Devonian Landscape - Mosses and Ferns

Vascularised Plants - Thicker Woody Larger Plants

- Lignin - Constituent of cell walls of all dry land plant cell walls
- Cambium - Plant tissue between xylem and phloem in stem and root of vascular plant

- Strengthening of vasculature allows for larger growth
- Organ differentiation was driven by Vascularisation
- Development of leaves and roots system:
- Leaves - P/S
- Roots - Nutrient Acquisition

Homospory to Heterospory - Sexes Introduced

- Plants - Need to protect reproductive cells

- Better but fewer, more invested reproductive cells (ovaries)
- Less efficient but abundant, less invested reproductive cells (sperms)

Carboniferous Landscape: Large Seedless Vascular Lycopsids

Complex Multicellularity - Measured by distinct cell types an organism has

Humans have 200 ~ 250 possible cell types
Land Plants - 50 types
Algae - 5 diff types

Multicellularity - Complexity spectrum from lil complex to greatly complex

Silurian Period - Not truly highly complex plants, but become complex multicellular orgs

1. Cuticle
2. Extremely Complex Vasculature
3. Seed plants (Devonian)

Development of Seeds - Gymnosperms

Ovaries produced around the reproductive cells
- Tough outer coating protection of seed to allow for their dispersal
- Moving reproductive cells - To reach other plans and disperse offspring
- Example - Pinecone

Gymnosperm - Naked Seed

Development of Angiosperms

- Surrounding protective reproductive cell to attract pollinators
- Allow structure to develop to fruit, used to attract vectors for dispersal
- Development of seed into fleshy body to attract things
- Enters age were flowers begins to co-evolve with animals
- Plants have co-evolved with pollinators and other animals which move them around
- Now they are impacted on by humans
- Offering bribes and rewards to animals

Phylogenetics

READ: Molecular Evolution - A phylogenetic approach by Page and Holmes (chapters 6&7)

Phylogenetic's

- Processes that underpins patterns seen in evolution
- Evolutionary trees show evolutionary history of orgs

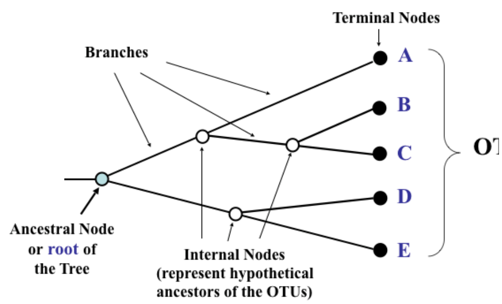
Russian naturalist Peter Simon Pallas:

"But the system of organic bodies is best of all represented by an image of a tree which immediately from the root would lead fourth out of the most simple plants and animals a double, variously contiguous animals and vegetable trunk; the first of which would proceed from mollusks to fishes, with a large side branch of insects send out between these, hence to amphibians and at the farthest tip it would sustain the quadrupeds, but below the quadrupeds it would put forth birds as an equally large side branch.

Phylogenetic's - Phylogenetic systematics method of taxonomic classification based on evolutionary history

- A given branch of a tree is defined by key transitional characteristics of num of diff changes (some major changes defines lineages)
- Study of evolutionary history and relationships among individuals or groups of orgs
- Relationships discovered via phylogenetic inference methods evaluating observed heritable traits (i.e. DNA seq. or morphology)
- Result of analyses = Phylogeny (phylogenetic tree) - Hypothesis about history of evolutionary relationships

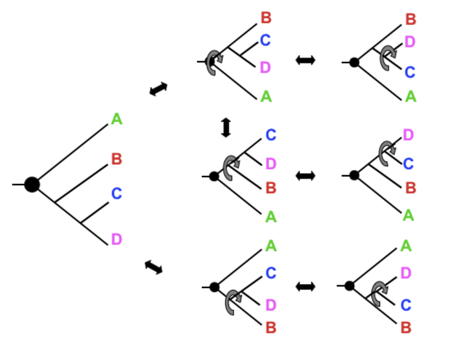
Basic Structure



OTU: Operational Taxonomic Units (i.e. species, individuals, pops etc.)

- Tree is formed from branches and nodes
- When branches converge they form nodes
- Base is an ancestral node (root of tree)
- Order of nodes is not important, however pattern of nodes and closeness of branches are
- Internal nodes - Represents hypothetical ancestors of OTU's

Phylogenetic Tree like a mobile - Order at nodes is irrelevant



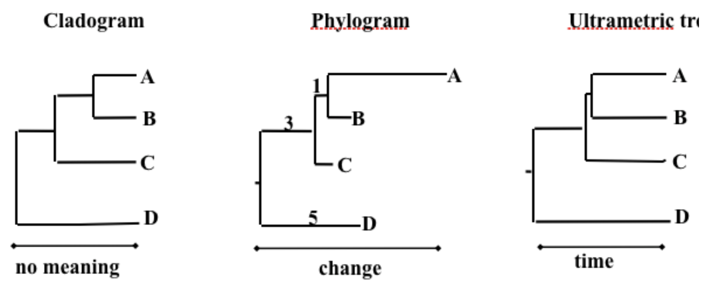
- Nodes are informative in terms of structure of lineages (C and D diverging from CA)

Types of Phylogenetic Trees

Cladogram: Simply shows clusters of orgs (ABC together D outlier)

Phylogram: Relates length of branches to amount of change (i.e. morphometric, genetic etc)

Ultra-metric: Relates length of branches to divergence time (i.e. constant rate of change)



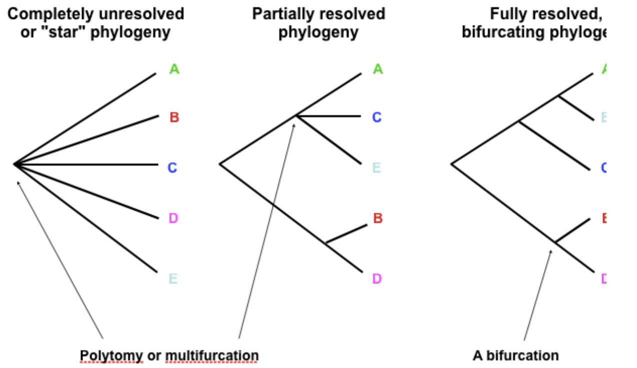
Goal of Phylogeny Inference - Resolve branching orders of lineages in evolutionary trees

Ability to do this is determined by info available:

Star shape, multi-furcation (polytomy), nothing is known about sequence of evolutionary events

Partially resolved: Contain some bifurcations, but also some multi-furcations

Fully resolved: Contains only bifurcating branches

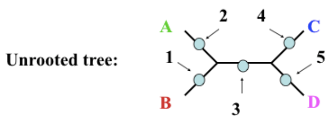


Rooted and Unrooted Trees

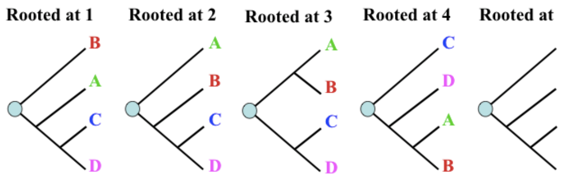
- Position of root makes important diff to the implications for pattern of evolution
- Where you root tree determines who becomes ancestral (i.e. 1 - B becomes ancestral)

Unrooted Trees - Clustering is known but seq. of evolution unknown

Rooted Trees - Know who is ancestral

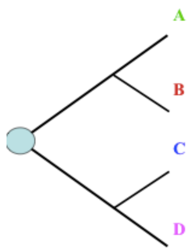


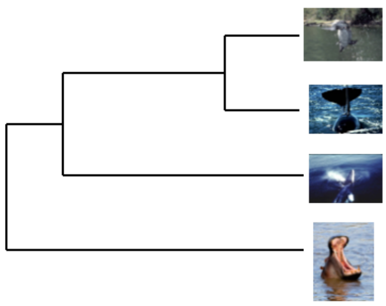
- Common to root at midpoint (position 3)
- Assumes a constant ‘clock-like’ rate of evolution across tree and sets root at half-way point between the 2 most distant taxa



Defining an Out-group:

- Allows inference to be made about course of evolution over time
- Allows determination of which org is ancestral (basal) to another
- A distantly related org usually chosen as the out group
- i.e. Basal org - Hippo

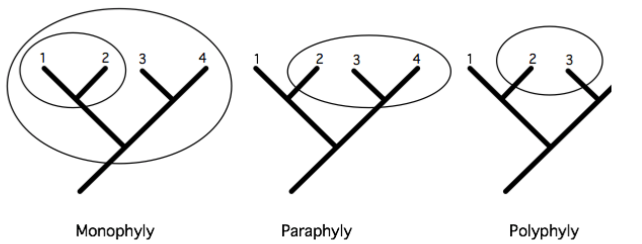




Midpoint Routing

- Assumes a constant “clock-like” rate of evolution across tree, and sets root at point half way between 2 most distant taxa

Relationships Among Taxa Within a Phylogeny



Relationships between OTU within trees can be defined by groups

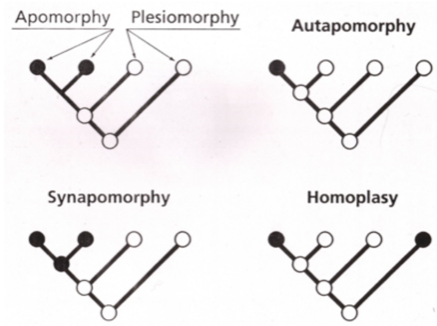
Categories for Grouping Taxa

Monophyly: 1&2, as well as 1,2,3,&4 are in same lineage, defined by broader lineage

Paraphyly: 3&4 share lineage, but 2 is separate lineage, defined by descendants but not all ancestors

Polyphyly: 2&3 in 2 diff lineages

Cladistic Terminology:



Concerned with ancestral vs derived states

Pleisiomorphy: Shares character with ancestral state, old forms

Apomorphy: A derived state, new forms

Autapomorphy: A unique derived state, single new form

Synapomorphy: Shared derived characters (homology), represents shared evolutionary ancestor

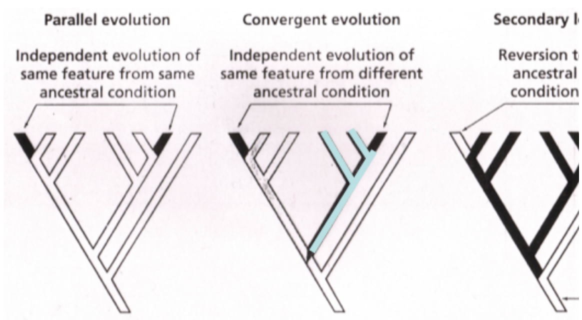
Homology: Shared character due to inheritance from shared ancestor (CA)

Homoplasy: Shared character due to independent derivation, looks artificially similar but evolved independently, no recent CA, shared characteristics not inherited from recent ancestor,

Determining whether homology or homoplasy exists is important when constructing trees

Homoplasy:

Can arise in various ways:



Parallel Evolution: Independent evolution of same feature from same ancestor

Convergent Evolution: Independent evolution of same feature but from diff ancestors, from 2 lineages

Secondary Loss: Reversal to an ancestral condition, ancestral state evolves to something else and reverts back to ancestral state

Computational Methods:

Clustering Algorithms

- Single tree constructed according to rules of a specific algorithm (a pattern of similarity)
- Tends to be very fast
- Uses matrix of similarities
- Doesn't compare possible alternative trees (even if more than one could explain the data well)
- Doesn't necessarily find "true" tree

Optimality Approaches

- Define optimality criterion (minimum branch lengths, fewest number of events, highest likelihood etc.)
- Use specific algorithm for finding trees with best value according to optimality criterion
- Produces many equally optimal trees
- Optimal tree may not be "true" tree

Constructing Molecular Phylogenies - 2 Main Strategies

Distance-based (phenetic) Methods:

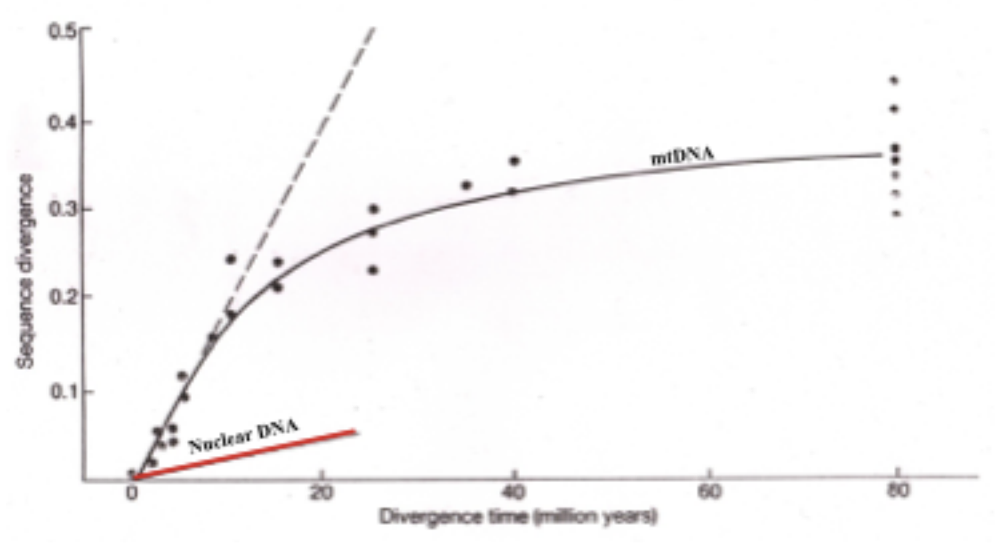
- Compare genetic data to determine genetic distance (similarities) between OTU's
- Depends on an evolutionary model (similarity in morphology, behaviours, DNA seq. etc.)
- Phenetic trees are based on matrix of similarities

Example - Focus on comparing DNA seq.

- DNA is composed of 4 letters, so mutation could change a nucleotide, and then revert back
- therefore there are changes which have occurred which we are unaware of (saturation)

Phenetic Method - Jukes-Cantor Model
- Corrects for saturation due to back-mutation by using k (percentage diff between 2 seq.)
- Saturation (mutation -> back-mutation)

JC = - 3/4 ln (1 - 4/3 k) to produce a sequence divergence value



Shows mtDNA evolves much faster than nuclear DNA
- Without saturation effect, represented by dashed line
- Nuclear DNA - Pretty linear in rate of change

Other Evolutionary Models

Kimura 2 Parameter Method

- Corrects saturation effect and differing mutation rates for transitions and transversions

2 Diff kinds of Mutations in DNA:

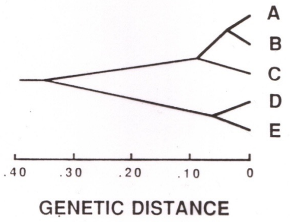
Transitions: Change between purine->purine (A->G) or pyrimidine->pyrimidine (C->T)
Transversions: Change between purine->pyrimidine (A->C) or pyrimidine->purine (T->G)

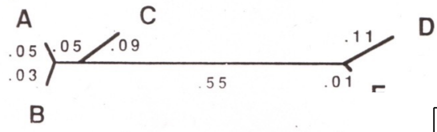
Tamura-Nei Model

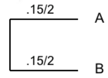
- Considers rate of evolution along a sequence as mutational rate is not constant across stretch of DNA

For both models - Matrix of distances created

	A	B	C	D	E
Species A	----				
Species B	0.08	----			
Species C	0.19	0.17	----		
Species D	0.70	0.75	0.80	----	
Species E	0.65	0.70	0.60	0.12	----







OTU	(AB)	C
C	$d_{(AB)C}$	
D	$d_{(AB)D}$	d_{CD}

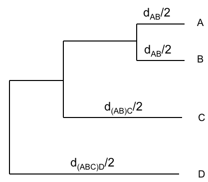
2 Phenetic (distance-based) Clustering methods:

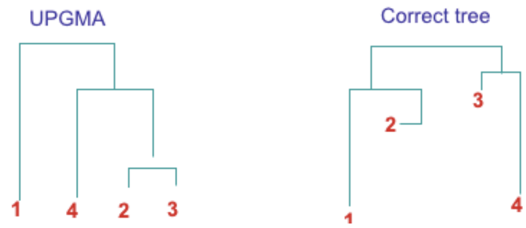
1. ***UPGMA*** - Unweighted pair group method using arithmetic mean, construct tree through successive pairing of closest nodes, doesn't allow for variation in rate of evolution among taxa

   (ultra-metric tree), look at most similar species and find midpoint, constant rate of change

   Constructing UPGMA

   1. Start with distance matrix
   2. Find pair with smallest distance between orgs (A and B)
   3. Group these orgs
   4. Determine branch length = Distance between AB divide by 2
   5. Recalculate distances from AB to other taxa as avg: d(AB)C = (dAC + dBC)/2
   6. Generate new distance matrix using avg. distances
   7. Find smallest distance in new tree and repeat process
   8. Repeat until all taxa are on tree

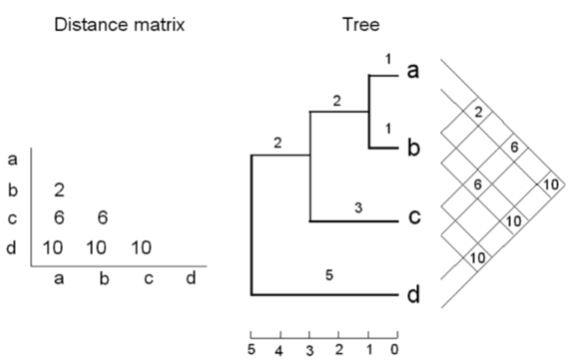




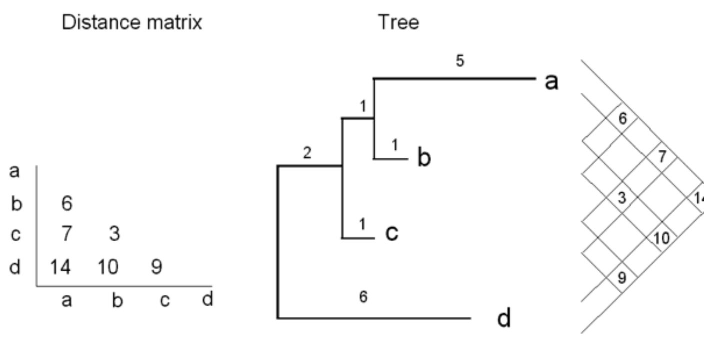
   - Constant molecular clock rate is assumed for all species
   - However, certain species (e.g. mouse and rat for some genes evolve much faster)
   - UPGMA tree is ultra metric - Assumes that rate of evolution constant across tree

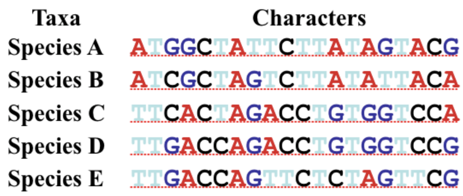
2. Neighbour-joining - More sophisticated, allows rate of change to vary across tree (metric tree), illustrates relative genetic distances through diff branch lengths. An additive tree allowing rates to vary, branches illustrates degree of diffs between OTU of tree

UPGMA vs Neighbour-Joining:



vs





Character-based Methods:

Maximum Parsimony:

- Optimality method
- Generates most parsimonious tree (with shortest evolutionary path)
- Generated by determining how many steps to get from 1 character state to another in DNA seq.
- Compare DNA seq. between character states
- Find which tree gives smallest num of steps
- May produce many equally parsimonious trees

Example - Max Parsimony (Likelihood) Trees:

Input: 4 Sequences
- ACT
- ACA
- GTT
- GTA

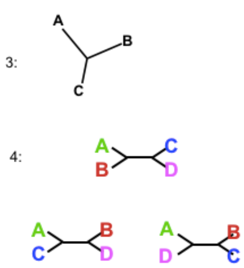
Note when there are many possible trees, there may be many equally parsimonious trees

Maximum Likelihood Trees:
- Optimality method
- Evaluates phylogenetic hypotheses in terms of probability proposed model of evolution and a proposed unrooted tree would give rise to observed data
- Tree with highest max likelihood value considered to be preferred tree

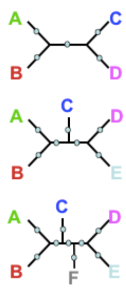
All Phylogenetic Reconstructions:
- In each case - Many possible trees can be constructed from a given set of data
- The more OTUs, the more possible trees there are (more than exponential increase)
- Can be many equally good tress (i.e. equally parsimonious trees) - Consider a consensus tree
- Tree is our best hypothesis about pattern of evolution, but not definite.

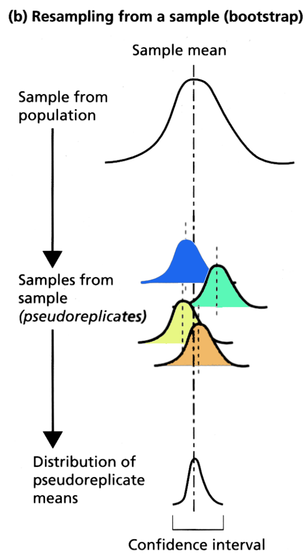
Number of possible trees, unrooted trees, (arranged randomly) increases more than exponentially with increasing taxa num

- Each unrooted tree theoretically could be rooted anywhere



# Taxa (N)	# Unrooted trees
3	1
4	3
5	15
6	105
7	945
8	10,935
9	135,135
10	2,027,025
.	.
.	.
.	.
30	3.58×10^{36}





With so many trees, how to choose particular tree?

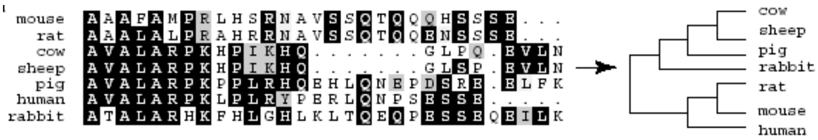
Can attempt by re-sampling from same set of data crating "pseudo-replicates" - subsamples from data

Boot-Strapping

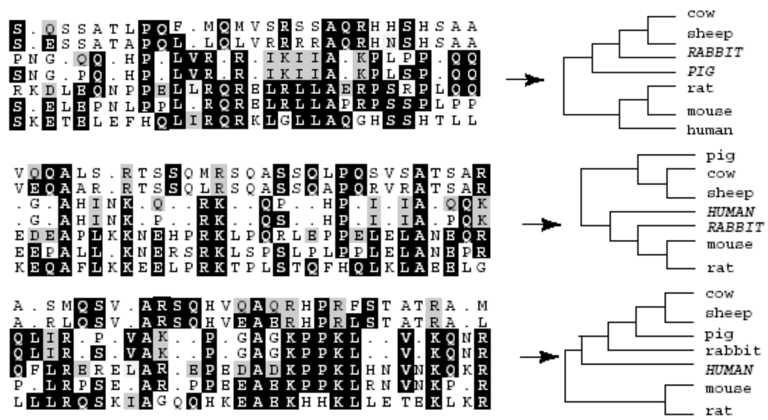
- To assess confidence in a particular tree, amongst many trees
- Re-sampling from same set of data creating pseudo replicates (sub-sampling)
- Distribution of means of subsamples allows us to determine confidence interval

Method:

1. Sequence to make initial alignment and tree in normal way (AA or DNA)
2. Each aligned site considered independently



3. Throw all sites into hat to randomise
4. Take random samples (with replacement) to reconstruct a new phylogeny (replacement: site can be picked multiple times, other sites may be absent from new alignments)
5. Multiple replicates (1000+)
6. New alignment may contain several sites numerous times
7. Other sites may be absent



8. Number of times a given branch occurred in all bootstrap resamples gives bootstrap value (higher num more reliable - interpreted as confidence interval for clade, low is unreliable)

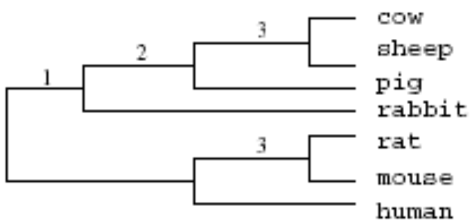
3 Replicates:

Cow-Sheep

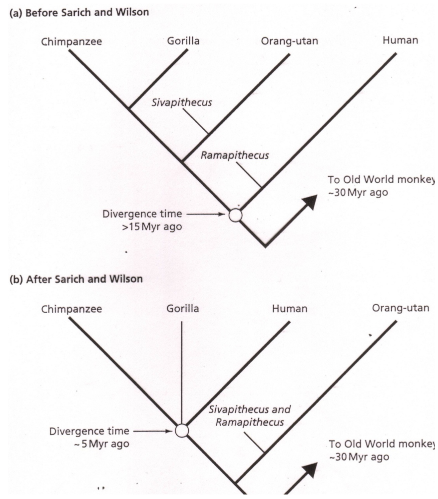
Rat-Mouse

Building Trees:

Molecular phylogenetic compared to trees based on morphologies revealed some novel info,



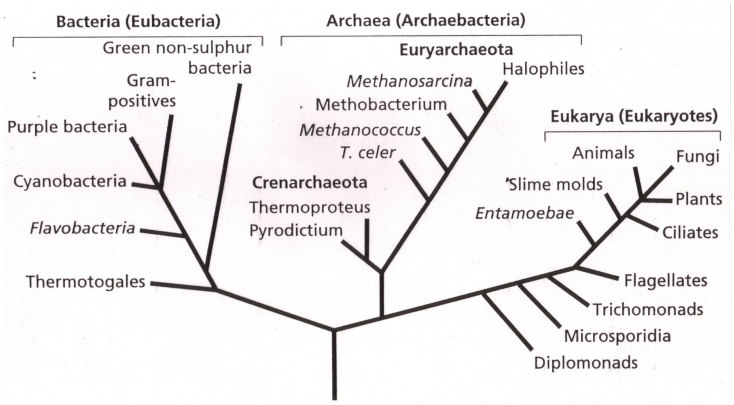
Example - Immunological distances (based on serum albumin) to redefine our human evol. understanding, showed divergence of humans from chimps and gorillas more recently (15 MYA) than orang-utans



Molecular phylogenies address questions impossible to answer based on morphologies (i.e. cryptic species)

Example - rDNA evolve very slowly as highly conserved (purifying selection) so can produce phylogenies between very distantly related orgs

Species Discovery - Possible using molecular markers when taxa cant be easily distinguished by



morphology.

Example - Bottlenose Dolphin

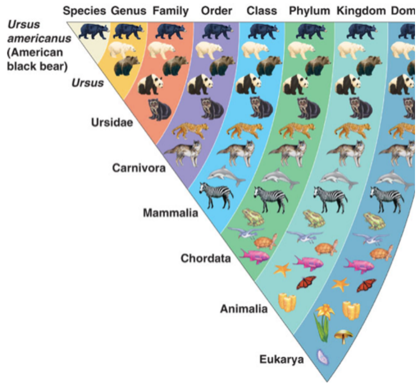
Found world-wide, an aduncus type described separately in Asian and South African waters. The 2 pops (asian/south african) were found to be highly genetically diverged, and probably are diff species, although morphologically similar

Using trees provides between understanding of evolutionary processes

Phylogenetic's Summary:

1. Features of Tree: Nodes, Branches, OTU (terminal node)
2. Trees rooted or unrooted - Rooted tree allows inference about sequence of divergence
3. Synapomorphy is shared derived character implying homology - homoplasies are uninformative towards construction of trees (similar but not related evolutionary)
4. Character-state phylogenies, i.e. maximum parsimony, based on evolutionary steps and optimality model
5. Phenetic Phylogenies, i.e UPGMA and neighbour-joining (variation in rate), based on similarity or distance measures and a clustering algorithm
6. Many possible trees could be constructed from modest num of OTUs
7. We work out best consensus tree based on resampling method called bootstrapping
8. Molecular trees can complement and support trees based on morphology or some other phenotype
9. Molecular trees can offer analyses morphological trees cant, i.e. those representing very deep evolutionary time and can sometimes refine morphological phylogenies in important ways

What's a species and where do they come from?

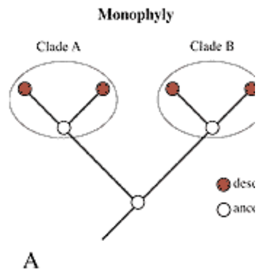


Hierarchy of Classification:

- Some sp easily recognisable and clearly distinct
- Others harder to classify due to morphological similarities (e.g cichlids) whilst some have many forms/sub-species (e.g dogs)
- DNA analysis methods such as AFLP (amplified fragment length polymorphism - genetic markers) can separate sp. look very similar but evolutionarily separate

Species Criteria:

1. ***Separation*** - Species clearly separated from each other by some characteristic (i.e. morphological, behavioural, genetic, geographical) - usually a combination of these



2. ***Cohesion*** - Species should be genetically and ecologically internally cohesive, individuals can interbreed and occupy same habitat
3. ***Monophyly*** - Orgs within species should share single most recent common ancestor
4. ***Distinguishability***:
    1. Diagnosable traits unique to species and distinguish from all other species (i.e. Synapomorphies)
    2. Phenetic Clusters - Describe groups of traits which collectively distinguish species, may not individually (i.e. morphology, observable traits)
    3. Genetic Clusters - Identify diff species even if morphologically indistinguishable (i.e. cryptic sp.)

Species Concepts:

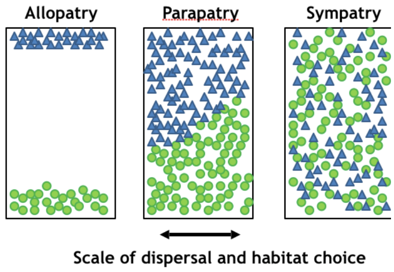
Bio Species Concept: Species are groups of actually or potentially interbreeding natural pops reproductively isolated from other such groups

Issues with BSC:

- Difficult to determine if there's on-going reproduction (i.e. between individuals of same species from diff pops)
- Sexual recombination of chromosomes in species with 2 sexes mix genomes and unifies gene pool - But not all species are sexual
- Some species, morphologically and behavioural distinct, may be able to hybridise (although possibly with reduced fitness)
- BSC has no historical dimension, and can only be applied to living orgs

Phylogenetic Species Concept: Monophyletic group composed of smallest diagnosable cluster of individual orgs - within which a parental pattern of ancestry and decent. Uses entire genome

Issues with PSC:

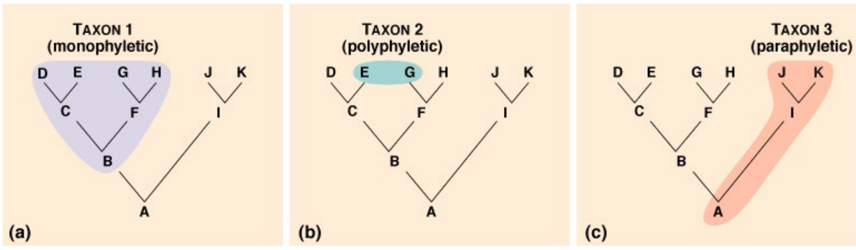


- Resolution of phylogeny depends on type and quantity of characters used - very fine scale splitting possible

- Recent species may still be polyphyletic for genetic markers (carry genotypes from ancestor), takes time for lineages to sort (extinction or fixation characters) and become monophyletic (unique characters represented and shared characters go extinct)

- Method itself may not tell you about current gene flow or hybridisation, depending on character used to construct phylogeny

Advantages: PSC consider historical relationships among taxa, identify cryptic species that are morphologically identical



DNA Barcoding:

- Initiative launched worldwide building on very simple version of PSC
- Using just 1 mitochondrial DNA gene (COI) and phenetic phylogeny method (neighbour-joining)
- Issues - Particularly for species discovery and lots of work
- Can be effective with some known taxa

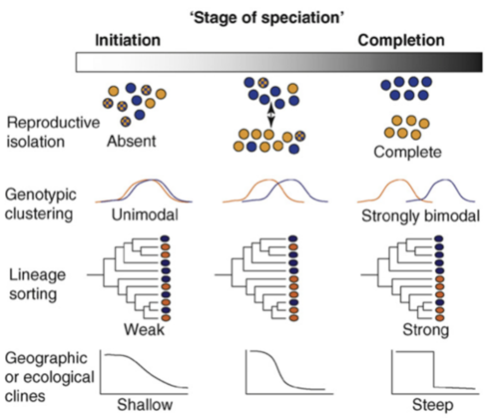
How Does Speciation Proceed?

Key Issues

- Can same processes that lead to evolution within pop (i.e. genetic drift and natural selection) drive speciation on their own? Is 1 process sufficient to explain speciation process

- What starts process of speciation?

- How important are sudden events (genetic, developmental or environmental) in generating new species by saltation (big leaps)?



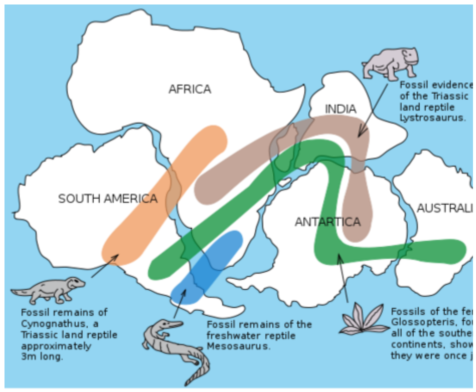
Speciation process often depends on envi factors and time - Continuous series of stages

Driving Factors -> Ecological and Environmental

Geography

- Major factor in determining potential for gene flow among pops
- Allopatry - Pop separated by some distance opportunity for dispersal reduced
- Parapatry - Origin of pops next to each other
- Sympatry - Origin of pops in same geo region
- Harder to understand for parapatry and sympatry

<u>Allopatric Speciation:</u>

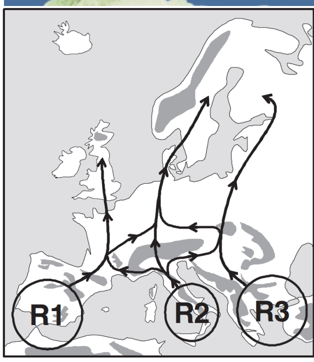


- Barriers - Mountain ranges, sea etc.
- Prevents dispersal and mixing
- Allopatric isolation can occur when habitats change to create new barrier (i.e. tectonic plate movement)
- Separates section of previously contiguous pop (vicariance)
- Pops diverge by genetic drift and local selection pressures

Tectonic plates carried continental plates distributing orgs across continents - When pops separated, isolated and thus evolved into new species (Vicariance Event - imposed barrier between pops)

<u>Establishment of Refugia - Important Allopatric Mechanism</u>

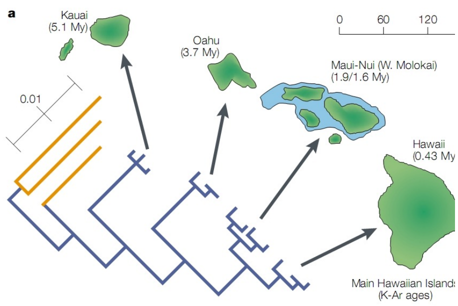
- Location of an isolated or relict pop of once more widespread species - isolation (allopatry) can be due to climatic changes, geo, or human activities (i.e. deforestation and overhunting). Forced movement of pops
- Example - During last glacial maximum (20,000 years ago) European habitat changed forcing species adapted to continual land mass in North into more southern peninsula areas (separate)



- Once barrier recedes (e.g. glacier/snow cover), pops may come into secondary contact, or follow diff migration corridors back to their original habitat

Crickets Oak Tree Bears

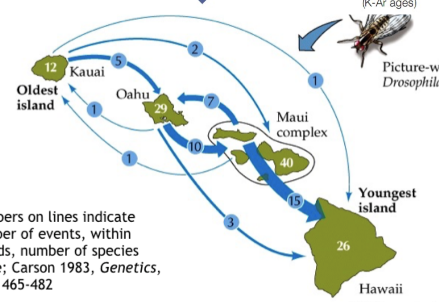
<u>Island Biogeography - Important Allopatric Mechanism</u>



- Founder effect - Peripatric speciation (new sp. form in isolated peripheral pops, cant exchange genes)
- Arc island emerge sequentially.

- Colonisation and speciation follows emergence of islands

- Example - Hawaiian islands, bird speciation follows timeline for volcanic origin of Hawaiian islands



Numbers on lines indicate number of events, within islands, number of species there; Carson 1983, *Genetics*, **103**, 465-482

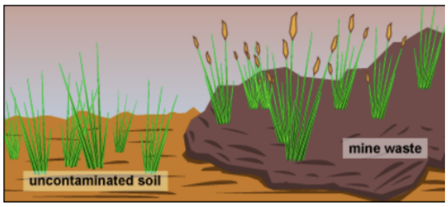
- Example - Hawaiian fruitless, process involved founder events, each island with new species, species moved numerously between islands

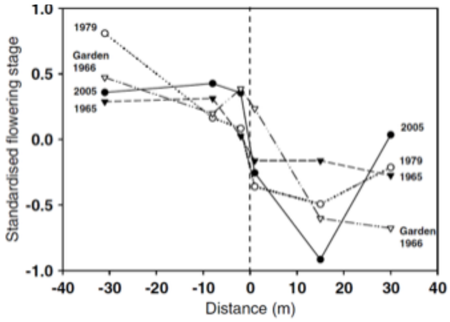
Founder Events: Small groups or individuals (females) founding new islands and starting new species (peripatric speciation), genetic drift strong due to small size of pops
-> Diversity and relatedness determined by working out num of founder events and direction of movement.

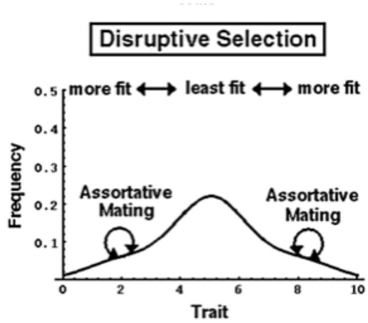
Parapatric Speciation:

- Differentiation occurs along shared boarder (neighbouring pops isolated by a boarder)

Example - Evolving diffs in metal tolerance isolating parapatric pops of Anthoxanthum odaratum (grass). Diffs in flowering stages, changing breeding times thus reproductive isolation - differences consistent over 30 years. Boundary affected the propensity for individuals on 1 side to mate with individuals on other side.



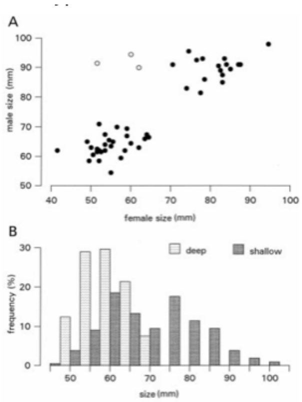




Sympatric Speciation (Hardest):

- At some stage there is likely to be continuing gene flow before it will eventually cease
- How can sub-pops differentiate if they are interbreeding?

- Possible Mechanism - Competitive Speciation: Co-evolution of disruptive selection and assortative mating (mating restricted to certain types)



<u>Example - Fish Talapia in Western Cameroon</u>

- Deep and shallow water morphs are diff sizes - Tend to mate within same types
- Shallow (bigger) and Deeper (smaller) pops
- Maintenance of small and large types is a reinforcement of divergence
- Often seen in littoral and pelagic types

<u>Example - Killer Whales (Orca)</u>

- Highly social - Distinctive fin colourations for identification
- Highly stable groups: Resident or Transient groups
- Distributions of groups overlapping
- Distinguished species using genomic work - Genetic markers
- Prey type (fish vs. marine mammals) determined diff physiology - Certain physiologies confer advantage for eating certain prey type - physiologies have genetic foundation
- Fish marine mammals - Greater physiological factors (i.e. larger teeth etc.)
- Even in similar water, groups preying on fish differ genetically from groups preying on marine mammals
- Disruptive selection - Choosing genotypes for suiting behaviour of eating fish

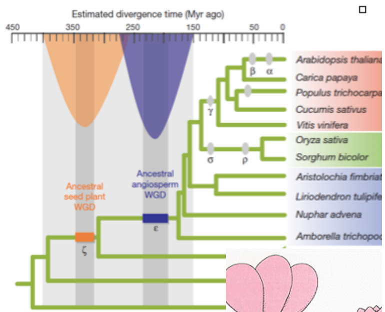
- Geographically distant groups are also genetically diff
- Geographically close groups are also genetically different (e.g Alaska residents vs Alaska transients)

Host Shifts - Key category of sympatric speciation

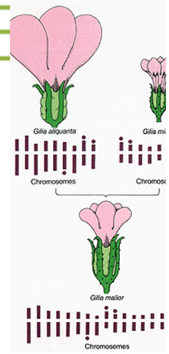
Example - Hawthorn fly
- Evolved to parasitise and lay eggs in hawthorn tree berries
- Apple orchards introduced into same area - New potential host
- Some hawthorn flies laid eggs in apples (unable to distinguish)
- Larvae group up in diff envi (habitat)
- Mechanism for isolation
- Speciation between hawthorn and apple laying types

Example - Coral Reef Fish
- Very specific affinities to particular species of coral
- Proposing evolution of new species by host switch to unoccupied coral species (take adv.)
- Series of founder events: Pops on new coral host types, adaption to coral type and speciation

Speciation Common Mechanism - Polyploidy



- Common mechanism for speciation in plants
- Generation of more than 2 copies of each chromosome (polyploidy)
- Cross between orgs with diff chromosome num leads to reduced fitness or sterility
- Plants can combat by doubling their chromosome = Instantaneous speciation
- Instantly diverge from ancestors
- 2 major ancestral divisions originated by polyploidy (seed plants and angiosperms)

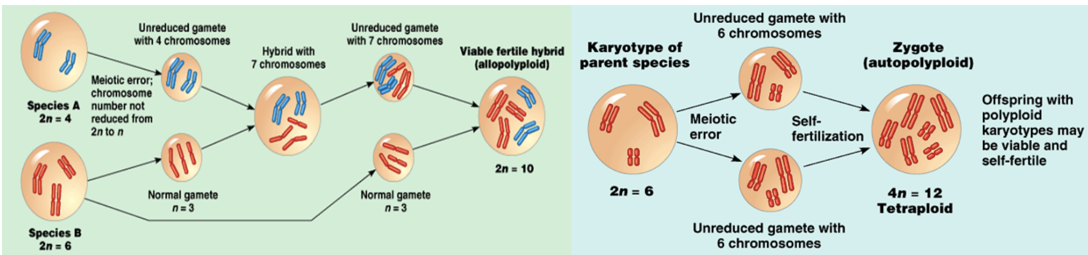


2 Primary Mechanisms for Polyploidastion

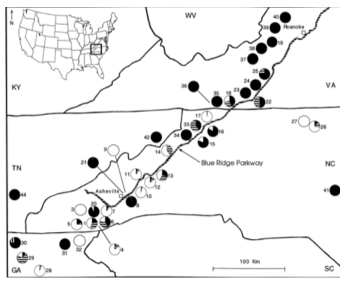
A. ***Allopolyploidy***: Common, hybridisation followed by chromosome doubling, Offspring retain chromosomes from both parent species

Example - A and B species with diff chromosomal num, meiotic error un-reduced gamete (diploid - 2n), hybridisation with 7 chromosomes -> Unreduced gamete with 7 chromosomes mixes with normal gamete (n = 3) -> Viable fertile hybrid (allopolyploid - 2n = 10)

Example - Wildflowers species had origin from 2 diff parent species (each parent had 9 chromosomes - new species has 18)



B. Autopolyploidy: Doubling of chromosomes due to inability to divide in meiosis. Self fertilisation produces polyploid offspring - Same genome duplication within same species/individual. Meiotic error (unreduced gamete - 2n) - Combining diploid gametes - Zygote (4n = 12)



Example - Beetle weed, diploid and tetraploid pops, sometimes including triploid hybrids (with reduced fitness, persistent hybridisation occurs) Map shows: diploid (black), tetraploid (white) and hybrids (striped)

Reproductive Isolation - Key Part of Process

Pre-zygotic Isolation:
- Mechanisms reduce mating between species or incipient (beginning to develop) species
- Associated with mate choice, mating time, or mating in diff habitats etc.
- Mate choice (sexual selection) itself be a speciation mechanism

Post-zygotic Isolation:
- After gametes have come together
- Mating between pops or species results in offspring less fit or infertile
- Can evolve over time (via genetic drift due to allopatric isolation)
- Or occur quickly - Speciation by polyploidisation

Summary of Isolation and Speciation Process

Example - Cichlids Fish:

- Various species in Lake Malawi

1. Initial segregation occurred by habitat
2. Morphology -> Adaptation to distinct rocky and sandy habitats, radiation of trophic morphologies within each habitats (i.e diversification in feeding apparatus - jaw diffs)
3. Finally - Assortative mating based on female mate choice and male display colour variation (diversifying male colour patterns within each lineage)

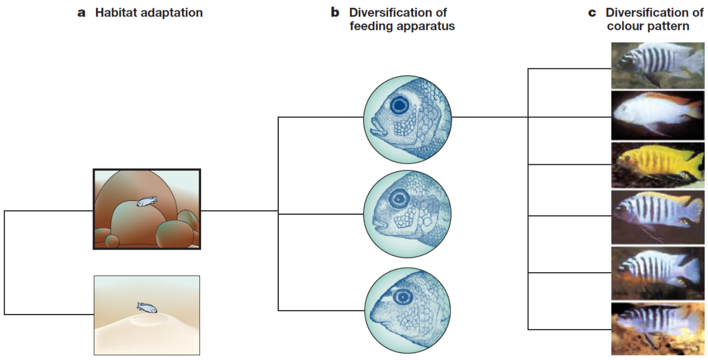
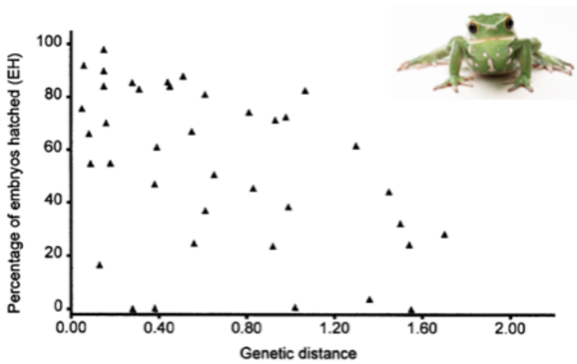


Figure 1 | **Three-stage radiation of cichlids in Lake Malawi. a** | The first stage of cichlid radiation involves adaptation to distinct rocky and sandy habitats in the lake. **b** | The second stage is a radiation of trophic morphologies within each habitat, which is represented by the jaws of *Metriaclima*, *Tropheops* and *Labeotropheus* (top to bottom, respectively). **c** | The third stage is a diversification of male colour patterns within each lineage, which is represented here by species of the genus *Metriaclima*. Modified from REF. 11 © (2001) Blackwell Scientific.

Example - Frogs:

- Proportion of embryos that hatch for interspecific crosses inversely proportional to genetic distance between species (higher proportion of embryos hatched - closer genetic diffs)
- Post-zygotic: More genetically different mates are - Less viable offspring



Summary:

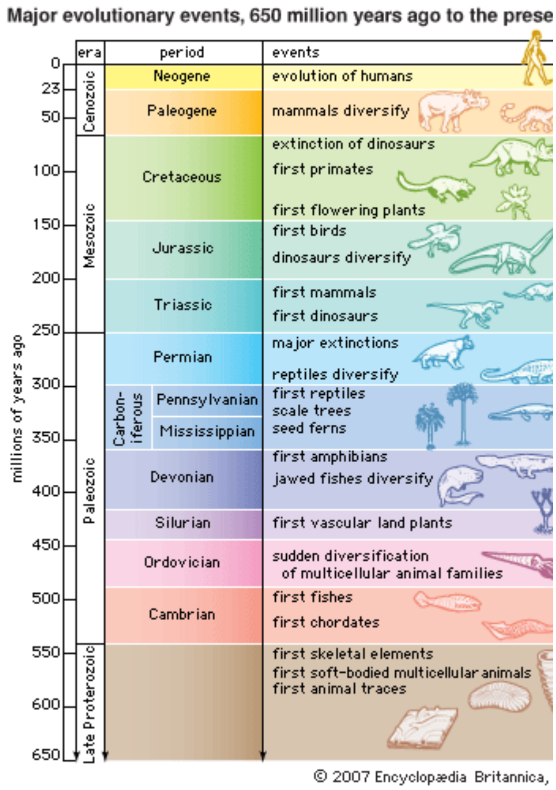
1. Basic criteria against which species status judged, rules aren't hard and fast. Associated with separation, cohesion, monophyly and distinguishability

2. Many species concepts, 2 most prominent are bio species and phylogenetic species concept (both issues)

3. Speciation process can be promoted in allopatry - Simplest and best supported scenario

4. Allopatry - Long-term or temporary (related to vicariance or refugia) and may be associated with founder events (i.e. island biogeography)

5. Speciation may occur in parapatry or in sympatry - Requires some mechanism promoting reproductive isolation by behaviour (pre-zygotic) or genetic (post-zygotic) mechanisms



Co-Evolution

Summary

- Cretaceous (130 MYA) -> New Angiosperms
- Pattens seen in fossil record shows increase in num of species (linked to abundance) in 130 MYA
- Steep rise in Angiosperms - Rapidly out competition Gymnosperms

1. Plants invaded lank back in 440 MYA (Devonian)

2. Initially, inbreeding favoured (selective advg.) as there weren't many plants around - As just colonised land - Not many available mates around thus reproductive assurance through inbreeding

3. Inbreeding also favoured as reproductive cells of first plants couldn't travel via air, only in water (mosses vs. ferns). Adaptation for life in water

4. Plants developed ability to disperse using wind vectors (first gymnosperms) - Improving ability to find mates, favouring spread of outcrossing - Thus development of separate sexes and mechanisms of assortative mating/mating systems

Likely that increase in angiosperms reflects selective advantage that allowed out competition of other clades

- Plants first eukaryotic organism
- Set up land ecosystems via primary production
- Followed soon after were animals - Insects

Evolution of Insects

- Colonisation of the land by arthropods - few million years after plants
- Arthropods followed plants onto land
- Insects evolved in the Devonian
- Rise of angiosperms reflects process of coevolution of plants and insect
- Driven diversification of angiosperms
- Advantage of angiosperms was ability to co-evolve with insects through vectors for pollination and dispersal of offspring

- First insect in Mid-Palaeozoic (spring tail - Cambrian ~ Permian)
- All insect orders had evolved by carboniferous (except later ectoparasites and lepidoptera evolved with flowering plants in Mesozoic and Cenozoic)

Jurassic 170 mya (dinosaurs)
Triassic 220 mya (ectoparasitic insects on mammals)
Permian 250 mya (first flowers, endopterygotes diverge)
Carboniferous 310 mya (exopterygote insect orders present)
Devonian 370 mya (age of fish, first land Hexapods, Collembola)
Cambrian 515 mya (marine arthropods abound)

Changes in selective pressures caused outcrossing to become advantageous
Comp with other orgs, disease vectors etc.
Sexual Reproduction - Advantage to develop mating systems which allowed for better, faster outcrossing >> Angiosperms >> Insect Dispersal

Co-Evolution

- Co-evolution is reciprocal adaptation between interacting orgs (usually ones ecologically linked)
- Adaptations - Anatomical, metabolic or behavioural
- Patterns formed are distinctive, predictable, and often very beautiful
- "Co-evolution" often used loosely and, in strict sense, co-evolution is rare and may not be that important

Certain types of Insects tend to feed on certain types of plant -> Peacock and white cabbage butterfly

Why might this be?

- Plants produces particular chemicals which repel certain classes of insects but not others
- Close interaction of plants and animals
- Each have some kind of benefit
- Coevolution: reciprocal adaptation between closely interacting species

Principles of Co-Evolution

Co-evolution can occur in any interaction between bio entities, at any scale (i.e. links aren't always at ecological scale)

Broadly speaking, either both individuals benefit (mutualism) or only 1 (antagonism)

Mutualism: Trophic, Defensive, Dispersive - Positive interaction
Competition: Negative interaction
Parasitism: Very negative interaction

Coevolution between Eukaryotes

- Most obvious examples of antagonistic coevolution between diff eukaryotes are reciprocal adaptations that develop in predator and prey
- Behavioural adaptations in Bats and Moths - Flight patterns and hinting behaviours
- e.g. Reciprocal adaptations to echolocation seen in bats and moths
- Most obvious example of mutualistic co-evolution, on the other hands, would be plant-animal or plant-insect interactions, where plant feeds animal vector in exchange for pollination

Darwin - Hawk Moths and Madagascar Star Orchid

- Nectar found at bottom of orchid tube
- Insects pollinate orchids
- Darwin predicted moths with large tongue to allow to reach nectar
- Found to be the case
- High degree of specificity of interaction
- Relatively few species found with this specificity
- Range of scales of co-evolution

Coevolution between Eukaryotes and Prokaryotes

Example - Soybean Nodulation
- Specific bacteria form associations with specific plants (usually beans) and nutrient exchange occurs

- Something similar happens in your intestine (your micro-biome)
- Both interactions are mutualistic; infection would be an obvious antagonistic one

Coevolution between Single Cells

- We all carry around with us evidence of Coevolution between single cells
- Mitochondria (and, in plants, chloroplasts), remnants of an early endosymbiosis between our ancestral eukaryotic hosts and α-proteobacterial-like cell

Coevolution between Diff Genomes (at genomic level)

- About half our genomes consist of viral-derived material
- Action may sometimes be antagonistic - 'Selfish' genes cost us energy to replicate
- Sometimes may be mutualistic - Provide raw material for variation: Rag1 and Rag2 proteins that cut antibody genes during somatic recombinations are derived from TE genes
- Transposable elements cut up DNA - helps to reshuffle DNA - Antibody generation
- Hypervariable regions in antibodies
- Enzymes are RAG1 and RAG2 -> Come from transposable elements

Other 'Co-evolutions'

Does it make sense to talk about 'coevolution' when looking at links between culture and biology?

BUT Interspecific adaptations don't always involve strict 'coevolution'

Do interspecific interactions and adaptations always mean coevolution?
Examples are not "true coevolution"

Example - Baitsian Mimicry

- Not co-evolution as interactions are not reciprocal
- Where harmless species evolved to imitate warning signals of harmful species directed at the predating species of them both
- Unilateral

Example - Bird-Insect Adaptations

- Blackbirds predate wasps and hover flies
- Not coevolution as adaptation is not species-specific
- Wasp-hoverfly interaction - Hoverfly evolved to look like wasp but wasp hasn't changed in anyway

Split Coevolution into 2 Broad Types:

I. Specific Coevolution ('narrow sense') - One species adapts specifically and reciprocally with another. This is 'true', bilateral, coevolution

II. Diffuse Coevolution - More general term for generalised adaptations to bio entities (e.g. predator adaptations to catch range of prey, rather than 1 single, specific, prey species)

Leads to 2 Questions on Strict co-evolution:

- How common is true coevolution?
- Whats the point in studying coevolution?

How Common is True Co-evolution ?

- Probably not that common
- Safest to assume diffuse or unilateral adaptation unless proven otherwise - Look for 2 specific patterns:

Convergent Phylogeny

- Convergent evolution - Independent evolution of similar features in species of diff lineages
- Creates analogous structures that have similar form/function, not present in last common ancestor of those groups
- Adaptation, at its extreme, leads to speciation
- If co-speciation occurs between 2 orgs, resulting in convergent phylogenies, then reasonable indication that coevolution is linking these 2 species
- It's not a guarantee

Intimate Adaptation

Only way to identify true coevolution is to make sure we look in detail at suspected coevolution to see whether adaptations really are intimate and bilateral.

True Co-Evolution

Antagonistic Interaction - Association between orgs where 1 benefits at expense of another

Coevolution is a subset of evolution

Essential mechanisms that drive and pattern coevolution are exactly same as ones in 'normal' evolution:

A. We need heritable variation in a trait that affects interactions
B. Trait may be monogenic or polygenic
C. Usual rules of pop genetics hold, so coevolution can be swamped by drift in small pops, etc.

All points mean we see geo-variation in occurrence and direction of coevolution ('geographical mosaic theory')

- Sometimes factors will favour mutualistic interactions between 2 species, sometimes they'll favour antagonistic interactions
- Sometimes they'll be strong, sometimes weak, and so on
- BUT what makes coevolution interesting is tightness of the interaction
- Gives us a coupled system

Game Theory

- Essence of Game Theory is that choices you make aren't judged against any absolute standard, but against choices somebody else makes
- Leads to patterns that depend upon how game is being played
- Broadly, there are 2 ways to play a game with somebody:
    A. You co-operate
    B. You compete
- If you co-operate, you need to keep checking that your partner isn't cheating
- Tight coevolution tells us about how those trajectories work - Stable mutualism, or Coevolutionary chase
- This cuts down variables involved - if we looked at non-specific, noise might overwhelm signal

Geographical Mosaic Theory:

- Role envi plays on trait evolution
- Theory states that the close interaction between 2 species exists, depends upon envi factors
- In some envi conditions there is an advantage to co-evolve, in others there is not
- Species interact in diff ways given the envi conditions
- May compete, Interact or Coevolve
- Coevolved in past -> change in envi conditions allowed relaxation of selective pressure to coevolve etc.

Allows us to study how game theory drives evolutionary trajectories

- Evolving in response to another org -> Effectively playing a game
- Making choices about adaptation in response to what other org is doing
- Can follow trajectories when either player makes a choice
- Can dissect how evolutionary trajectories will play out as 2 species are isolated from others
- Patterns in coevolution -> Closely related to Red Queen (constant evolution to stay in same place with occasional break outs)

Example - Cuckoo

- Lay eggs in other species nests
- 4 Species used
- Fairly long standing co-evolution
- Evolved measures against cuckoo laying -> By laying eggs in dunnock nests (recent visitor)
- Other 2 species (meadow pipit and reed warbler) recognise eggs and throw out
- Cuckoo is probing evolutionary space where victims have not adapted to

Example - Evolution of Insects

- Beetles - Numerous species
- Due to 200MYA probing in evolutionary space
- Mandible Evolution - Due to the range of eating plant material
- Clades of beetles evolved mouth pieces - Enormous selective advantage over other clades due to large range of food which could be consumed -> Radiation occurred
- Spread through evolutionary space fairly rapidly
- Beetles gaining upper hand
- Both sides locked on to co-evolution - One not losing ground on the other
- Gives insight into how evolutionary adv. can be translated into occupancy of evolutionary space
- Process seen in many diseases

Patterns in Antagonism

- 1 benefits at expense of other (zero-sum)
- So negative frequency-dependent selection (harsh alleles are selected against)
- Fitness of phenotype decreases as it becomes more common (phenotype fitness dependent on freq. relative to other phenotypes within given pop)

I. Coevolutionary Alternation
II. Escape and Radiate
III. Arms races. With MRSA we've effectively chosen to up stake, virulence tends not to increase, so we've shifted into a vicious cycle. Usually, speed of selection slows

MRSA - Type of bacteria resistant to number of widely used antibiotics, means MRSA infections can be more difficult to treat than other bacterial infections

Patterns in Mutualism

- If both benefit (non zero-sum)
- So positive frequency dependent selection and alleles often swept to fixation
- Fitness of phenotype increases as becomes more common
- Sweeping can lead to rapid evolutionary change (e.g. endosymbiosis; SAR1 bacteria)
- Gene transfer, residual independence, maternal inheritance, etc.
- Here, tend to see steady state being reached
- Need to defend against cheaters - gene transfer?
- Very tight can give diversifying coevolution, although trumped by geo
- Too tight gives alga and corals and global warming.

Selective pressures were met by angiosperm plant
Shed light on way in which species can coevolve together
Strict definition of coevolution tends to get lost at species level
Coevolution at the taxon level can be seen

Genome Evolution

<u>Gregor Mendel - Showed units of inheritance are discreet -> Don't blend and persist over time</u>

- Crossed pure bred pea plants to demonstrate laws

	T	t
T	TT	Tt
t	Tt	tt

<u>Law of Segregation</u>

- 2 alleles at (diploid) locus separate during process of forming gametes (meiosis) and randomly unite at fertilisation forming a diploid (in zygote)
- Gametes -> Haploid

<u>Law of Independent Assortment</u>

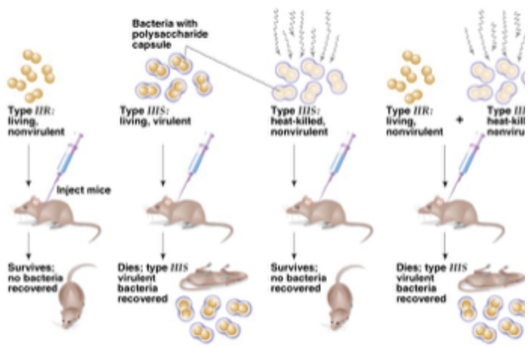
- 2 alleles separate independently during formation of gametes -> Traits transmitted to offspring independent of each other

<u>Thomas Hunt Morgan</u>

- Found role chromosome plays in hereditary
- Studied mutations -> Fruit flies demonstrated that genes carried on chromosomes are mechanical basis of hereditary
- Shows white-eye mutant in Drosophila was sex linked -> Inferred link to chromosomes from it
- Discovered that genetic traits are found on chromosomes

<u>Oswald - DNA is Transforming Principle</u>

- Unit of evolution is found on chromosomes -> What is the unit of evolution though?
- Most thought the proteins carried info
- Adding killed bacteria to a non-virulent (no coat) live bacteria and injecting into live mice -> Death
- Showed DNA was transferred between bacteria and not proteins during transformation
- Chromosomes made up of Histones and DNA carry genetic information



<u>James Watson and Francis Crick</u>

- Determined Double-Helix Structure of DNA
- Allows unwinding and template structure determines details of transcription
- Allows mechanism of replication and translation

Nuclear genomes vary in size and divided into chromosomes in eukaryotes

- Many reasons for variation but one correlation with taxa is body size

<u>Genomes are Composed of Genes</u>

- Genes code for polypeptides and more
- Much of non-coding DNA is repetitive, includes large and small repeated arrays
- Proportion of genes is shown to decrease with increasing genome size, and increase in repetitive DNA
- Introns are spliced out during post translational modification
- Very small portion of genome encodes functional genes
- Human genome - Made up of only 30,000 coding genes - Remainder by various non-coding unique and repetitive seq.
- Repetitive seq. includes satellites, mini satellites and micro-satellites

2014 -> 228,000 human genomes had been sequenced - Allow comparison of whole pops at genome level

<u>DNA Elements</u>

- Short seq. that act as signals impacting expression of genes, and RNA transcription found for ~75% of genome
- Function of "junk" DNA = Non-coding, repetitive regions

- RNA Extraction - Map it back against genome
- Allows find out how much of genome actually encodes RNA product
- 30~40% of genome is transcribed and has some function

- Genes are controlled by transcription elements - Switched on or off and level of transcription is controlled
- MicroRNA regulates genes
- Non-coding Long RNA
- Pseudo genes - Originally existed and had a function but became non-functional, but still RNA produced is involved in regulation instead of original gene product

<u>Gene Family</u>

- Repetitive arrays of genes, gene product usually very important, so there are many copies of it within genome (e.g. ribosomal DNA), duplication from ancestral gene, dispersed around genome or occur in consecutive array

<u>Synonymous vs. Non-synonymous change</u>

Within coding seq. of gene still non-coding residues - those which are synonymous - 3rd positions within codon can vary without changing amino acid codon codes for
Redundancy within code —> Which is translated into amino acid
Last position (synonymous) usually changed but gives same amino acid

No changes to phenotype
Non-Synonymous are first and second positions of codon

Mammalian Mitochondrial Genome - Closed circular molecule

- Only non coding part is 1kb long out of 17 kb molecule = Control region

Plants - Chloroplast genome (plastids)

- Circular genome
- Variable in length
- Much larger in size
- Have introns
- Majority of DNA is non coding
- From symbiosis events giving rise to organelles

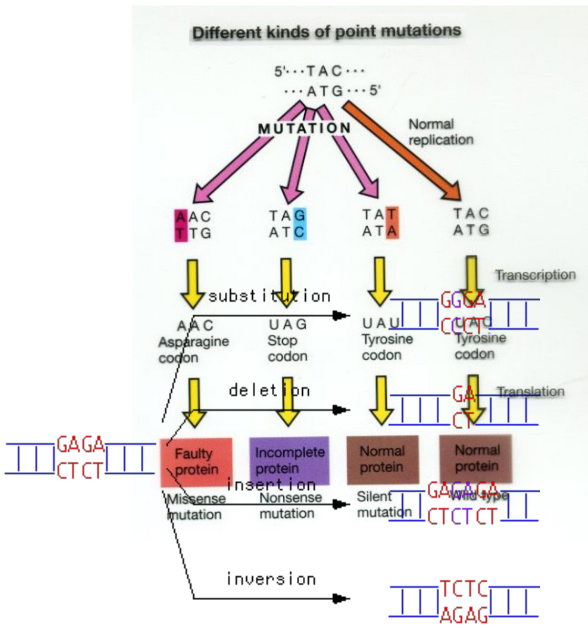
<u>Mutations</u>

Point Mutations (substitution):

- Missense mutation (diff AA)
- Nonsense mutation (stop codon)
- Silent Mutation (same AA)

Deletion Mutations

Insertion Mutations



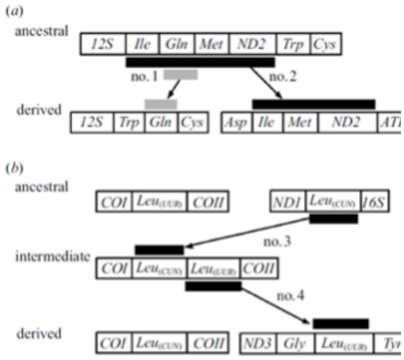
<u>Mutation Rate for Point Mutations</u>

Within Exons:
0.004 x 10^-9 per bp/year

Synonymous Sites and Introns:
1.7 x 10^-9 per bp/year

Average Synonymous Rate:
5 x 10^-9 per bp/year

- Slower mutation rate in introns than within exons
- If functional coding region has mutation, it'll leave an effect
- Introns mutate -> Non functional so no effect
- Mitochondrial DNA has faster mutation rate due to less sophisticated repair mechanisms



Mutation Hotspot

- Not evenly distributed across Genome
- High freq. of mutations in hotspot regions along gene

Impact of Mutation - Dependent on Where it Occurs:

Insertion into coding region causes Frame Shift

A. At Promoter region - may increase or decrease rate of transcription,
B. At Response element/operator site - May disrupt ability of gene to be properly regulated
C. At 5'-UTR/3'UTR - May alter ability of mRNA translation, may alter mRNA stability

May effect expression of gene due to interaction with transcription factor

Transition/Transversion

Type of Substitution Mutation

Transition
- Interchange of 2-ring purines (A <-> G) or interchange of 1-ring pyrimidine (C<->T)
- Substitute adenine base with guanine
- Substitute cytosine with thymine

Transversion
- Interchanges of purine for pyrimidine bases
- Substitute Adenine base with either Cytosine/Thymine
- Substitute Cytosine base with either Guanine/Adenine
- Are slower and harder to occur

How do Point Mutations Occur (?)

Deamination - Replacement of an amine group (swapping Cytosine into Uracil)

Chemical Mutagens (nitrous acid, UV light) can change bases (swapping cytosine into Uracil which pairs with Adenine rather than Guanine)

Larger Scale Mutations
- Chromosomes can mutate in ways that may change DNA content
- Overtime reassortment of chromosomes occurs

A. Deletion - Results in loss of DNA (deletion)

B. Inversion - Changing direction of seq. (inversion)
C. Translocation - Moves DNA among chromosomes

<u>Example - Radiation of Crab Sp.</u>

- Rearrangements and translations occur in mitochondrial genomes
- Radiation of crab sp. -> sequencing of mtDNA genome has been done
- Dark bands show rearrangement which leads to evolution into diff crab sp.

Repetitive DNA

- Simple repeats making up majority of vertebrate nuclear genome
- More than single-copy coding genes
- Tandem repeats

Satellite DNA - Named for segregation of many similar sized DNA on centrifuge gradient as a satellite distribution, determines size classes by shearing and running through caesium chloride

Motif - Array (repeated motif elements)

Mini-Satellite DNA - Named as length of repeat arrays were shorter than satellite DNA arrays -> Discovered DNA fingerprinting technique

Micro-satellite DNA - Repeat arrays are even shorter

<u>Mutation of Repetitive DNA</u>

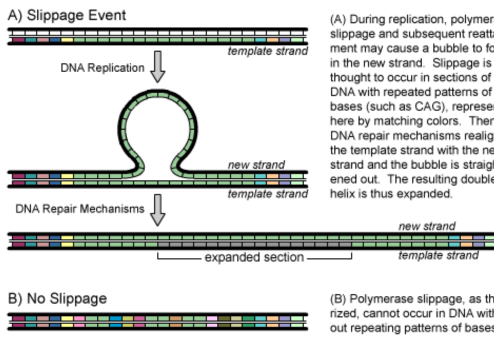
Repetitive DNA evolves very quickly but not via point mutation -> DNA turnover mechanisms generates variation in length of repetitive arrays

DNA turnover - Changes size of an array

1. DNA slippage - Within chromatids or during replication

- Within single chromatid - Combination of strand breakage, looping and DNA repair leads to expansion or repeat array or contraction
- Breaking and folding of chromatid
- Extension - Endonuclease cuts to allow loop to relax, filled using polymerase and ligated
- Much faster mutation than point mutation (1 x 10^-4 base pairs per year)
- DNA slippage during replication - Misalignment of repeat elements during replication with either excision or repair leads to extraction or contraction (loop and repair) ->

Figure Q-5: The Polymerase Slippage Model



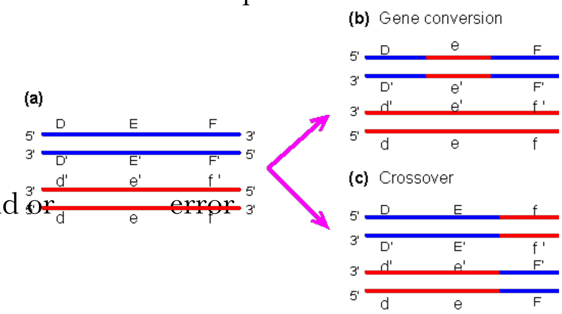
Results in diff copies depending on which strand the error occurs on

2. **Unequal crossing-over - Within repetitive non-coding arrays or within gene families**

- Hypothetical recombination of chromatids through misalignment
- 2 chromosomes misalign during crossing over results in 1 strand longer than the other
- Unequal crossing-over involving gene families - Unequal recombination at diff levels, repeats in spacer region, changing num of repeats
- Mutation in 1 gene of gene family leads to spread of mutation throughout gene family (copies of same gene)
- Eventually expressed

3. **Gene conversion - Promotes greater or less diversity**

- Results between genes that share similar seq. through formation of heteroduplex
- and Subsequent repair either converts seq. of invaded strand or preserves it
- 2 Chromosomes come together, conversion of one into other
- Repair either results in original (conversion) copy of strand or error into strand

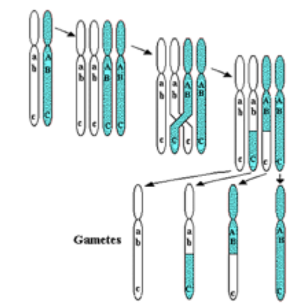


4. **Transposition - Jumping genes**

Transposable Elements - Transposons generate short interspersed elements, jumping gene inserted all over genome, interspersed nuclear element

<u>Shuffling Genomes - Role Of Recombination</u>

- In sexual orgs, gametes generated during process of meiosis
- Homologous chromatids overlap and exchange DNA = Recombination
- Crossing over causes shuffling of alleles during meiosis -> Gene combination change
- Important in evolution, as evol. occurs at level of pops based on raw material available and sometimes combination of genes available is important



Crossing-over and recombination during meio

<u>Conclusion</u>

- Nuclear genomes are in constant state of change/flx
- Composed of much seq. for which we know lil about
- Much repetitive DNA may be generated as by-product of errors generated when normal genomic processes related to DNA rep, transcription, repair and recombination go wrong

- Take advg. of these region to learn more on genomic function and evol.

<u>Summary</u>

1. Genome is full complement of DNA carried by single gamete -> Considered in terms of organelle (nuclear, mitochondrial, chloroplast)
2. Genomes vary greatly in size among taxa - Due to diffs in amount of non-coding DNA
3. Proportion of genomic material that is coding genes is small
4. Genes are structured and rate of change over time (interaction between mutation and selection) varies in coding and non-coding parts of genome
5. Repetitive DNA is common and changes quickly over evol. time via Point mutations and driven by errors made during alignment and replication of repetitive region

So Few Genes

So Few Genes but So much Diversity !!

- 10,000 ~ 30,000 genes in vertebrate genome -> Expresses so much phenotypic diversity both within and among species?

<u>Simples Case - 1 Gene —> 1 Phenotype</u>

- Rarest and simplest case
- Example Sickle Cell Anaemia
- Single base mutation in gene coding for Haemoglobin changes
- Morphology of RBC altered resulting in disease
- GAG (glu) —> GTG (val)

<u>Mendelian Segregation</u>

- Show if a trait is behaving as a single locus
- E.g. Medel's Pea Color

aa Genotype —> Green (recessive)
AA Genotype —> Yellow (dominant)

Gene is segregated based on punnett square through Mendelian law of segregation

P: Aa x Aa
G1: AA, Aa, Aa, aa

3 - Yellow
1 - Green

<u>Molecular Genetics resolving Mendel's Pea Plant Color Gene - *sgr* (stay green)</u>
-> Why are mendel's green pea plant a recessive trait

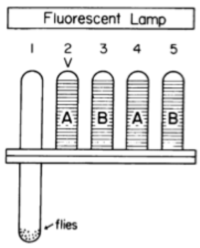
- Mendel's green peas are result of a broken gene (mutation)
- Single Locus - *sgr* gene - Breaks down color
- *sgr* inhibits opening of ring of pheophorbide in chlorophyll breakdown pathway
- If sgr gene is present then pea plants are Yellow
- If sgr gene isn't present then pea plants are Green (chlorophyll not broken down)

1. *sgr* turned on in peas

2. SGR protein produced
3. SGR protein turns on other genes in peas to produce chlorophyll destroying proteins
4. Proteins can break down chlorophyll
5. Peas are yellow

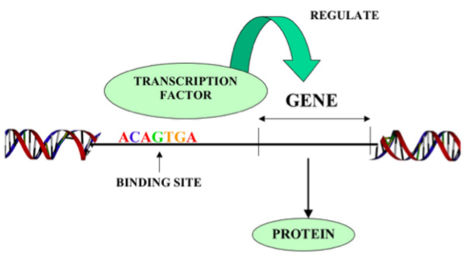
<u>Domestication - Provides Info on Genetics of Phenotypic Traits</u>

- Example - Mirror Phenotype in Carp
- Another single locus effect (mendelian segregation) - Found out via Breeding
- Scaled carp (wild type) - Fibroblast growth factor receptor 1
- Mirror carp (mutation) - Mutated fibroblast growth factor receptor 1
- *fgfr1* - Developmental gene
- Loss of function is compensated for by a duplicate copy - Paralog (second copy of gene)
- Genome duplication can carry history of genome -> Genes with 2 copies
- Paralogs have redundant function in early development but diff function in Adult stage
- Timing of gene expression can change phenotype



<u>Example - Learning Olfaction Memory in Drosophila - "Dunce" and Associate genes</u>

- Phenotype is Behaviour
- Experiment on Drosophila
- Flies are kept in chamber
- Chamber A - Voltage and thus flies will be shocked
- Chamber B ~ D has no voltage
- Normal flies will learn to go into other chambers (avoid shock) but memory decays over hours
- Pathway of genes interact with one another
- Can alter genes to extend memory of flies (behaviour)



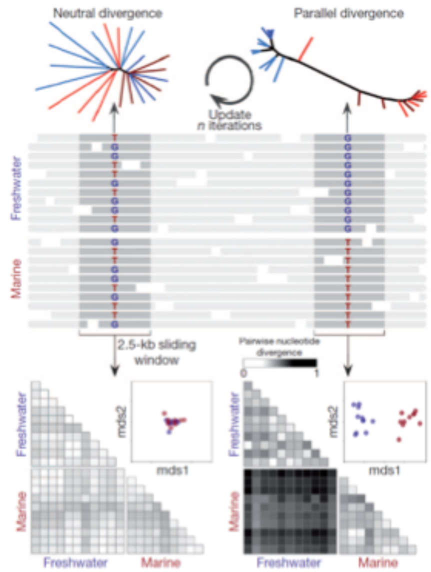
<u>Transcription Factor - Complex Interaction</u>

- Transcription factors and micro-RNA switches can Regulate:
  - Alter expression of gene
  - Determine level of transcription
  - Turn gene on/off

- Interacts with binding site - Upstream of promoter

<u>Example: Stickleback Fish</u>

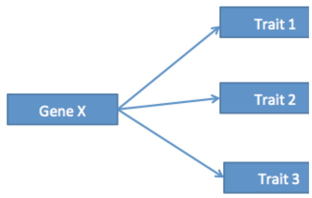
- Compared genomes of sticklebacks living in 2 diff envis: Marine (red) vs. Fresh (blue)
- Comparison of genome = Some loci show no diff
- Parallel divergence = Very distinct segregation of genes in evolutionary history
- 17% coding genes, 41% regulatory genes, 42% probe regulatory
- Regulatory genes are key



Another Example

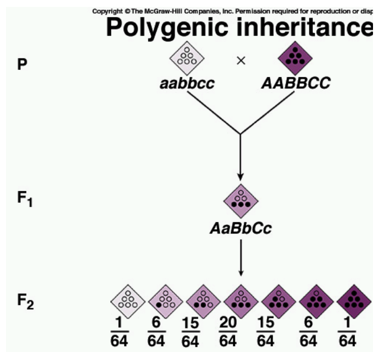
HPRT gene knocked out - Shows diff in expression profile effecting the resulting phenotype, HPRT locus changes expression at range of loci

Pleiotropy: 1 Gene —> Many Functions (multiple traits)



Example: Cytokine (EPO)

Erythropoietin (EPO) - Cytokine (immune system gene) involved in inhibiting programmed cell death (apoptosis) and other multiple pleiotropic effects
- Dependent on context of how much is expressed and when and where



Quantitative Traits (continuous) are Polygenic

Polygenic - Multiple genes —> 1 Phenotype

• Multiple genes interact to generate phenotype and can interact with each other in diff ways:

A. Epistasis - Interaction between 2 or more genes to control single phenotype (example: when genotype at 1 locus (allele) masks effects of genotype at another locus) = Multiple genes control 1 phenotype

B. Additive - Each relevant gene has independent effect on the phenotype

Heritability

Phenotype (P) determined by Genotype (G) and Envi (E) - esp. developmental envi
Varies quite a lot between traits

V - Variance

Vp = Vg + Ve

Variance in phenotype = Variance due to Envi + Variance due to Genotype

Variance due to Genotype can be broken into components:

Dominance (D)
Interaction (I) - Epistasis
Additive (A)

$V_P = V_A + \mathbf{V_D + V_I} + V_E$

Non-Additive Genotypes = Variance due to dominant genotype + Variance due to interaction

<u>Heritability can be quantified in 2 ways:</u>

Broad Sense Heritability

H = Vg/Vp

Heritability dependent on Genotype divided by Phenotype

Narrow Sense Heritability

Additive genetic variance (important) explains more of diffs among phenotypic traits

h^2 = Va/Vp

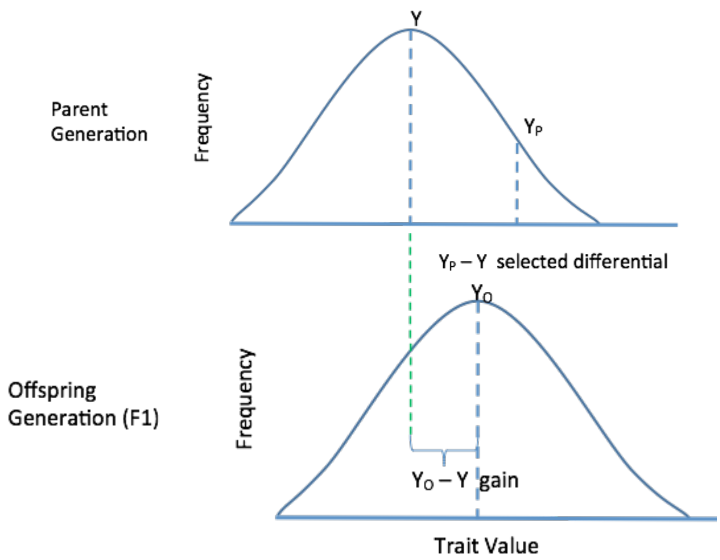
Heritability squared dependent on additive variance divided by phenotypic variance

<u>Calculating Narrow Sense Heritability</u>

In Parent Generation

Y - Mean height
Yp - Parent's height

Yp - Y = Selected differential



In Offspring Generation

Y0 - Offspring height

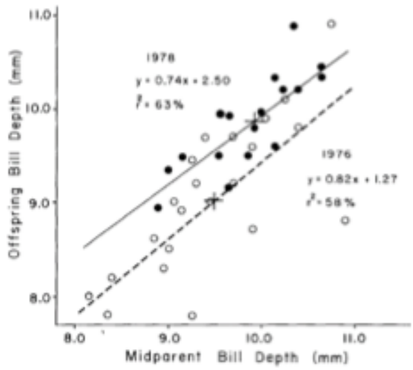
Y0 - Y = Actual Gain

Narrow Sense Heritability found by: $\boldsymbol{h^2 = (Y_O - Y)/(Y_P - Y)}$

- Selecting tall members results in mean height of population to gradually increase

- Heritability is actual gain divided by what we wanted

- This proportion due to genetics and not environment



<u>Example for Galapagos ground Finch</u>

- Can also measure h2 regression analysis
- Seeds became harder thus Finches bills need to become bigger
- Strength of regression on graph determines heritability of that trait
- Vary in heritability (h2) - High heritability close to 1
- Low heritability - Close to 0
- Weight of Finches - h^2 = 0.91 - High heritability
- Bill width of 0.9 - High heritability

<u>Summary so Far</u>

1. Most often genes function part of pathway or through interaction among genes (transcription factors, epistasis, additive) meaning traits are polygenic (Many genes -> 1 Phenotype)

2. Changes in genes in a pathway can alter outcome in variety of ways, meaning same set of genes can lead to diversity of functions (infinite num of ways to get numerous phenotypes)

3. Individual genes may affect multiple traits (pleiotropy), often part of 1 or more complex pathways - Pleiotropy

4. Not all aspects of traits are based on genotypes - Since envi factors also influence heritability of trait - Can test heritability to find what % is up to genetics

<u>Pleiotropy - Gene Sharing or Moonlighting</u>

Version of Pleiotropy where given gene can function in very diff way in diff context = Gene Sharing or Moonlighting

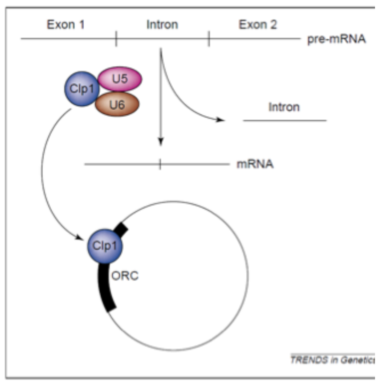


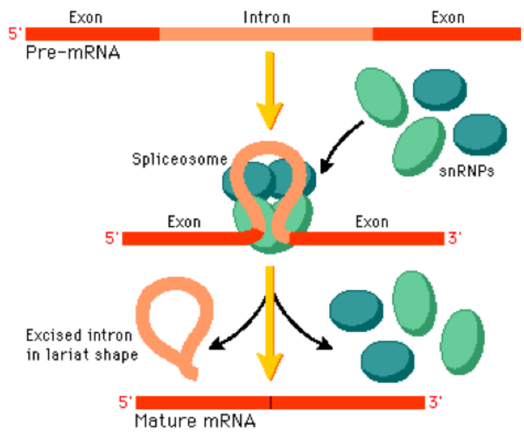
Fig. 1. The two roles of Clp1 in splicing and DNA replication. Clp1 interacts splicing factors U5 and U6 in pre-mRNA processing to produce mature RNA.

First Example:

Yeast Protein (Clp 1) 1 Gene having 2 functions:

1. Gene Splicing
2. Replication Control

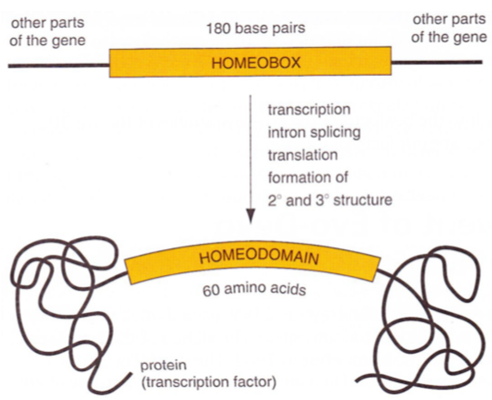
Another Pleiotropy Path - During transcription introns spliced out of mRNA



1. Pre-mRNA (Exon-Intron)
2. Spliceosome
3. snRNP's (Small nuclear ribo-nucleo-protein particles)
4. Excised intron in lariat shape
5. Produces Mature mRNA

Alternating splicing events create alternative mRNA iso-forms -> Results in diff gene expression even at same locus

- Skipping exons
- Retaining introns
- Alternative last or first exon etc.



Homeobox Genes, Homeodomain and Development

- Homeobox genes are developmental control genes which undergo transcription -> Splicing -> Translation -> Protein
- Results in Homeodomain Protein - Which are regulatory proteins (transcription factors)

Features of Developmental Control Genes:

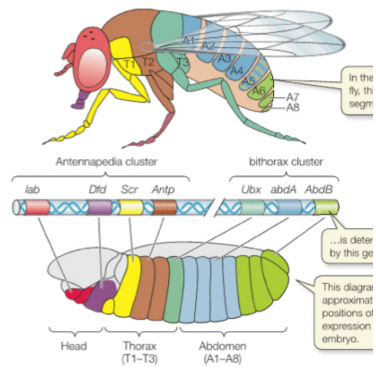
1. Homeobox genes involved in developmental control and at early stages of embryogenesis

2. "Homeobox" from Homeotic mutations cause major transformations (e.g. antennapedia - ant gene mutation causes legs to grow from fly's head) - Not all have mass effect

3. Homeodomain (encoded protein) usually transcription factor, regulates other genes

4. HOX genes - Sub group important role in development along anterior-posterior (head-tail) axis of body - Genes clustered (4 in mammals), heavily conserved across vertebrates for structural programming of head —> tail structure of embryo

5. PAX Genes - Critical role in forming tissues and organs during development (like eye)

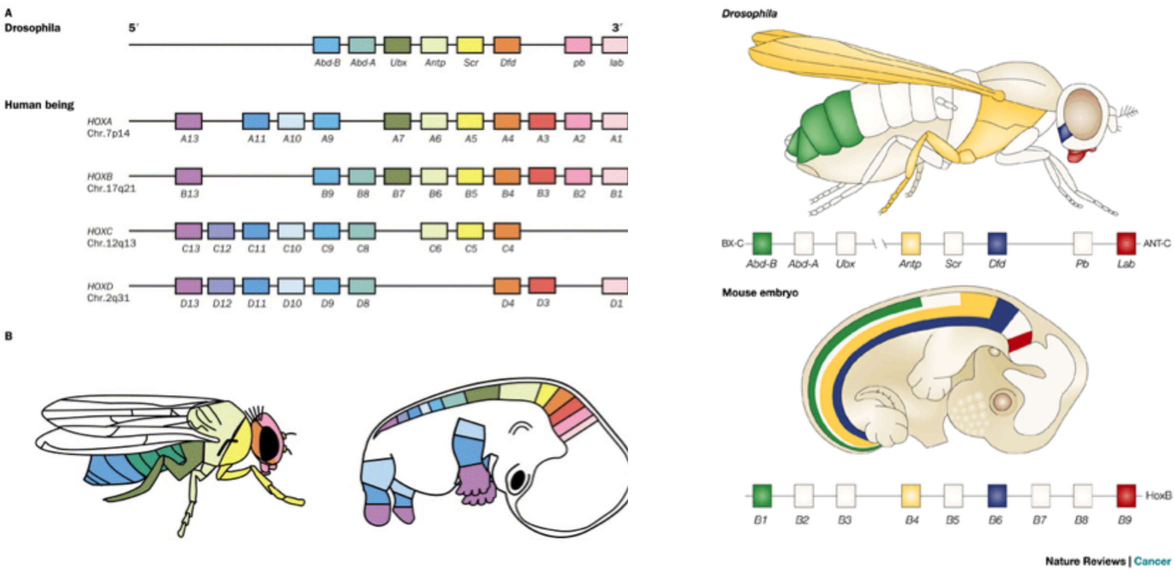


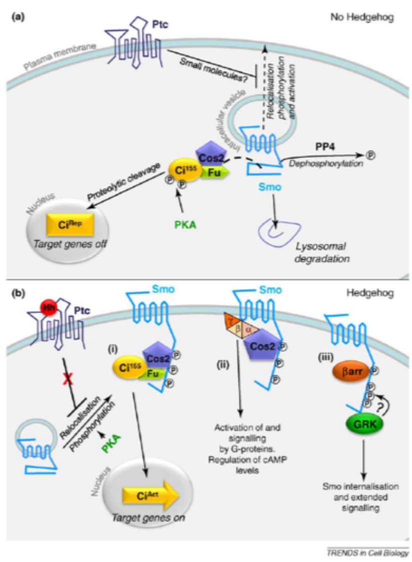
Drosophila - Example

- Relevant genes (HOX) clustered together on chromosome in same sequence as reflected in segments of developing fly
- Organisation of gene locus same organisation of body it expresses

Key Discovery - Same homologous set of genes appeared in diversity of other orgs, close to same function - Similar seq. in mouse and fly

Even in comparing flies and humans (fetus)





Example - Hedgehog Locus (ligand)

- Maintains segment boundaries in drosophila
- Red dot - Hedgehog interacting with Patch (transmembrane protein)
- Produces cubits (CI) interrupts from smoother (smo) turning relevant target genes on
- 1 gene control bunch of other genes at same time
- Homeotic Genes = Master switches = Control numerous processes

Summary

1. Single Gene Effects: 1 gene —> 1 phenotype (very rare - simplest)

2. Gene products part of pathway - Changing pathway changes phenotypes many ways - interacting with each other = Polygenic

3. Proteins encoded by genes interact with other proteins in pathway (inhibition/promotion), can interact with DNA to promote/inhibit transcription (epistasis - interaction)

4. 1 gene —> multiple traits (pleiotropy), and phenotypic traits typically polygenic

5. Polygenic "quantitative" traits involves genes with independent additive effects or interaction between genes (epistasis)

6. Some parts of phenotype typically due to genotype rest is Envi -> Defining Heritability

7. Single genes multiple roles - Differ or even opp depending on location of expression and context

8. Alternative splicing during transcription lead to diff results/functions for given gene

9. Set of developmental control genes (HOX) has a large effect on developmental process thus on phenotype and are typically associated with control of transcription (transcription factors)

10. Complexity means although there are few genes compared to the size of genome, they determine much greater range of phenotypes than would be possible if 1 gene had only 1 function

Evolution and Ontogeny

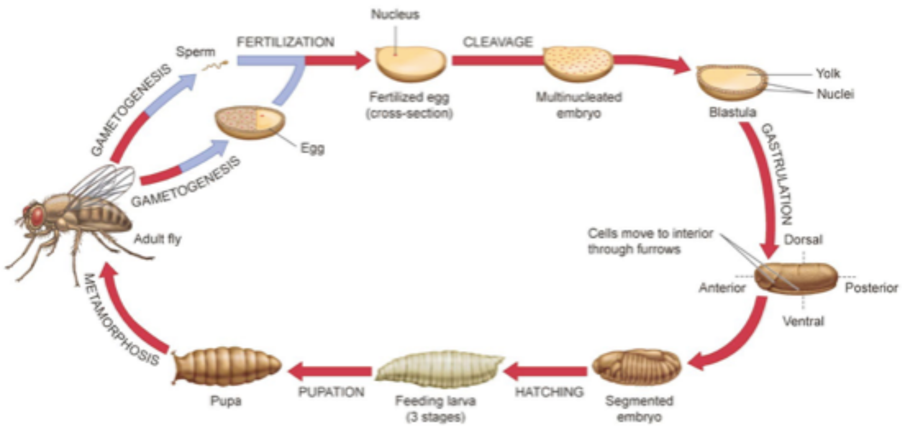
Evolution

Ontogeny

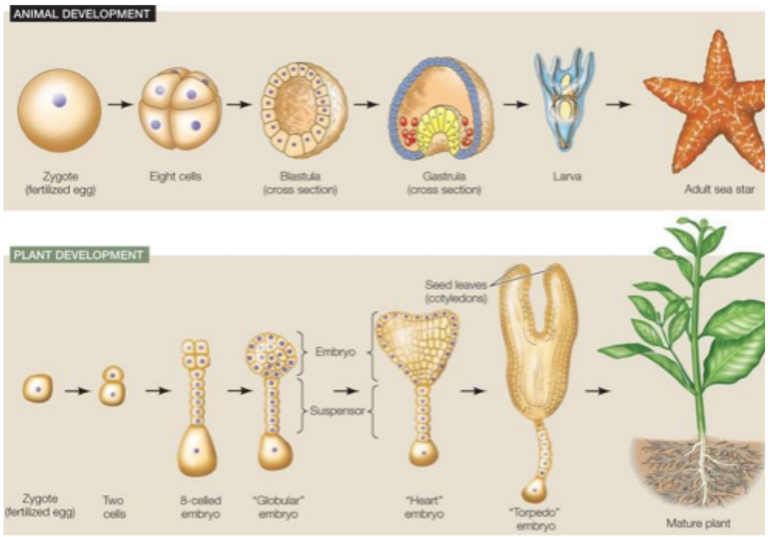
- Complete developmental trajectory from egg to adult
- Many orgs process is "indirect" including separate larval and adult stage (mostly in invertebrates)

Process in Fruit Flies:

1. Start in generation of Gametes in Adul flies
2. Fertilisation of sperm and egg
3. Cleavage - Multinucleate Embryo
4. Blastula (separate yolk and nuclei) = Cell proliferation and segregation
5. Gastrulation forming positional body axis
6. Segmented Embryo hatching into feeding larva (larval stage)
7. Pupates into Pupa
8. Metamorphosis -> Fruit fly (adult stage)



Common themes across broad taxonomic groupings



Animals

Zygote -> 8 cells -> Blastula -> Gastrula (Multicellular Stages) -> Larval Stage (or non-present) -> Adult Stage

Plant

Zygote -> Multicellular stages from embryo -> Mature plant

Darwin - Heritable Variation

Process of Pan-genesis

- Hypothetic mechanism for heritability
- Blending inheritance
- Offspring merely struck an avg between characteristics of their parents
- Cells in orgs combine with others and blend
- Problem: Blend every generations would diminish trait resulting in an avg.

Both adults and earlier life stages could be subject to natural selection

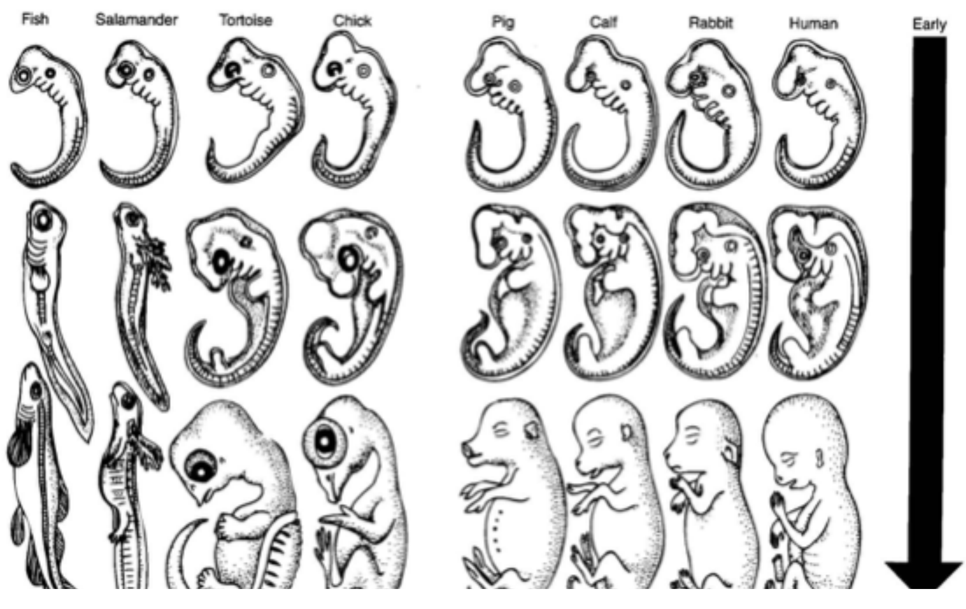
19th Century Embryologists:

Karl Ernst von Baer - Known as father of embryology, came up with "law of divergence" first of which is "general features of large group of animals appear earlier in embryo than the special features". Later stages represent more refined stages, earlier stages more broader

Ernst Haeckel - Biogenic law here he says that ontogeny is a "recapitulation of phylogeny" -> Looks through developmental stages of org and finds evolutionary history

Von Baerian Divergence

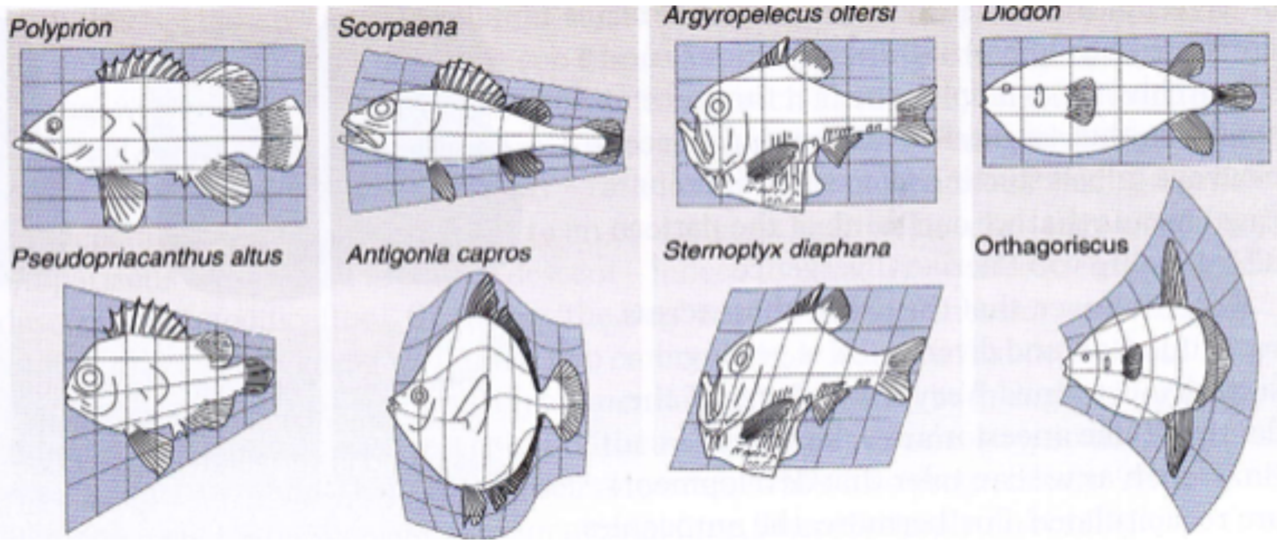
- Earlier embryonic stages in diff orgs look very similar
- Onwards in Ontogeny > Greater specialisation
- Earlier forms have general characteristic => Leads to theory of progressive evolution
- Building Org: Use general inherited processes -> Refine -> Change phenotype -> Change specifics in later stages



D'Arcy Thompson (1860 ~ 1948) - Allometric Pattern Transformation

- Proposed theory of "transformation" where morphological characters evolved as co-ordinated changes in body form - Allometric patterns during later stages of ontogeny
- Take org (fish) put on a grid and distort the grid
- Creates things that look like existing families of orgs
- "Transformation" - Coordinated process - Potential for diff parts of body to grow at diff rates - Changes consequent structure of org
- Start with original template and change that -> Changes the adult form

Allometry - Growth of body parts at diff rates, resulting in change of body proportions



Richard Goldschmidt

- Discovered homeotic mutations
- Developed theory of Saltational evolution (hopeful monster)- Cause big diff in small change
- Developmental mutation creating something so diff -> Finding a niche
- Issue of: Where's it going to find mate and how will huge change be suitable/adaptable to envi

Homeotic Mutations - Replacement of part of one segment of an insect or other segmented animal by structure characteristic of a diff segment

Gavin de Beer

- Worked on implications of evolutionary changes in timing of developmental events
- ***Heterochrony - Change timing of events during Ontogeny***

Birth of Evo-Devo

- From discovery of homeobox genes by 2 labs
- Providing molecular basis for homeotic mutations and bette understand of process of developmental re-patterning
- Homeobox Genes - For huge changes
- Provided basis for big developmental changes
- Wild type fly vs. Antp (legs growing out of antenna sockets)

Homeobox Genes - DNA sequence, found within genes are involved in regulation of patterns of anatomical development (morphogenesis) in animals, fungi and plants

Developmental Re-Patterning

- Process of change during ontogeny
- Framework for evolution of new phenotypes
- Evol process by changing genes and having selection work on it changes form of an org
- Developmental trajectory provides raw material on which natural selection can act
- Mutations changing developmental process have one or more of following effects:

A. ***Heterochrony*** - Changes in relative timing of developmental processes of descendants compared to ancestors, Changing timing

B. ***Heterotopy*** - Changing relative spatial positioning of developmental processes

C. ***Heterometry*** - Changes in relative size of parts of an org, or in relative conc. of gene products

D. ***Heterotypy*** - Evolution of new form within org, evolution of new type of structures

** All 4 make up Developmental re-patterning

Cell Activity During Development is Genetically Controlled - Following Processes:

1. Cells Divide and Proliferate
    - Rate, plane and duration of proliferation needs to be controlled to generate specific adult form

2. Cells Differentiate (stem cells)
    - Over 200 cell types in adults, which start from very similar cells early on
    - Cell as embryo grows differentiate into diff types of cells

- Each cell has same genome so differentiation is about differential switching on and off of genes

3. Cells Move
- An esp. important feature of gastrulation in animals
- When cells stream from 1 part of embryo to another
- Movement can be induced by trans-membrane proteins among other processes

4. Cells die
- Programmed cell death known as apoptosis and necessary part of development where some cell types need to have shorter lifespan (epithelial cells) than others

* Changes in 1 of these 4 processes (or some combination) could result in heterochrony, heterotopy, heterometry or heterotypy

<u>Heterochrony</u>

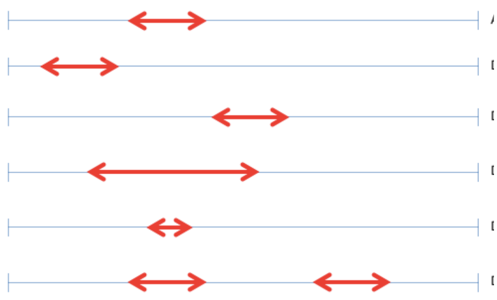
- One way change in timing of development can impact on phenotype of adult form is by having adult form reached at an earlier stage of development
- ***Pedomorphosis*** - Retain characteristic perviously only seen in juveniles (earlier stages) but now seen in adult stages and neoteny (slows development down) and progenesis
- Progenesis - Earlier sex maturation

Example: Adult Axolotl looks like larval stage (juvenile) of amphibious salamander ancestor

<u>Various Ways in which Heterochrony can be promoted at Molecular Level</u>

Model A - Ancestral stage of expression of particular gene

D1 - Occurred a bit earlier
D2 - Occurred a bit later
D3 - Occurred for longer period time
D4 - Occurred for shorter period of time
D5 - Occurred twice



<u>Example: African cichlid fish represent a rapid radiation of species</u>

- Used talapia (ancestral sp.) as a reference
- Genes governing light perception (opsin genes) studied
- 3 Gene sets corresponding to 3 pigment sets
- Compared various species that were either:

A. “Directly developing” (showing adult expression pattern from early age) showing typical increase of expression over time (like in Talapia)

B. Showed continued low expression from early developmental stages (suppression, reduction, lowering down of level of expression)

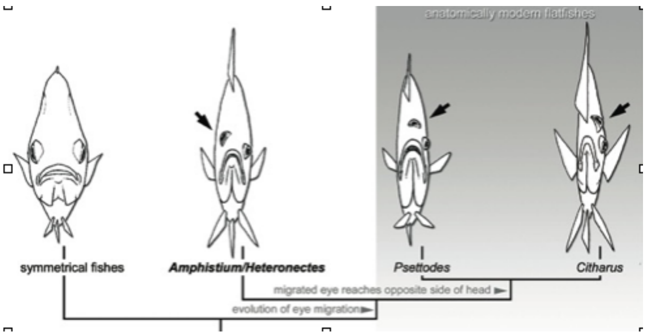
- Comparing species - Diff expression patterns corresponds to diff habitats

Heterotopy (Change in Position)

Example: Flatfish

- External features of adult vertebrates typically symmetrical
- Eyes all together on one side -> Sits on sandy bottom, only require eyes on 1 side to be abel to see and predate = Hopeful monster?
- At larval stage, flatfish symmetrical like ancestors - Like case of recapitulation (ontogeny repeats phylogeny) but may simply reflect a later stage modification of developmental process

- Are 500 species of flatfish the descendants of hopeful monster event 65 million years ago
- Discovery of intermediate forms from Eocene suggests gradual evolution
- From symmetrical fishes to -> Evolution of eye migration -> Migrating eye reaches opposite side of head



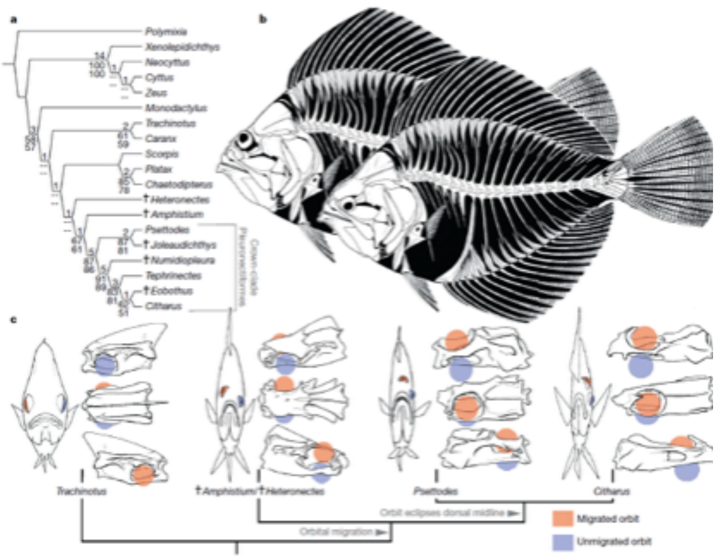
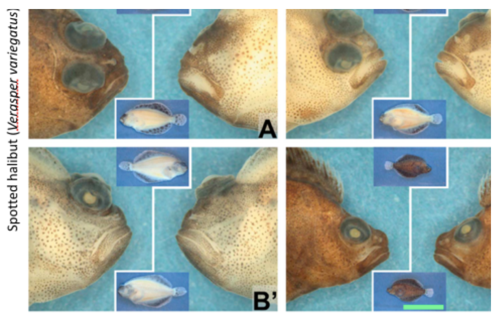


Illustration from Paper

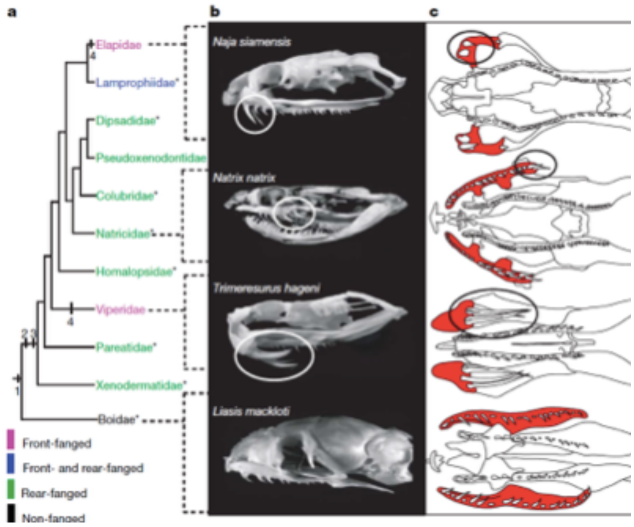
- Fossil of ancestral species with symmetrical heads/eyes
- Fossil of 58 morphological characters showing intermediate species with partial migration of eye
- Partial migration in extinct species —> Full migration
- Progression over evolutionary time



Molecular Mechanism not yet fully worked out

- May involve timing of hormone production from thyroid
- Thyroid hormonal changes during development affected color and symmetry
- Change due to genes -> Changes orientation of eyes

Another Example - Snake Fangs

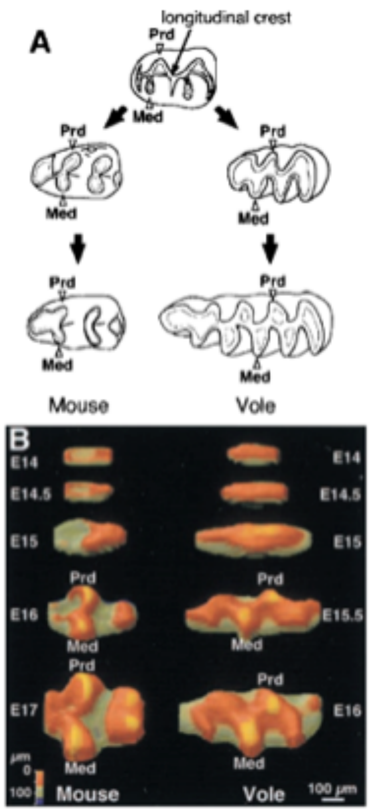


- Involves anterior - posterior axis - Position of fangs in snakes
- Ancestral form had no Fangs -> To Form with rear fangs -> Recent form with front fangs
- Evolving independently within lineage at least twice (front fangs evolved atleast twice)

Development of Fangs

- Controlled by Sonic Hedgehog (1 of 3 types of hedgehog loci in vertebrates)
- For ancestral forms (no fangs/rear fangs) expression of this gene is along extent of upper jaw
- For modern form (front fangs) expression localised at back of jaw not anterior where fangs form
- Expressed in initial position where ancestors grew fangs
- Fangs are then displaced during ontogeny ***(ontogenic allometry)*** to front of the head
- Starting from ancestral fangs and then refining during development

Example - Development of Teeth in Mice and Voles



Atleast 2 processes occurring: ***Heterotopy*** (positioning) and ***Heterometry*** (size)

Heterotopy ->Involves shift in orientation of dental cusps from alternating in ancestor and in modern vole and being parallel in mouse

- Cusps alternate in ancestor and modern vole
- Cusps parallel in mice

Heterometry -> Involving increase in num of cusps in vole (vole has more cusps than mouse and ancestral form)

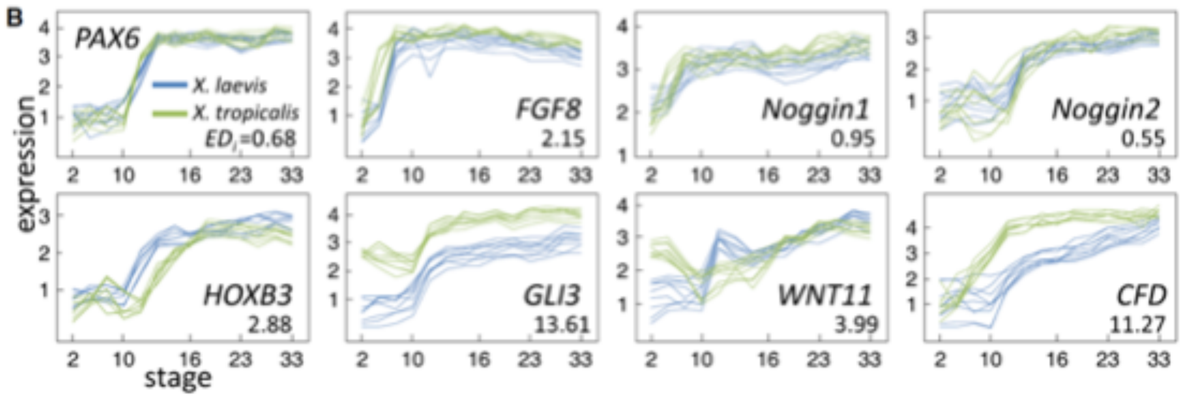
- Sonic hedgehog (shh) plays important role - Shows shift in orientation of expression in vole as development progresses

<u>Heterometry</u>

<u>Developmental controlling genes - Example: Frog</u>

Expression profiles of relevant genes during development for 2 congeneric species

1. Laevis - Larger
2. Tropicalis - Smaller



- Profiles match very well for many genes (reg genes) but in some cases amount produced is GREATER for tropical

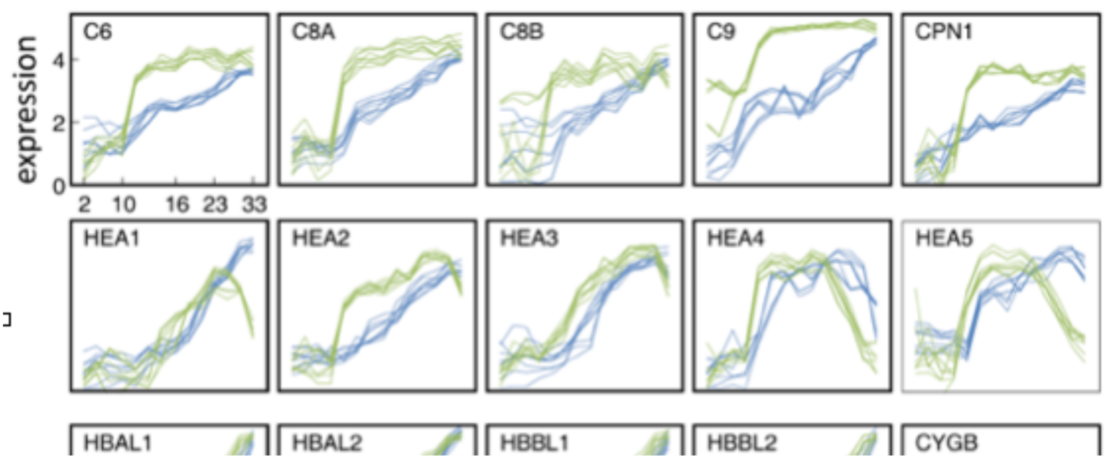
- Expression of many diff genes in diff timescale (Day 2 ~ 33)
  - Green = Expression profile for tropicalis
  - Blue = Expression profile for laevis

- Heterometry -> More expression of gene GlI3 in Tropicalis than Laevis

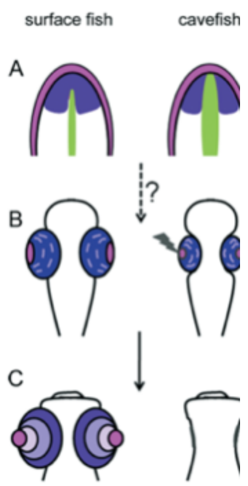
<u>Look at diff pathways:</u>

1. Top - "Complement system" genes shows heterometry (more gene expression in green)
2. Middle - Expression of hatching genes shows heterochrony -> Tropicalis hatching genes tends to be induced earlier and decreases sooner

Heterochrony - Genes shift in timing of expression



Example - Cave Races of Fish - *Astyanax mexicanus*



- Eye loss in cave races of fish represents heterometry with respect to gene expression (sonic hedgehog gene) and with loss of eyes

At 10-12 hours post-fertilisation, shh signalling along midline (green) greater for cavefish and eye field delineation by Pax6 expression is reduced (purple)

At 24 hpf lens apoptosis starts in cavefish - So eye forms then removed

In Adult fish eye completely regressed in cavefish whilst fully developed in surface fish

Issues raised by Cavefish Example?

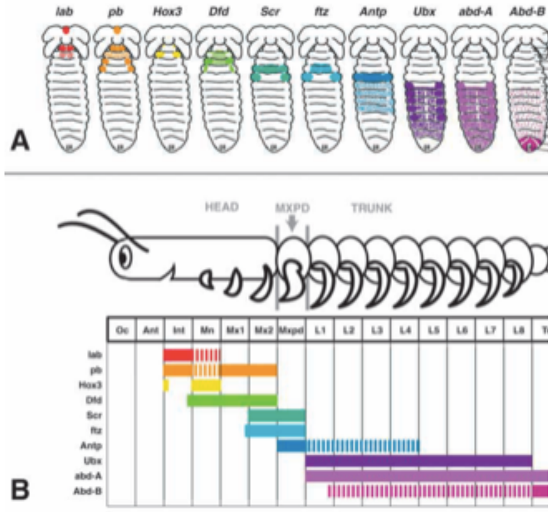
1. Why build an eye if your going to remove it (expensive?)
    - Answer - Normal forebrain development requires concomitant production for eyes, since cells for each intermingle from early stages, used to build fore brain with eyes then take away

2. Why remove the eye at all ?
    - Cant see in cave but why loose the eye
    - Antagonistic pleiotropy (1 gene influencing multi-phenotypes) = When investing in one thing, you repress something
    - Take away eye to build something else
    - Same genes enhance some features whilst reducing others

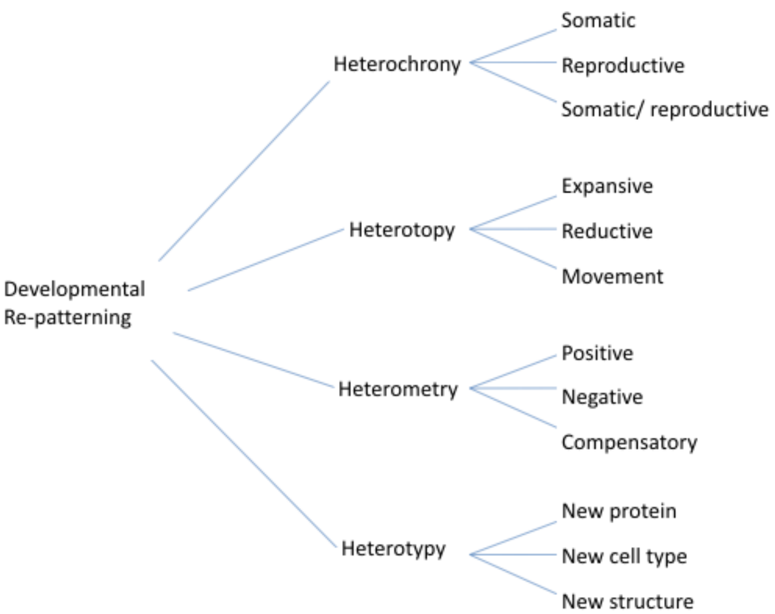
3. Heterometry can be positive or negative
    - In example both occur
    - While eye is being lost, other traits (e.g. taste buds) are increased
    - Heterometry is also often necessary heterotopy to compensate and associate with heterochrony

Heterotypy (new structures) - Example Centipedes

- Evolution of novel forms or appendages in this case poisonous claws in centipedes
- Ancestors didn't have poisonous claws
- Positionally displaying where genes are expressed in orgs
- HOX gene expression unique for this segment of body
- Likely to have evolved early (and then lost again in descendant lineages)



Arthropleura - Fossil myriad from Upper Carboniferous (335 ma) up to 2. 5 m long



Summary

1. Ontogeny - Developmental trajectory from eggs -> Adult, and evolution happens when there is re-patterning of developmental process

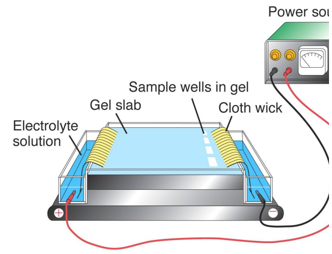
2. Key researchers proposed concept we continue to build on and test, including von Baer's observation that general features of group of animals appear earlier in embryo than special features

3. Field of "evo-devo" came with discovery of developmental control genes (like HOX cluster)

4. 4 Key processes of developmental repatterining (heterochrony, heterotopy, heterometry, heterotypy)

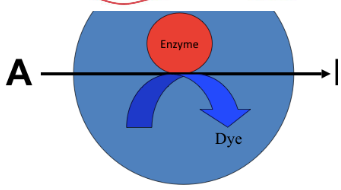
Molecular Methodology

Gel Electrophoresis of Allozymes



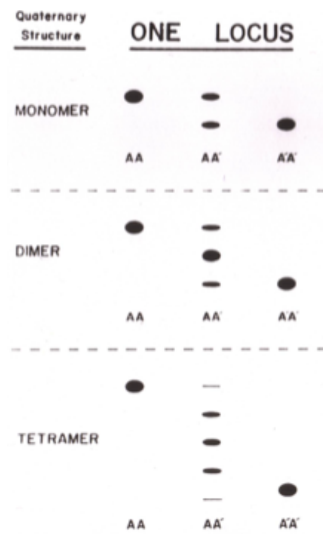
To find variation of individuals within pop scientists compared enzymes
Led to extensive screening for diversity and observation that there was much more natural variation than had been expected
A lot more diversity than expected

Allozymes - Variant forms of an enzyme that are coded by different alleles at the same locus



Experiment - Electrophoresis

Sample of enzymes in well in gel



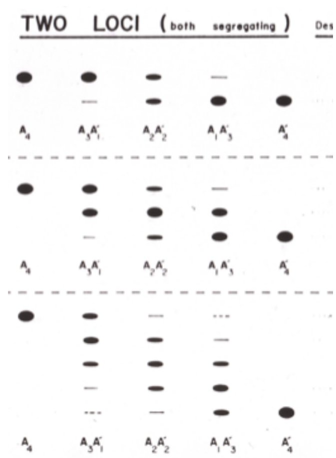
As proteins are negatively charged, travel towards +ve end across electrical field
Allozymes of electrophoresis -> Find diff form of enzymes
Enzyme is a catalysts therefore requires substrate (also to produce dye)
Led to extensive screening for diversity and observed that there was much more natural variation than had been expected

Enzyme Profile - Simplest Case (1 locus - 1 polypeptide chain)

Polypeptide (amino acid chain) enzymes consisting of more than 1 chain affected profile of gels, identifying heterozygotes and homozygotes
Enzymes can be made up of 1 or more polypeptides and can affect profile for heterozygote in gel

Homozygous - AA
Heterozygous - AA'
Homozygous - A'A'

2 or More Loci (2 or + polypeptide chains)



As num of loci encoding protein increases - complexity of gel profile increases
Still simple to determine homozygous
Heterozygotes gets complicated - Difficult to identify

Could see lots of variation at 1 locus vs. Multi-Locus systems

Limitations of Gel Electrophoresis of Allozymes:
Limitations: Differentiate between synonymous and non-synonymous change

Non-Synonymous change - AA changes
Synonymous change - AA doesn't change (Silent)
Only non-synonymous changes could be identified as looking at protein level and not DNA level
Must change the electrical charge of enzyme until it moves on gel electrophoresis

2D Gel Electrophoresis

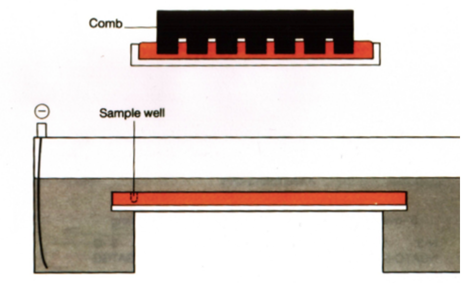
Proteins are stained
Proteins are run one way and then run again on same gel in different direction
Identify all spots and compare
Overall pattern compared for diff allozymes
Only indicate an overall pic but not any precise info -> Only identify patterns
Not where individual protein is

Working with DNA *transcribe and translate into protein*

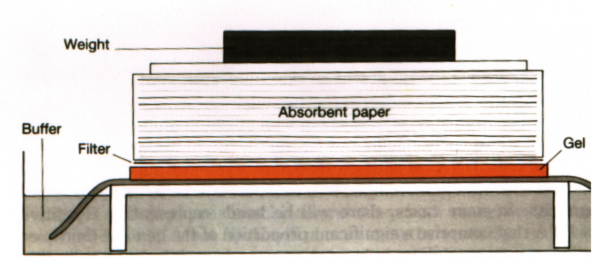
More useful for comparisons
Can identify synonymous and non-synonymous mutations

1. **DNA Extraction**
    1. Grind up tissues
    2. Digest proteins using SDS-proteinase K
    3. Phenol chloroform extraction (carbohydrates, proteins goes into phenol phase whilst DNA (polar) goes into aqueous phase
    4. End up with clean DNA solution
    5. Precipitate DNA from aqueous phase with salt and 100% ethanol

2. **Electrophoresis**
    1. To visualise DNA
    2. Run DNA through agarose gel, apply current
    3. DNA migrates through electrical field
    4. All fragments have same charge/property
    5. Distance DNA migrates depends on size of fragment
    6. Produces molecular weight band



3. **Restriction**
    1. Restriction endonuclease (from pro enzymes)
    2. Can detect particular seq. within in DNA (short 5~10 base pairs long) and cuts, creating either 5' or 3' sticky end or blunt end
    3. DNA cut several times overtime if enzyme finds repetition
    4. Example: EcoRI recognises GAATTC (red), Sequence 5'->3' cut leaves a 5' overhang or 3' overhang or blunt end (no overhang)
    5. Rerun out gel -> Cut into diff sized fragments

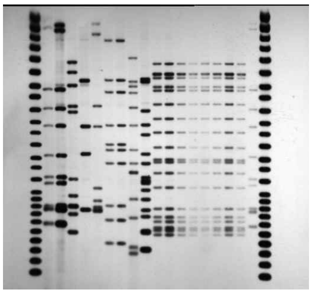


4. Southern Blotting
    1. Run smear of cut DNA onto gel
    2. Nitrocellulose filter above gel - DNA can bind to this filter
    3. Wick going across platform placing gel on top
    4. Absorbent paper and weight
    5. DNA transfers by capillary action onto nitrocellulose filter that binds
    6. Ethidium bromide allows visualisation under UV light

Southern Blotting -> DNA
Northern Blotting -> RNA
Western Blotting -> Protein

5. Probes
    - DNA is fixed onto nitrocellulose membrane
    - Create a probe using Cloning method(cloning techniques of plasmids)
    - Prokaryotes all have plasmids - Each plasmid has series of markers and restriction enzyme sites
    - Marker genes allow detection
    - Plasmid cut with EcoRI
    - Foreign DNA cut with EcoRI
    - Clone this DNA into plasmid using DNA ligase = Recombinant DNA
    - DNA inserted into bacteria cell = Clone -> Replicate DNA of interest

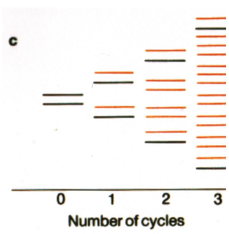
<u>Radioactive Probes</u>
Take stretch of DNA (isolated by cloning) -> Heat up for denaturing -> DNA single strand
Take short stretch of random DNA (hexameres - 6 bases) as primer
Primer anneals onto single stranded DNA
Polymerase finds single and double stranded difference
New synthesised strand has radioactive nucleotides
Insert filter into medium with radioactive probes
Radioactive probes more commonly used in modern DNA techniques
Probes will bind where specific locus exists that has complementary sequence.
On x-ray film can detect newly synthesised DNA



- Example of DNA fingerprint = Clone (right) vs. Diff Individuals (left)

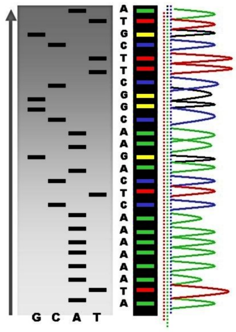
<u>Polymerase Chain Reaction (PCR)</u>

Most enzymes (polymerase) destroyed at high temps except for pro enzymes function at high temps (Use TAQ polymerase - heat resistant)
Heat separates DNA - Denatured - Single stranded DNA formed



Anneal primers and polymerase - Works by synthesising DNA strand
Exponential amplification of DNA: Denaturing, Annealing, Extension

<u>Micro-satellite DNA Loci</u>



Short repetitive sequences occur very freq.
Tend to be variable
Efficient way to screen for diversity using PCR
PCR used to amplify single locus
Primers anneal to flanking seq. which are unique
Levels of diversity are likely to be high (as length of repeats vary)
Variation amongst individuals within a pop easier to read

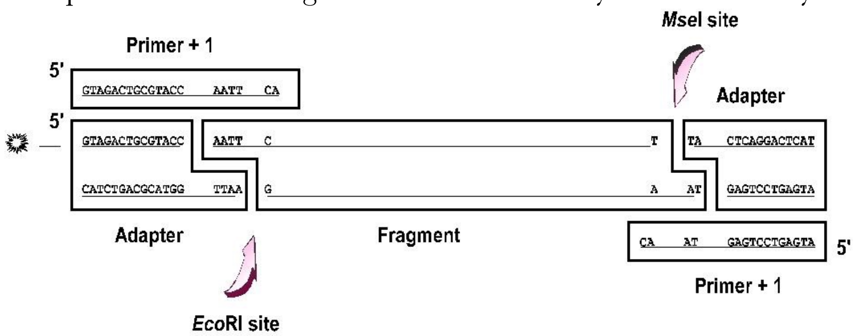
<u>DNA Seq. By Chain Termination</u>

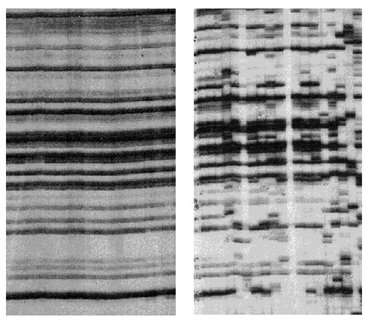
Set up 4 reactions, in each reaction - All components present for copy of DNA
In each case, diff labelled dideoxynucleotide (causes chain termination) used (A, T, C, or G)
Polymerase synthesises a copy but when hits particular nucleotide (dideoxy) terminates chain
One for G, C, A and T
Run DNA through a gel and sections segregates based on size
4 reaction run side by side -> Simply read seq. off that
Automated sequencer -> Gives print out of sequence using coloured dye (fluorescent dye)
1000 bases per run can be sequenced (1 Gene)
Allows building up of reference database allowing design of primers to analyse a specific stretch of DNA more thoroughly
Inexpensive technique

<u>AFLP - PCR Based method for screening for Diversity</u>

<u>Attempts to look at many Loci across Nuclear Genomes:</u>

Reference Database
PCR-based methods for screening for diversity - AFLP (amplified fragment length polymorphism)
Found way to find diversity across whole genome
Cut DNA and produce fragments, using restriction enzyme that give sticky ends (hangover)
Subset of fragments selected for amplification
Find adapters that stick onto sticky ends
Design primers to be complementary to adaptor seq., restriction site seq. and a few nucleotides inside restriction site fragments
Amplified all those fragments that were cut by restriction enzyme

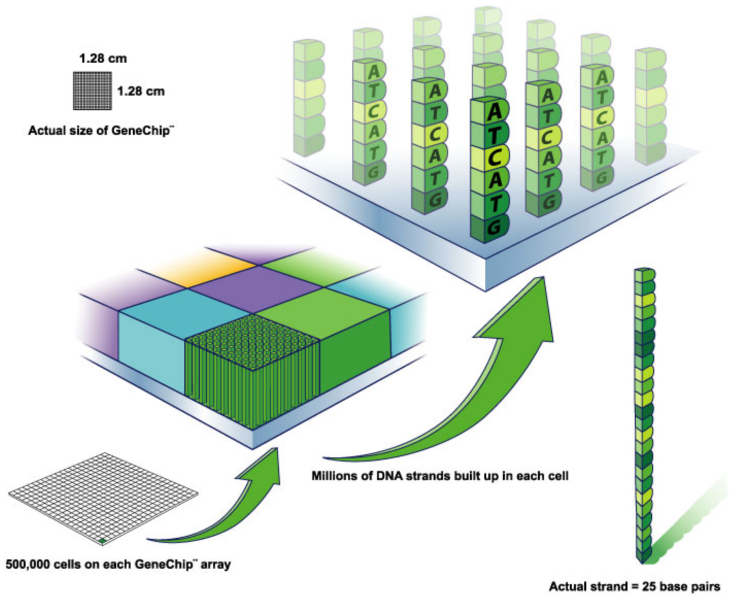




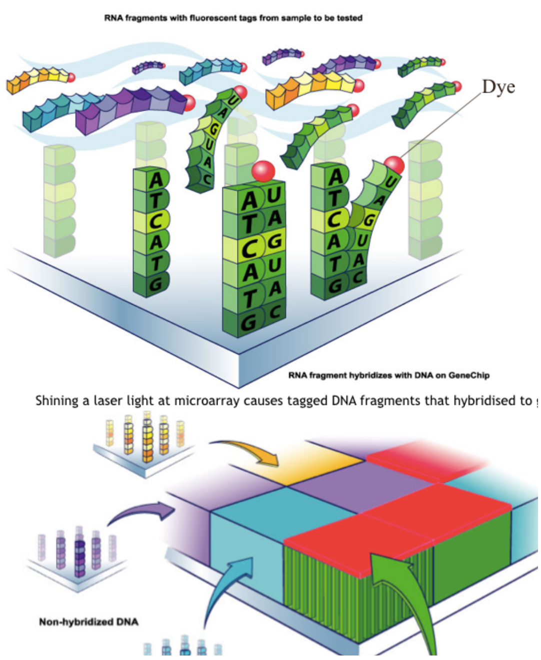
Radioactively labelled - Black and white (when in straight line - all clones) (non straight line - all diff individuals)
Can identify how similar profiles are - However not detailed info

DNA Microarrays

Genomic tool to monitor thousands of loci at once
Microscopic spots of single-stranded DNA (ssDNA oligonucleotides) - Attached to solid surface called chip
Microarray assays are based on hybridisation of a ssDNA labelled with a fluorescent tag to the complementary molecule attached to the chip
When each spot in microarray is attached to unique DNA molecule, used to detect presence/absence or even concentration of particular type of DNA molecule
One spot on a microarray contains many DNA strands of same sequence



Labelled DNA fragments from 1 sample hybridises to array
Shining laser light at microarray causes tagged DNA fragments that have hybridised to glow
Can identify homozygotes and heterozygotes for specific loci



Latest Technology

Massively Parallel
Very many fragments can be sequenced at same time
Genome sequencers - Repetitively sequence same sample
Before used pyrosequencing - Chemiluminiescent reaction marks polymerase addition of specific nucleotides

Illumina (sequencing by synthesis)

Provides short reads (125 ~ 250 basepairs)

Single run can now produce a terabase of data (3.2 billion bases in human genome -> Good sequence of genome requires that redundancy)

Need a num of copies read for that seq.

Each read not all that accurate however, after numerous times, accuracy improves (depth increase)

Can seq. a dozen human genomes in a week

PacBio Machine

Single molecule real time -> Provides long reads (up to about 8kb or so)

Relatively low accuracy per read (accuracy met through redundancy)

Attempting to make pacbio much smaller (smaller than mobile phone)

Hosptial beds -> Seq. patients genome and find diseased gene

Next Generation Sequencing

Pyrosequencing - DNA fragments are bound to a substratum and the incorporation of nucleotides by polymerase is marked by the emission of light, generated by Luciferase.

1. Hybridise primer and incubate with enzymes and sequentially with nucleotides
2. Polymerase - Double and single strand boundary
3. Polymerase incorporates nucleotides and PPi (pyrophosphate) is released in small amount that reflects amount of incorporated nucleotide (eg. repeats)
4. Conversion of PPi to ATP drives luciferase-mediated production of light, detected and quantified by a chip
5. Apyrase degrades unincorporated nucleotides and when complete another nucleotide is added
6. Addition of dNTPs is sequential and nucleotide seq. is detrained by signal peaks in pyrogram trace.

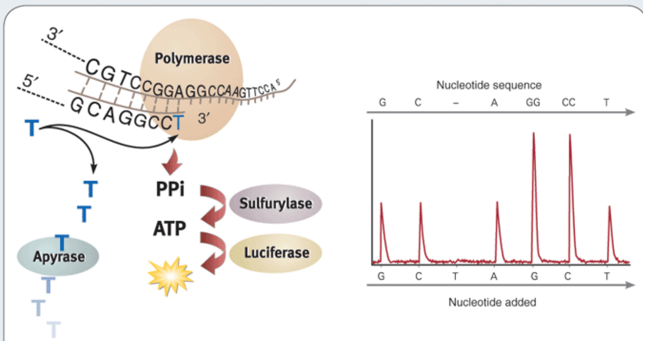


Figure 1 | The principle of Pyrosequencing and the output Pyrogram™. Double peak heights indicate incorporations of two nucleotides in a row.

2001 Human Genome Sequenced

228,000+ Human genomes sequenced

Many other projects underway for other sp.

Summary

1. Gel Electrophoresis of Proteins - First method to permit large-scale screening of natural pops, led to unexpected discovery that there was substantial variation in natural pops at molecular level (only coding loci were compared - non-synonymous change), useful and informative, but limited, only looks at non-synonymous changes

2. DNA Extraction and Electrophoresis - Permitted the analysis of DNA directly for the first time, through use of restriction enzymes and DNA probes, Identify gene region (particularly Gene of interest), Higher resolution than protein analysis and can identify gene regions and restriction site diffs - Can distinguish between synonymous and non-synonymous change

3. DNA sequencing - Chain termination method most direct and efficient method standard today, but sequencing by other methods began in early 70's - Became easier with PCR, distinctly see synonymous and non-synonymous change, limited as only can seq. up to 1000 base pairs, revealed how much variation there was in a genes

4. PCR - Changed everything, because it facilitated analysis of specific genes without the need for cloning. This method allowed the analysis of microsatellite DNA markers, which became a standard in population genetic studies. (1985 – present). PCR facilitated sequencing and use of micro-satellites. Made many aspects of sequencing much easier. Lot easier to sequence and possible to investigate micro satellite DNA

5. AFLP, Microarrays, Next generation seq. - Methods to access info across genome have been developed, and this is the future – challenge is to work with all those data (bioinformatics). Whole genomes can now be sequenced and compared very easily to put things into context. A lot easier to do so, whole genome allows everything be put into context

Intro to Population Genetics

Genetic variation within and among pops -> Basis of evolutionary change

Asex. Pop

- Genetic change determined by mutations
- Reflected in lineages that may survive or go to extinction (if envi changes)
- Mutation lineage continues in straight line (if envi stable) but may go extinct if envi changes

Sex Pop

- Diversity spread out among individuals in pop according to rules of Mendelian segregation (independent assortment and crossovers)
- Mixes up genes - law of segregation
- Spreading of genetic types -> Independent assortment

Mendelian Inheritance

Mendel's laws of inheritance

Law	Definition
Law of segregation	During gamete formation, the alleles for each gene segregate from each other so that each gamete carries only one allele for each gene.
Law of independent assortment	Genes for different traits can segregate independently during the formation of gametes.
Law of dominance	Some alleles are dominant while others are recessive; an organism with at least one dominant allele will display the effect of the dominant allele.

Terminology:

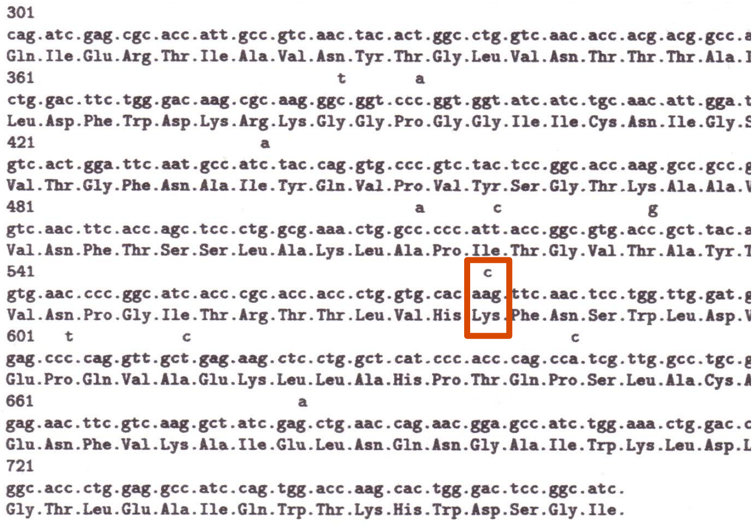
1. Locus - Position within genome (like address), can be a gene or specific location, defines location within a genome

2. Allele - DNA at a locus, can be many alleles for 1 locus, creating variation within pop. In diploid orgs, alleles at 1 locus may be same (homozygous) or diff (heterozygous)

3. Sexual diploid org has 2 alleles at each locus, 1 from mother and 1 from father

DNA seq. comparisons revealed great deal of variation among individuals

What evol forces could've led to so much divergence among individuals within species ("great obsession")



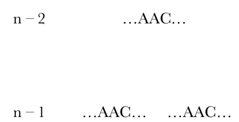
Example - ADH gene from Fruit flies

- Individual seq. from diff flies
- Reveals great diversity
- Mostly synonymous mutations occurred to produce variations (no AA change)
- Only 1 non-synonymous mutation occurred at 578 led to diff AA (lysine -> threonine)
- Change was detected when variation was detected at enzyme level (slow vs. fast form allele - slow doesn't migrate as far on gel)

<u>How Alleles Differ from Each Other - 3 Ways they can Differ:</u>

1. By ***origin*** - Alleles differ by origin are from same locus but located on diff chromosomes

2. By ***state*** - Alleles are identical by state if have same genotype - Context important, all slow alleles at ADH locus when sequenced showed diff states



3. By ***descent*** - Usual concern is with alleles that are *recently* diff by decent

Due to mutation, alleles which are identical by descent may be diff by state

Example - N pop differs by state (AAG*) but identical by descent

<u>Alleles in Pop: Accuracy of Estimating Freq.</u>

Accuracy in estimations controlled by sample size. Larger sample size gives more representative allele freq. for entire pop. Confidence limits more defined (smaller range) when large sample size

p - Frequency of allele

p = 5 % of pop (n= 20)
95% Confidence limits are 0% ~ 15%

p = 5% of pop (n = 100)
95% Confidence limits are 1% ~ 9 %

Calculating Allele Freq - Hardy Weinberg Equilibrium
For now assume 2 alleles in a pop of sexual diploid orgs: A1 and A2

2 alleles at a locus in a diploid org genotype could be:

	Homozygote	Heterozygote	Homozygote
Genotypes	A_1A_1	A_1A_2	A_2A_2
Frequencies	x_{11}	x_{12}	x_{22}
Relative freq.	0.6	0.3	0.1

Given genotype freq. can calculate allele freq. as follows

Frequency of A1 = p
Frequency of A2 = q

p = x11 + .5(x12) = 0.6 + .5(0.3) = 0.75
q = x22 + .5(x12) or q = (1-p) = 0.25
p+q = 1

Knowing freq. of genotypes -> Determine freq. of alleles by plugging in numbers

p = 0.75
q = 0.25

2 ways of thinking of Allele Freq p (A1):

1. Relative freq. of A1 in pop among all A alleles

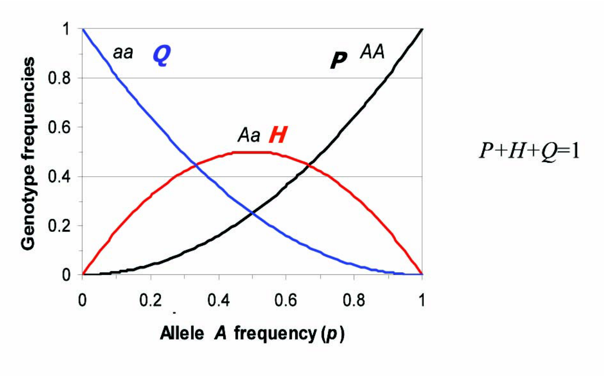
2. Probability that an allele picked at random from pop is an A1 allele - broken down into series of paired actions - Picking genotype at random and then picking allele at random from chosen genotype

$$p = (x_{11} \times 1) + (x_{12} \times 1/2) + (x_{22} \times 0)$$

As we are looking for A1, 100% chance this will be found if A1A1 homozygote, 50% chance in A1A2 (heterozygote) and 0% chance in A2A2 homozygote

Hardy-Weinberg Law

- Describes equilibrium state of a single locus in randomly mating, infinitely large diploid pop free from other evolutionary forces (i.e. mutation, migration, genetic drift and selection)



$P+H+Q=1$

- Because of the independent assortment of gametes, and multiplicative rule for probability of combining independent events - Equation given by:

$$p^2 + 2pq + q^2 = 1$$

Genotype freq. can be calculated via allele frequency by using Hardy-Weinberg equation

genotype	A_1A_1		A_1A_2		A_2A_2
HW freq	p^2	+	$2pq$	+	$q^2 = 1$

$p = 0.90$
$q = 0.10\ (= 1 - p)$

genotype	A_1A_1		A_1A_2		A_2A_2
HW freq	p^2	+	$2pq$	+	$q^2 = 1$
	0.81		0.18		0.01

Y-Axis - Genotype freq.
X-Axis - Allele freq.

P = Freq. for AA
H = Freq. for Aa (heterozygous)
Q = Freq. for aa

Low A1 allele freq. (rare) - Low aa genotype freq.
High A1 allele freq. - High AA genotype freq.
Middle A1 allele freq - High Aa genotype freq.

Important Assumptions

- When forming a zygote, probability of choosing male gamete that is A1 is same as probability of choosing a female gamete that is A1 = p

- True when genotype freq. are same for males and females, and individuals have equal probability in mating (aka - all individuals are hermaphrodites)
- Mating behaviour can affect genotype freq. (not allele freq.)

- HW equilibrium is reached after 1 generation of random mating among hermaphrodites
- Reached after up to 2 generations for dioecious species when allele freq. differ for two sexes

Important Implications:

- Mating behaviour can affect genotype frequencies, but not allele frequencies. Once equilibrium is reached, genotype freq. will also remain same

- To calculate genotype freq. need to know allele freq.

If assumptions aren't true, predicted and observed frequencies may differ (e.g selection occurring, pop not infinitely large)

Useful Observation - Rare Allele

When allele is rare (q - A2) -> Most likely found in a heterozygote

Proportion of heterozygotes to homozygotes (q^2)

2pq / q^2 = 2p/q = 2/q

If q small then p close to 1

q = 0.01, A2 allele 200x more likely to be in heterozygote state

- Even if allele stays around it will be a rare allele -> Recessive trait
- Must be homozygous to be expressed
- Can be carried in pop among heterozygotes - Not expressed unless homozygous recessive

More Than 2 Alleles

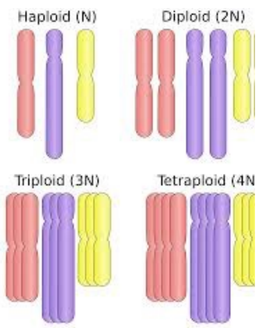
For loci with multiple alleles freq. of A_iA_i homozygote, allele is squared = p_i^2
Freq. of A_iA_j heterozygote is $2p_ip_j$

Example - 3 Alleles (a, b and c)
- Determined by binomial expansion => Very complicated

$(p + q + r)^2 = p^2 + q^2 + r^2 + 2pq + 2pr + 2qr$

Instead, can use measures of homozygosity and heterozygosity:

Total freq. of Homozygotes (homozygosity) $G = \sum p_i^2$



Sum of allele freq. squared (No matter how may diff alleles there are)

Total freq. of Heterozygotes (heterozygosity) H = 1-G = 1- $\sum p_i^2$

Total freq. of Homozygotes - 1

Worked Example

$H = 1 - \sum p_i^2$

A1	A2	A3	A4	A5
0.30	0.20	0.25	0.15	0.10

$H = 1 - (p_1^2 + p_2^2 + p_3^2 + p_4^2 + p_5^2)$

$H = 1 - (0.09 + 0.04 + 0.0625 + 0.0225 + 0.01)$

$H = 1 - (0.225) = 0.775$

What About Polyploids ?

Polyploid - Cells or nuclei containing more than 2 homologous sets of chromosomes

Predict those frequencies as well, still using binomial expansion

Example - Triploid Species (3 sets of chromosomes)

For 2 alleles: $(p + q)^3$

For 3 alleles: $(p + q + r)^3$

Example - Tetraploid Species

For 2 alleles: (p + q)^4

For 3 alleles: (p + q + r)^4

Practical Uses of HW

Wahlund Effect

- What is believed to be 1 pop is in fact 2 distinct pops
- Affects allele frequency calculations

Example:

- 2 pop (n = 80)
- 2 Alleles: Red and Green with equal frequency in overall single pop (p = q = 0.5)
- If this had been 1 pop, num of heterozygous individuals should be 40

2 pq x N = 2 x 0.5 x 0.5 x 80 = 40

- However only 2 heterozygotes (H = 0.025)
- HW saying 50% however reality is only 1/40
- Assumed 1 big pop but is in fact 2 very diff pops

<u>In Reality - Whalund Effect</u>

- Effect occurred in Scandinavian lynx pop
- Unknown division of pops between Norway and Sweden and that distinct sub-pops also existed within these
- Predictions of frequencies did not match observations
- Heterozygosity calculated over total pop - rather than considering substructure (geo division)

Summary:

1. High levels of variation in natural pops revealed by DNA sequencing

2. Pop genetics concerned with diffs among alleles: Differences by origin, by state and by descent

3. Estimate measures of pop genetic structure based on allele freq. and larger sample sizes give us better estimates

4. Genotype freq. can be calculated from allele frequencies according to Hardy-Weinberg rule:

Genotype:	A1A1	A1A2	A2A2
HW freq:	p2	2pq	q2

Assumes random mating in large diploid pop free from evolutionary forces that affect allele frequency, such as mutation, migration, genetic drift or selection.

<u>Question:</u>

Population Genetics lecture exercise: Calculate allele frequencies from these genotype frequency data.

Genotype	Number	Frequency
SS	141	0.4096 (X_{SS})
SF	111	0.3507 (X_{SF})
FF	28	0.0751 (X_{FF})
SI	32	0.1101 (X_{SI})
FI	15	0.0471 (X_{FI})

II	5	0.0074 (X_{II})
Total	332	1.0000

X = Frequency

Method 1 - No HW

Work: Best way making no assumptions and simply calculate allele frequencies from all of the genotype data provided. For example, for 'S' allele:

p_S = (X_{SS} x 1) + (X_{SF} x 0.5) + (X_{FF} x 0) + (X_{SI} x 0.5) + (X_{FI} x 0) + (X_{II} x 0) = 0.4096 + 0.1754 + 0.0551 = 0.64

Method 2 - Use HW

However, you could also assume Hardy-Weinberg Equilibrium and calculate pS as the square route of XSS = 0.64. So, for this example the population is in H-W equilibrium.

Sq. Root of 0.4096 = 0.64

Genetic Drift

Evolution

Hardy-Weinberg applies in an ideal population where all assumptions are true

Genetic Drift

- Natural Pop sizes are finite
- In finite pops there will be random changes in allele frequencies due esp to chance events, like variation in num of offspring between individuals, differential offspring survival, and offspring mating success
- This is Genetic drift
- Diversity at gene level is driving force for evolution
- Doesn't work to produce adaptations
- In each generation, some individuals may, just by chance, leave behind a few more descendants (and genes, of course!) than other individuals. The genes of the next generation will be the genes of the "lucky" individuals, not necessarily the healthier or "better" individuals. That, in a nutshell, is genetic drift. It happens to ALL populations — there's no avoiding the vagaries of chance.

Modelling Genetic Drift

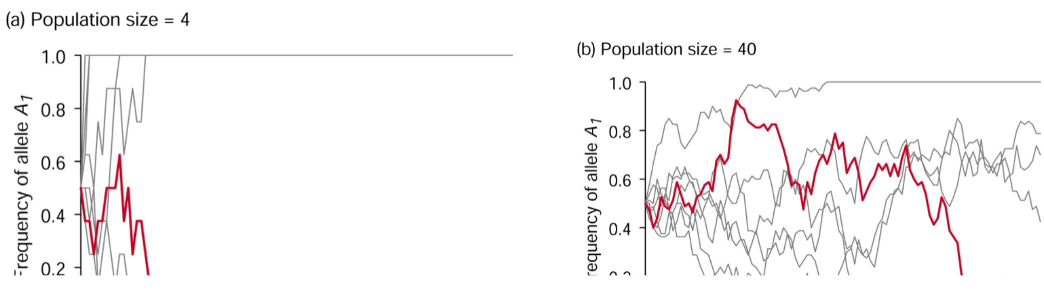
- Fate of allele is governed by chance -> Well seen in small pops
- Simulation based on Wright-Fisher model (assume neutrality - no natural selection) each new generation is obtained from previous generation by repeating 3 steps

1. Choose an allele at random from among 2N alleles in parent generation
2. Make exact copy of allele
3. Place copy in new generation

N = 20 (40 alleles - num of alleles in parent generation)
Repeat steps 4 time

Key is that each of 2N alleles have equal chance of having a copy appear in next generation
Model simplifies real life predictions

Modeled Graphs:

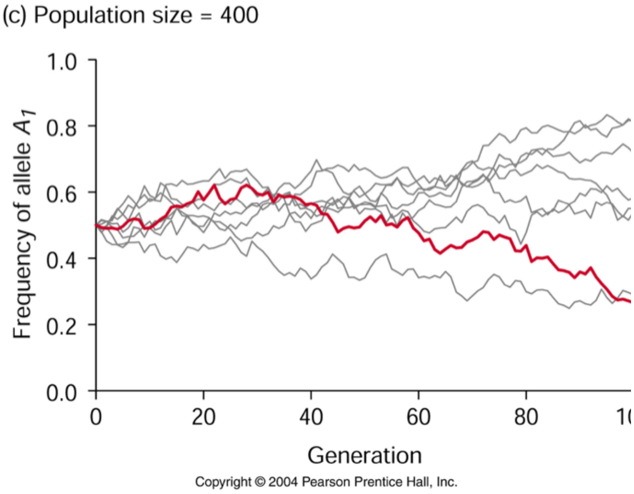


Vertical axis shows allele frequency

Horizontal axis shows generation number

<u>From Models:</u>

- Models show even with same starting conditions, very diff outcomes will be produced when seq is repeated
- Diff pops also show very diff outcomes
- In small pops, alleles go to extinction or fixation much more rapidly than in larger pops
- Process of evolution when governed by random effects gives diff outcome each time
- Smaller the pop -> More powerful genetic drift is
- Genetic drift leads to loss of diversity over time as alleles go extinct



<u>Implications of Genetic Drift:</u>

1. Random changes in allele freq. - Same start but diff outcomes - Evolution can never be repeated

2. Alleles are lost from pops, genetic drift always removes variation from pops

3. Direction of change is Neutral

	A	a
A	AA	Aa
a	Aa	aa

<u>Decay of Heterozygosity:</u>

Simple model with only 1 hermaphroditic individual with Genotype Aa and pop size remains 1

Next Generation: Probability of being heterozygote is half probability of being heterozygote than in previous generation (now half as many heterozygotes in pop)

Probability of being a heterozygote after t generations is **(1/2)^T = Decay Equation**

<u>General Case for Sexual Diploids:</u>

$$H_t = H_0 \left(1 - \frac{1}{2N_e}\right)^t \qquad H_t = H_{t-1} \left(1 - \frac{1}{2N_e}\right)$$

H0 = Original heterozygosity

Ht = Heterozygosity at time t
Ne = Effective population size (reproducing individuals)
Ht-1 = Heterozygosity in previous generation

Effective Pop Size (Ne)

- Size of ideal pop that would loose heterozygosity at same rate as real pop
- Includes those reproducing and also depends on how many reproducing individuals were in the past as both affect how much diversity is present to pass onto next generation
- Ideal pop has constant size, random mating, discreet generations, sex ratio of 1, no migration, mutation or selection

Another way to look at loss of H in diploid, sexual species

Chance that 2 identical alleles unite to form a zygote is:

1/2 Ne

When they do -> Heterozygosity is lost

Chance they don't unite is:

1 - 1/2Ne

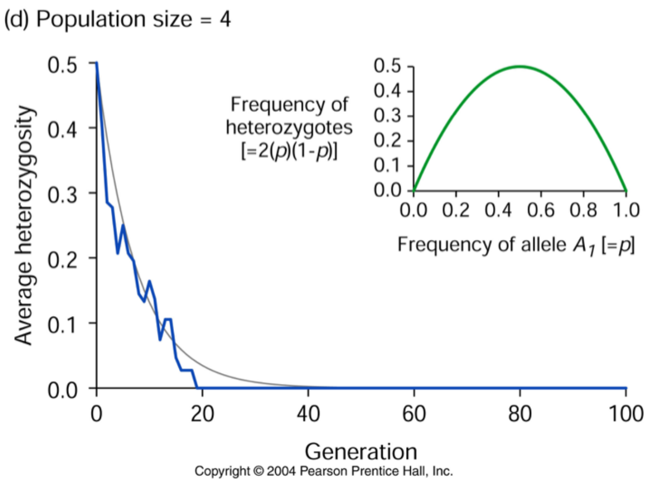
So… Heterozygosity in next generation will be:

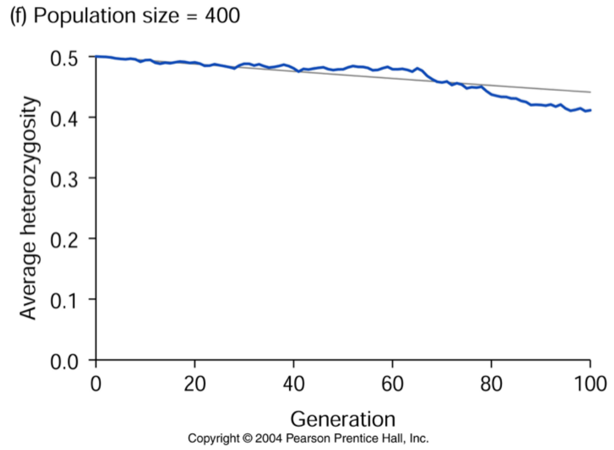
$$H_{t+1} = (1 - \frac{1}{2N_e})H_t$$

Heterozygosity in next generation = Equals present heterozygosity multiplied by probability that 2 identical alleles don't unite to form zygote (ie. probability of forming a heterozygote)

Heterozygosity across a whole pop:

- Decreases over time
- Very rapidly in small populations
- Slower rate in large pops





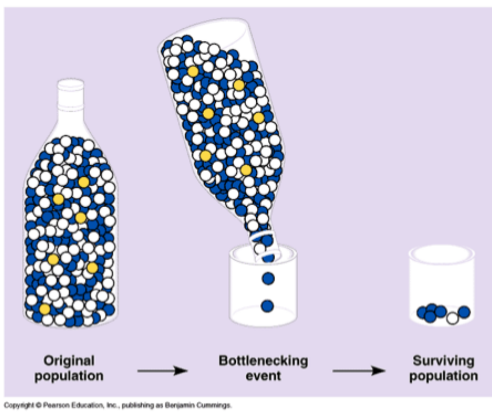
- Very slowly in very large populations

<u>Example - Empirical Study on *Drosophila melanogaster*</u>

- 107 Drosophila pops
- All founders were heterozygotes for eye color gene Brown (genotype bw*/bw)
- No dominance of either allele
- Initial freq. of bw* = 0.5
- Followed pops for 19 generation and kept pop size at 16
- Effective pop size Ne = 9
- Overtime num of extinctions and fixation of bw* allele increased
- Prediction using effective pop size matched actual observation of heterozygosity decay predictions

<u>Population Bottleneck</u>

- When pop is suddenly reduced in size
- 2 Consequences
    1. Stochastic (very random) sampling of alleles
    2. Loss of heterozygosity over time due to small pop size



<u>Homozygosity:</u>
G - *Probability that 2 alleles different in origin are identical in state (homozygosity chromosomes however they are identical*

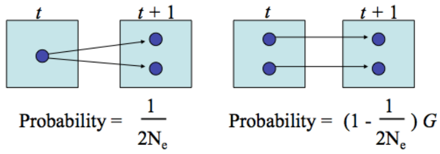
Neutral Alleles - *All alleles assumed to have equivalent fitness with respect to*

When no variation in alleles
G = 1

When all alleles are different
G = 0

<u>2 Ways alleles could be identical by state:</u>

1. Sharing a common ancestor
2. Not sharing a common ancestor, but still having identical states.



G' - Represents G in next generation

G is equal to sum of G due to descent and non descent

$$G' = \frac{1}{2N_e} + \left(1 - \frac{1}{2N_e}\right) G$$

1. When Ne is large this probability changes very slowly over time
2. Heterozygosity is lost over time scale of 2Ne generations

Drift occurs on timescale of 2Ne generations, but hardy Weinberg equilibrium can be reached after 2 generations of random mating

Thus Hardy Weinberg equilibrium only be greatly affected by drift when Ne very small (HW is valid inspire of drift in most cases)

Mutation and Genetic Drift

If genetic drift is removing variation over time, why do natural pops retain variation = Mutation
Mutation introduces variation

u = Mutation Rate
(5 x 10^-9 for neutral substitutions)

Mutation introduces variation at rate of 2Ne.u (num of gametes recombining in diploid times probability one will include mutation)

Genetic drift gets rid of variation at rate of 1/2 Ne

Equilibrium reached when evolutionary forces of drift (eliminates variation) and mutation (adds variation) balance

<u>Average rate of substitution for Neutral Mutations:</u>

As avg num of new mutations entering pop in each generation is 2Ne.u and chance of fixation of new mutation is 1/2 Ne

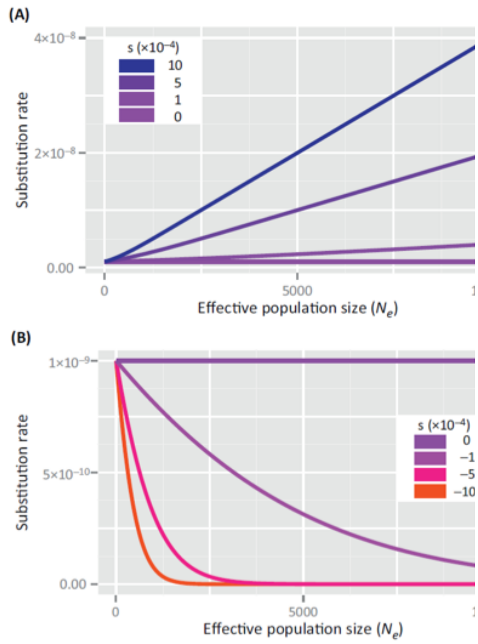
Average rate of substitution for Neutral mutations is:

$$2NeU \times 1/2Ne = U$$

Rate of substitution (1 AA changes for another AA) depends only on mutation rate and not pop size - Why?
Because both drift and mutation rate depends on pop size thus factor cancelled out

HOWEVER - Changes when selection occurs (non-neutral conditions)

<u>Example - How positive selection (A) and Negative selection (B) cause Ne to affect substitution rate</u>



Evolutionary effect much stronger when pop is large:

- When pop is small, drift is dominant factor, selection is insignificant and end result is random
- When pop is large, selection is dominant factor, drift is insignificant, and end result is directed

At equilibrium between mutation and drift, probability that 2 alleles differ by origin and also differ by state is:

$$H = 4N_e u / (1 + 4N_e u)$$

Assume that each new mutation is a new allele - Infinite allele model
* 4Ne.u often denoted as Theta

$$4NeU = \theta \text{ (Theta)}$$

Therefore:

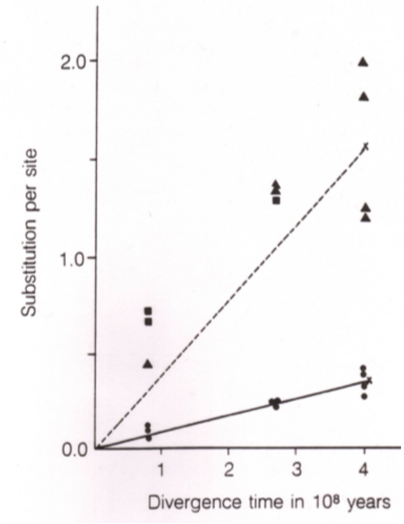
$$H = \theta / (1 + \theta)$$

If θ very small (u constant, so Ne very small), drift dominates and variation is eliminated

If θ is very large (Ne very large), mutation dominates and all alleles become unique

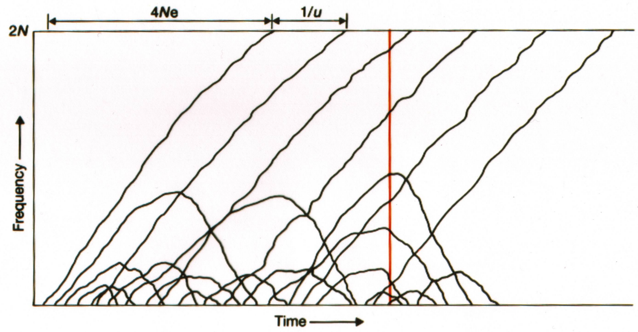
H = Heterozygosity indicates variation

Over time new mutations arise and either go to extinction or fixation over time, there will be lots of variation in natural pops that reflect the transient representation of new alleles



Neutral Theory of Evolution - Most DNA variation is neutral and this is basis for evol

- A pop free from selection accumulates many polymorphic neutral alleles by drift
- Following change in envi, some of neutral alleles no longer be neutral, but will be deleterious



- Purifying selection acts against deleterious mutations to remove them from population (selection)
- After alleles are removed, pop becomes more adapted to its new circumstance

Neutral Theory - Should be large variation in natural pops and that changes should accumulate gradually over time (provided mutation is random, neutral and selection acts to purge deleterious alleles).

Sequence data from ADH gene supports natural pops should have high levels of variation

Example - Gradual change in AA composition over time

- Data from AA composition of various proteins in evol. lineages demonstrates gradual change over geological time
- Rates of change at diff loci is diff because there are diff levels of purifying selection
- If all variation is being acted upon by natural selection, there wouldn't be gradual change across lineages
- Each selective pressure would be very diff and this would drive pops into very different directions, not produce a gradual change
- DNA seq. allowed assessment of change over time more accurate, and allowed comparison of synonymous and non-synonymous rates of change

- Solid - Rate of non-synonymous change much slower, due to selection acting (AA replacing)
- Dashed - Rate of synonymous change (silent) is higher (neutral alleles)

Observed rate of change did seem very constant = Molecular Clock
Given varying envis, natural selection is expected to create more erratic patterns of substitutions

Furthermore, observed avg rate of change by AA substitution in genes was measured to be about 10^{-9}, very close to estimated neutral mutation rate at nucleotide level (and prediction that substitution rate should be determined only by mutation rate).

However, in derivation of substation rate K = U given in units of generation, so substitution rate should be constant per generation rather than per year

Thus animals with shorter generation times should evolve more quickly - “Generation Time Effect” another prediction in Neutral Theory

Observed in non-coding DNA (not in proteins)

Something slowed down rate of evolution in proteins and led to theory that most amino acid substations are not neutral and are slightly deleterious

<u>Summary</u>

A. Genetic Drift: In finite pops will be random changes in allele frequencies due to chance events, such as variation in the number of offspring between individuals.

B. Important implications: **Evolution is unpredictable; genetic drift removes variation from population; the direction of change is neutra**l

C. Heterozygosity is lost in finite pops over time according to following formula:

$$H_t = H_{t-1} (1-(1/(2N_e)))$$

(Ne in this formula is effective population size - the size of ideal pop that would show same rate of decay in heterozygosity as observed pop)

4) At equilibrium probability that 2 alleles differ by origin and by state is:

$$H = 4N_e u \ / \ (1 + 4N_e u)$$

5) Mutation introduces variation at a rate of $2N_e.u$, where u is mutation rate to neutral alleles, and genetic drift gets rid of variation at a rate of $1/2N_e$, so ***the average rate of substitution is $2N_e u$ x $1/2N_e = u$***

<u>Effective pop Size</u>

- Most pops are large however do not act large
- Rate of genetic drift isn't really promotional to census pop size
- Its proportion al more abstract effective pop size
- An ideal pop of sexually reproducing individuals

- Following characteristics:
  - Equal num of males and females all who able to reproduce
  - All individuals have equal likely chance to produce offspring and num of offspring each produces varies no more than expected by chance
  - Mating random
  - Num of breeding indiviauls is constant throughout generations

Anything that increases the variance among individuals in reproductive success (above sampling variance) will reduce Ne (the size of an ideal population that experiences genetic drift at the rate of the population in question)

Evolution of Invertebrate Metazoans

Geological Time Scale:

Eon	Era	Period		Epoch	Time Began (Million Years)
Phanerozoic	Cenozoic	Quaternary		Holocene	0.01
				Pleistocene	1.8
		Tertiary	Neogene	Pliocene	5.3
				Miocene	23.0
			Paleogene	Oligocene	33.9
				Eocene	55.8
				Paleocene	65.5
	Mesozoic	Cretaceous			146
		Jurassic			200
		Triassic			251
	Paleozoic	Permian			299
		Carboniferous	Pennsylvanian		318
			Mississippian		359
		Devonian			416
		Silurian			444
		Ordovician			488
		Cambrian			542
Proterozoic					2500
Archean					4000
Hadean					4560

Eon - Indefinitely long period of time, largest division of geo timescale

Era - 2 or more periods comprise an era

Period - Unit of geo time which a system of rocks formed, cross-referencing rocks and geo events from place to place

Epoch - Subdivision, longer than an age, time where geo series is formed

Metazoa -- Multicellular mitochondrial euks (with plants, fungi and some protists sometimes referred to as Crown Eukaryotes)

Invertebrates - “animals without backbones

Cambrian —> Cretaceous: Overview

Cambrian: (542 Ma) Cambrian explosion of diversity followed by mass extinction

Ordovician: (488 Ma) Spectacular radiation of marine invertebrates. Esp. animal life on sea floor or burrowing in marine sediments followed by mass extinction

Silurian: (444 Ma) Marine life rebounded. Swimming invertebrates and first terrestrial arthropods

Devonian: (416 Ma) Radiation of corals, cephalopod molluscs and of fishes.Terrestrial invertebrates included centipedes, spiders, pseudoscorpions, mites and insects. Amphibians begin colonising land as well as complexities in seas

Carboniferous: (318 Ma) Diversification of terrestrial orgs including snails, scorpions, centipedes and insects. Winged insects evolved. First reptiles evolved

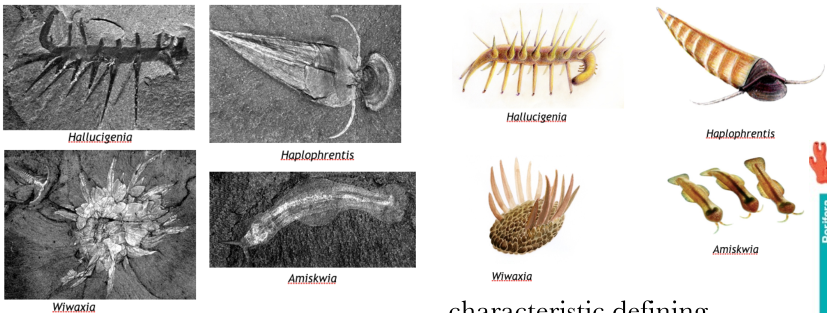
Permian: (299 Ma) Most modern groups of insects present. Reptiles diversify

Triassic: (251 Ma) Invertebrate lineages diversify. Many burrowers. Further reptilian radiation

Jurassic: (200 Ma) Radiation of fishes, reptiles (dinosaurs) and first mammals

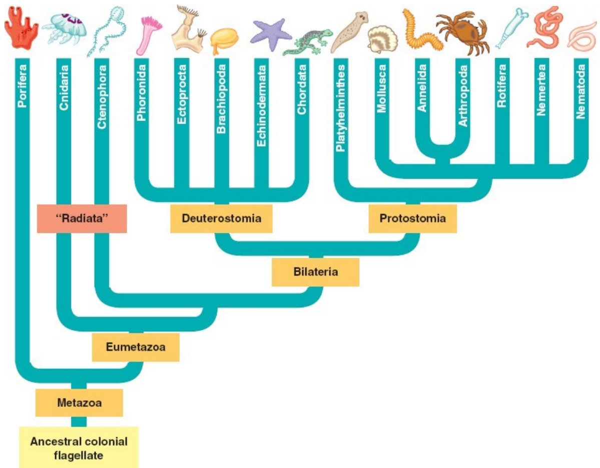
Cretaceous: (146 Ma) Extensive diversification of marine invertebrates. Flowering plants evolved, and with them coevolution of invertebrate pollinators.

Cambrian Fossil Record - ***Burgess Shale*** consisting of well-preserved collection of fossils showing, sponges, lobopods, arthropods, priapulids, polychaete annelids, chordates and more (Outer space looking orgs)



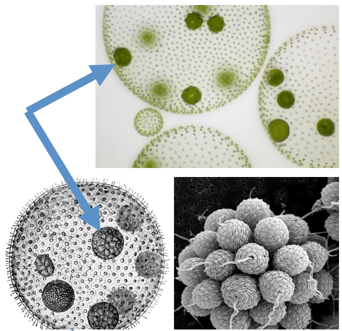
Radiation of Metazoans

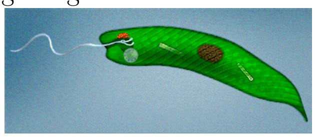
- Identifying key characteristic defining lineages (turning points within lineages which define whole new groups and structure pattern of evolution)
- Shared derived characters - Homoplasy within that group = Synapomorphies
- Phylogenies - Identify synapomorphies to define groupings



Earliest Metazoan Ancestor

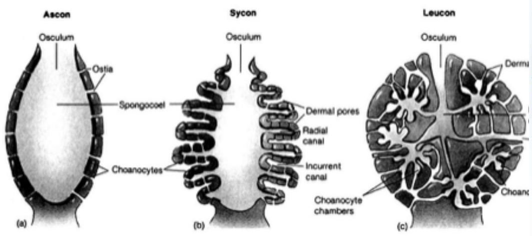
- Ancestral colonial flagellated Protozoan
- Most recent common ancestor of Metazoans
- Individual or in colonies like Algal volvox (circles)
- Main colonies are main circle and buds off producing daughter colonies

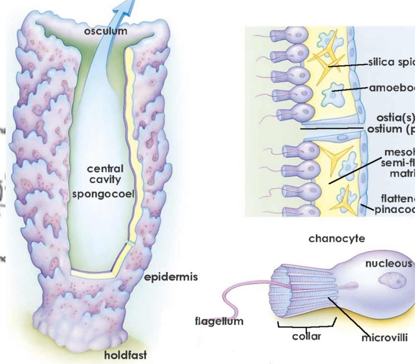




Porifera

- Most ancestral metazoan
- Colonial orgs with diff cell types (i.e. pinacocytes, choanocytes, amoebocytes)
- Internal cells are flagellated
- 3 main forms:
  A. Ascon - Bucket shaped
  B. Sycon - Convoluted
  C. Leucon - Bath sponge



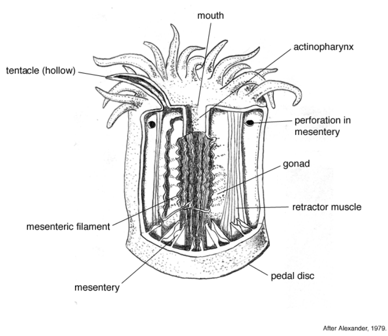


Radiation between Radiate and Bilateria

First major synapomorphy

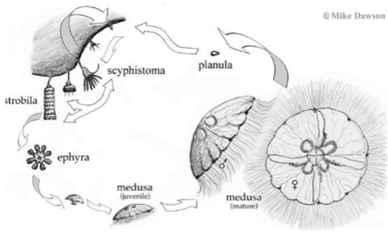
Radiata

- Show radial symmetry in adult and larval forms
- At which ever plane, orgs will divide up in same way
- Consists of 2 orders: Cnidarians and Ctenophores



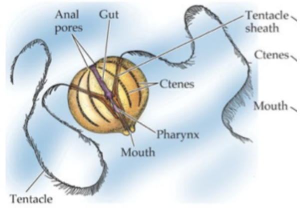
Cnidarians:

- Polyploid stage (attached tentacles), Medusoid stage, planula larvae
    - Anthozoans (Corals/Anemones) - Only have polyploid life history stage, and oldest
    - Scyphozoa (Jellyfish) and Cubozoa (sea wasps) - Polyploid and Medusoid stage (evolved later)
    - Hydrozoans - Loss of ancestral polyploid characteristic
- Nematocysts - Stinging cells, ejected into anything disturbing, toxic poison on long tentacles



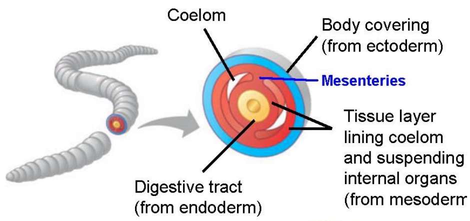
Ctenophore:

- Common form with tentacles and ctenes (comb-plate - locomotor organ)
- Jelly ball with ciliates



Synapomorphy Distinguishing Radiata from Bilateria:

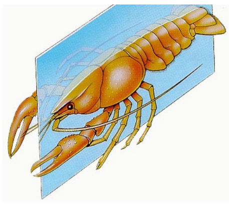
- Radiata actually have primitive form of symmetry (briradial symmetry)

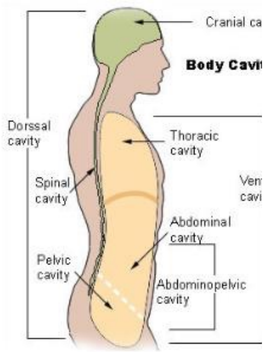


Main Synapomorphy:

- Radiata lack coelom

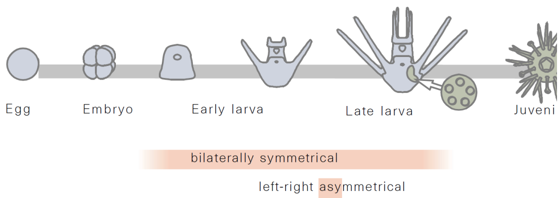
- Bilateria have coelom

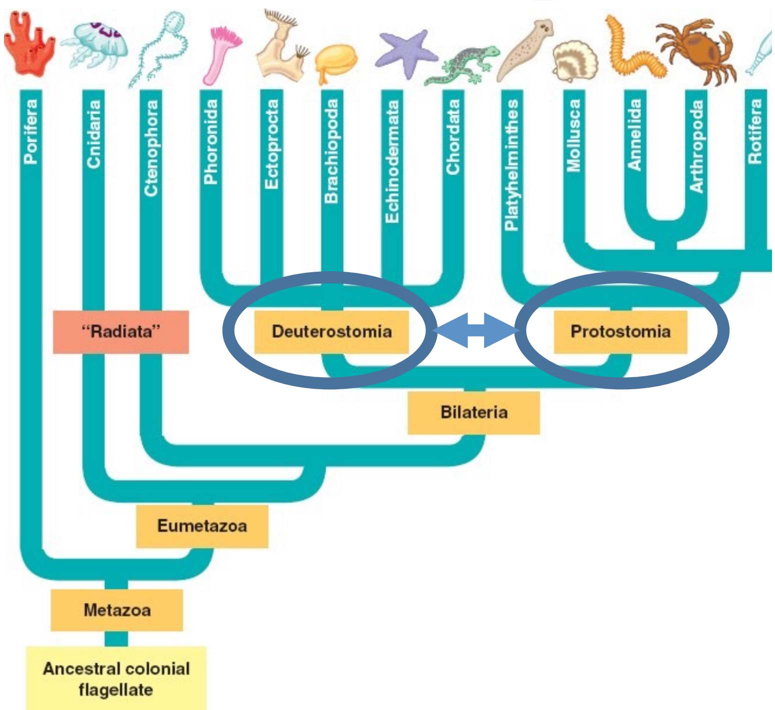




Bilateria:

- Very large group
- Division along symmetrical plane (1 plane)
- Many have evident bilateral symmetry in the adult form (i.e. lobster)
- Some not bilateral as adults, but bilateral in larval stages (i.e. sea urchins)
- Consists symmetry at some point in life history stages





Synapomorphy distinguishing Deuterostomes from Protostomes

- Coelom development differs

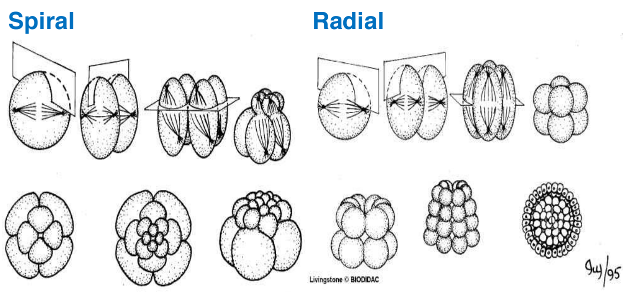
- Key diffs in early stages of development

Deuterostomes:

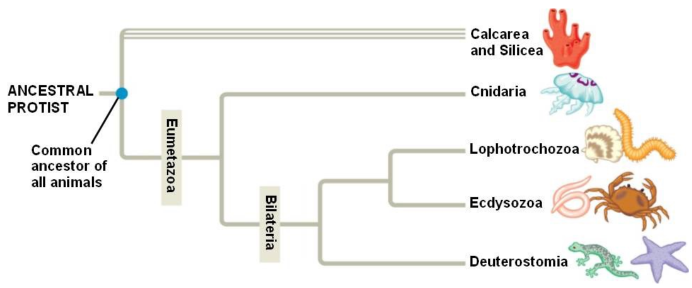
- Radial and indeterminate cell division (nice organised box of cells)
- Enterocoelous - Folds of archenteron forming coelom
- Coelom forms on other end of blastopore
- Anus develops from blastopore

Protostomes:

- Spiral and determinate cell division in 8 cell stage
- Schizocoelous - Solid masses of mesoderm split to form coelom
- Near blastopore, opening of ball of cells forms into coelom
- Mouth develops from blastopore



Further Division of Deuterostomes - Subdivisions:



1. Sensu lato - Deuterostome-like (phoronida, ectoprocta, brachopoda)

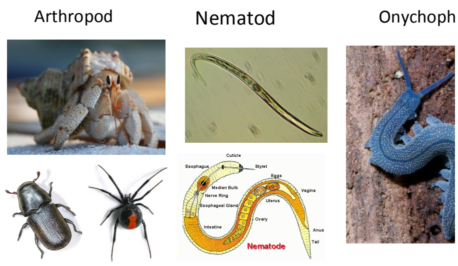
2. Sensu stricto - Proper deuterostomes (echinodermata, chordata)

Division of Protostomes:

1. Lophotrochozoa (Annelids, molluscs etc.)
2. Ecdysozoa (Arthropods, nematodes etc.)

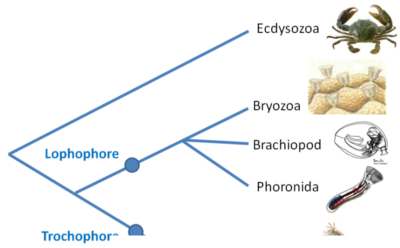
Ecdysozoa - Group of Protostomes

- Very large group and very diverse
- Arthropoda (insects, spiders, crustaceans), Nematoda, Rotifera, Onychophora, and several other groups
- All have cuticle - outer layer or organic material functioning as skeleton
- Many members periodically shed cuticle in ecdysis process

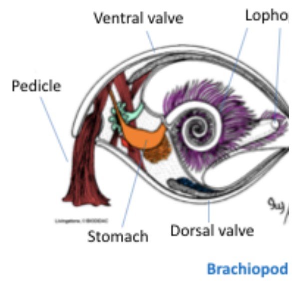


Lophotrochozoa - Group of Protostomes (+ Sensu lato deuterostomes)

2 Broad Groups

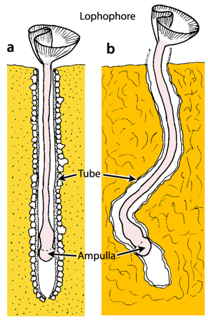


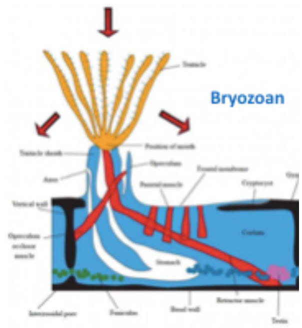
1. ***Lophophores***



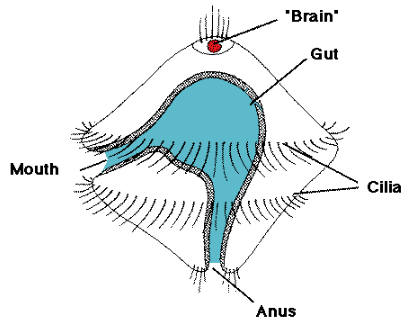
- Bryozoa, Brachiopods, Pharonida
- All share unusual feeding appendage- Lophophore
- Complex structure from 2nd of 3 division coelom forming hollow tentacles
- Mouth located within ring of hollow tentacles (covered with cilia)
- As complex structure unlikely to evolve independently - Seen as a synapomorphy
- Shared by diversity of creatures whom share ancestors
- Includes sensu lato Deuterostomes

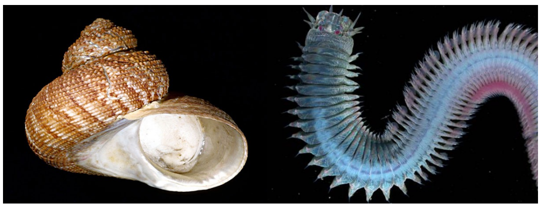
2. ***Trochophores***





- Molluscs and annelids (i.e. worms and squid) - Diverse
- All share similar larvae form - Trochophore Larvae with 2 cilia bands around centre and set of flagella at top and bottom
- Distinct structure of anus and brain





<u>Deuterostomes (proper) - Sensu stricto</u>

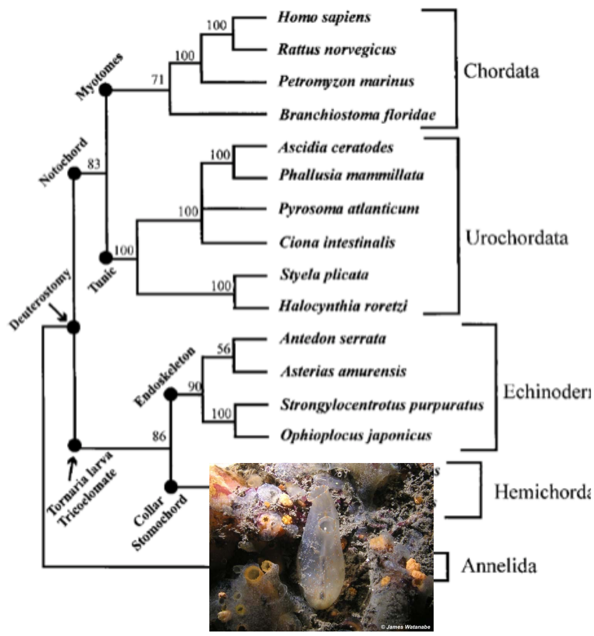
Includes Chordata (Humans)

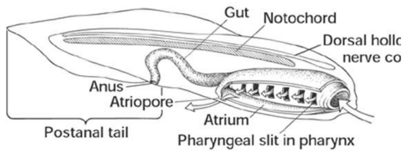
Other subdivision within lineages for grouping

Divisions by rDNA and Synapomorphies:

<u>Notochords:</u>

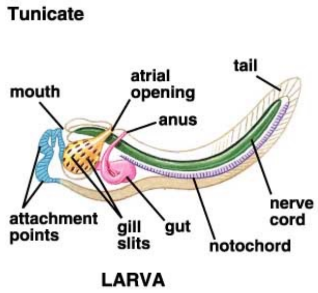
Chordata - Myotomes
Urochordata - Tunic

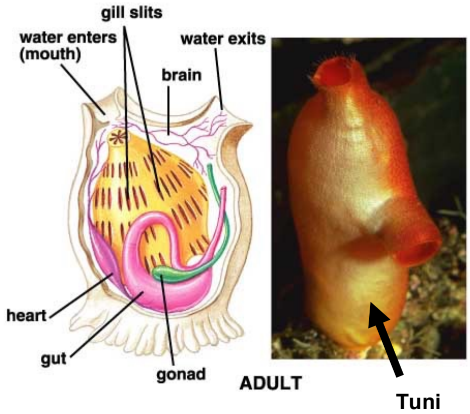


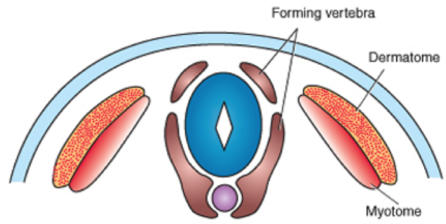


Lineage - Notochord - Cartilaginous skeletal rod - embryonic)

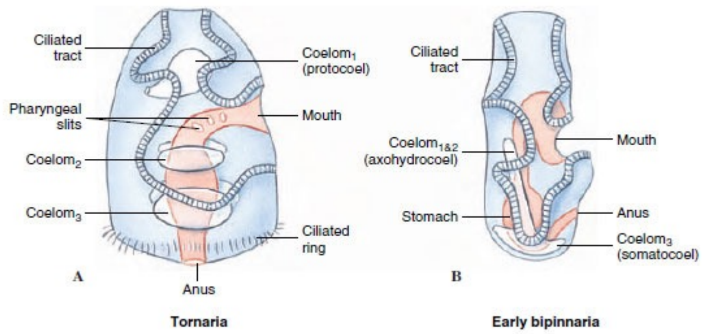
- Myotome - Dorsal part of each somite in vertebrate embryo, gives rise to skeletal musculature







- Tunic - Adult forms have outside encapsulating structure where rest of org exists, larval forms all have notochords

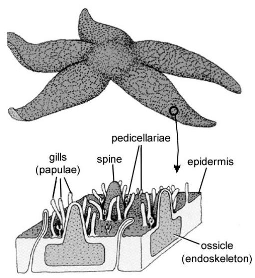


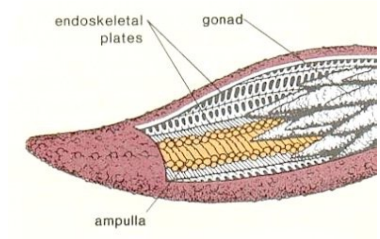
Lineage - Tornaria Larva Tricoleomate

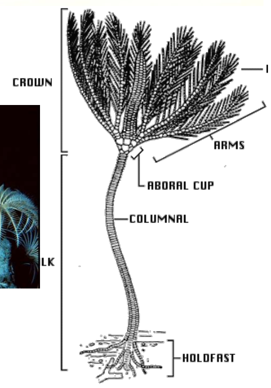
1. Endoskeleton = Echinodermata (sea stars)
2. Collar Stomochord = Hemichordate

Tornaria Larva - Tri-coelomate orgs

- Unifying feature
- With distinctive gut pattern
- In Echinoderms larval form is early bipinnaria where coeloms have merged
- Long ciliated tract
- Connection between mouth and anus
- Multiple (3) coeloms







Echinoderms (phylum):

Endoskeleton - Ancestral feature, set of interconnecting plates or separate ossicles, covered by epidermis on outside (Asteroidae in image)

Ossicle - Small calcified material forming part of skeleton of an invertebrate animal

5 Main Classes

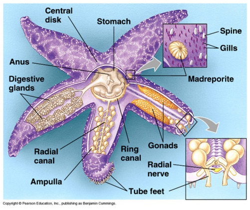
1. Crinoidae (sea lilies/feather stars) - Earliest radiation of group and have endoskeleton comprising calcareous hard plates (common in later radiation) and tube feet (like Asteroidae). Divided into stalk and crown with consistent relationship between mouth and anus

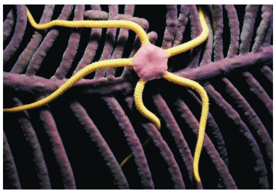
2. Holothuriadae (sea cucumbers) - Have endoskeleton, but comprised of microscopic ossicles embedded in connective tissue, quite squishy, endoskeleton within epidermis

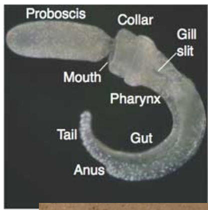
3. Echinoidae (sea urchins and sand dollars) - Radially symmetrical as adults but bilateral as larvae, more complicated body forms

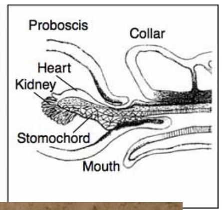
4. Ophiuroidae (brittle or basket stars) - Large group (1600 sp.), comprised of brittle stars with tubed feet and internal plate endoskeletons

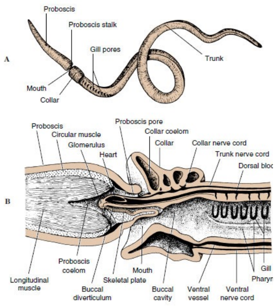
5. Asteroidae (sea stars) - Often 5 legs but can have more, use tube feet for locomotion and to prise apart bivalve prey

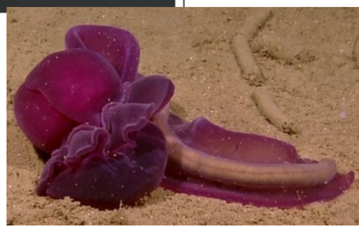








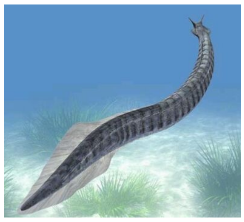




Hemichordata

- Acorn Worms
- Stomochord (flexible hollow tube) surrounded by a collar
- Deutrostomes with Tornaria larvae

Metazoan Evolution:



- Using rRNA - highly conserved and evolves slowly, can compare org which are very dissimilar in morphology (deep-lineage analysis)
- Leads to discovery of diff groupings
- Can build phylogenies on morphological basis with shared synapomorphies defining each group
- However other many characteristics to define groupings - Could be more critical defining evolution pattern
- DNA analysis allows homoplasy (look similar but arisen differently) to be distinguished from homology

- New Synthesis - Uses Morphological + Molecular Data
- Still represents characters (simple = 4 bases in DNA seq.)
- Molecular characters simplistic - Evolution according to molecular clock

Pikaia gracilens

- Chordate form Burgess shale - Possibly our earliest ancestor
- Not vertebrate, but shows chordate characteristics including signs of notochord

Summary:

1. Metazoan radiation starts with Cambrian species radiation, many current groups represented at time

2. Series of division points define radiation. 1. Division between Radiata and Bilateria. Radiata (Cnidarians and Ctenophores) radial symmetry throughout life history and lack a coelom. Bilateria have bilateral symmetry at some life history stage with all possessing a coelom
3. Division between Deuterstoma (subdivided into sensu stricto and sensu lato groups), and Protomstoma. Coelom forms differently between groups and cell cleavage is spiral (Protostomes) and radial (Deuterostomes)

4. Division between Ecdysozoa (cuticle) and Lophotrochozoa, which further divided according to their larval stage and feeding appendage

5. Morphological or life history traits are used to define synapomorphies to determine these lineages, but molecular and morphological data lead to a reinterpretation of which characters are most important in defining lineages

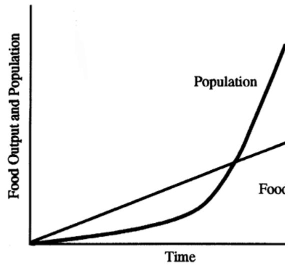
Natural Selection

Natural Selection:

Darwin:

- Differential survival of phenotypes vary in fitness
- Fitness is measure of relevant gene's representation in future generations.
- Purifying selection underlies neutral selection - Unfavourable traits removed from pops and favourable traits are positively selected

Malthus



- Reasoned while pops grow geometrically, resources to sustain them grow arithmetically
- However unaware tech would advance food resource production and pop growth doesn't occur exponentially exactly

Darwin drew on Malthus's Idea

- In natural envi, resources are limiting and pops grow exponentially.
- Comp for limited resources, keeping pop in check
- Some individuals do better than others -> confer this advantage to their offspring -> lineage survives
- = Idea of natural selection

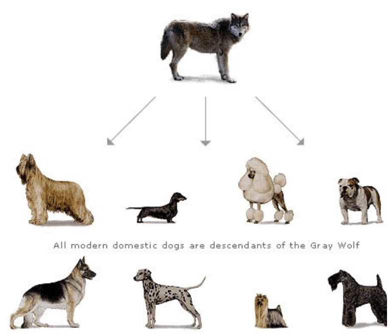
Basic Idea of Natural Selection

- Traits can become differentially represented in subsequent generations due to diff envi pressures
- Shown through Artificial Selection - Selective breeding of domestic animals or crops
- As demonstrated artificially, must also occur in nature

Example - Wild Mustard can be selectively bred to lead diff plants (i.e. broccoli, cabbage etc.)

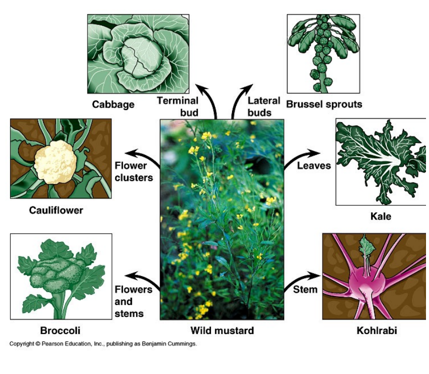
Example 2 - Grey Wolves are ancestors of modern domestic dogs, can now selectively breed a wide range of dog breeds

Falconer's Experiment:

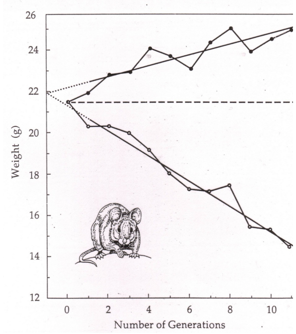


- Artificial selection for large and small mice (potential for selecting phenotype - weight)
- Weight at start was 21.5g (avg)
- Selection for heavier and lighter
- After 10 generations, weights diverged to 25g and 14g
- Only few generations are necessary for a heritable change to occur.

Natural selection works with ***available*** genetic variation in natural pops that has accumulated by mutation over time - Such variation will be going to fixation or loss due to genetic drift and rate of this transition depends on size of



Falconer's (1953) experiment on artificial selection for lar
mice and small mice, with weights at 6 weeks of age p
vided. The dashed line indicates the common weight at t
start of the experiment (generation 0).



pop. Therefore natural selection works within these constraints, but cannot simply create anything.

Fundamental Model of Natural Selection

1. Frequency of an allele after selection (p') is proportional to frequency of that allele among newborns, multiplied by their probability of survival

2. Probability of survival (w) is often called viability.

3. Example - Frequency of A1A1 adults in a pop is proportional to
   $p(A1, A1) = p^2 w_{11}$

Many Components to Fitness

- Fertility
- Developmental time
- Mating success
- Foraging ability
- Longevity

All aspects of phenotype affecting contribution of individuals genotype in next generation
-> Aspects are combined together to give viability (FITNESS)

w = Fitness (viability - probability of survival)

Fundamental Model - Based on single locus in diploid org 2 Alleles - A1 and A2

Genotype:	A_1A_1	A_1A_2	A_2A_2
Frequency of newborns:	p^2	$2pq$	q^2
Viability:	w_{11}	w_{12}	w_{22}
Frequency after selection:	$p^2 w_{11}/\bar{w}$	$2pq w_{12}/\bar{w}$	$q^2 w_{22}/\bar{w}$

$\bar{w}$ = 'constant of proportionality' *W = 1*

After selection freq. of genotypes:

Freq. of newborns x viability / constant of proportionality

After selection freq. of A1 allele is (p'):

$$P' = (p^2 w_{11} + pq w_{12}) / w$$

$$p' = \frac{p^2 w_{11} + pq w_{12}}{\bar{w}}$$

As A1 only present in half of heterozygous

$$q' = \frac{pq w_{12} + q^2 w_{22}}{\bar{w}}$$

$$w = p^2 w_{11} + 2pq w_{12} + q^2 w_{22}$$

Components add up to 1 by altering value of <u>w</u>

Allele Frequencies in Next Generation

p' = Freq. of A1 allele in next generation after selection

q' = Freq. of A2 allele in next generation after selection

Selection changes the probability of sampling the 2 alleles in the next generation

Genotype freq. remain in H-W equilibrium after selection at frequencies defined by p' and q'

Allele freq. changes under selection, however remains under H-W equilibrium but defined by new allele freq.

Equilibrium

Change in allele frequency across generations: p' - p

Change of 1 generation to next = After selection - Before selection

$$\Delta p = \frac{pq\left[p(w_{11} - w_{12}) + q(w_{12} - w_{22})\right]}{\bar{w}}$$

At equilibrium, delta p is 0. Equilibrium is given by:

$$0 = \hat{p}(w_{11} - w_{12}) + \hat{q}(w_{12} - w_{22})$$

Only fitness determines freq. of alleles in next generation. Can determine equilibrium allele frequency under selection by comparing fitnesses'. Fitness components - Viability (w)

$\hat{p}$ = Allele freq. at Equilibrium

$$\hat{p} = \frac{w_{12} - w_{22}}{2w_{12} - w_{11} - w_{22}}$$

For example
w11 = 0.9
w12 = 1
w22 = 0.8

$$\hat{p} = \frac{w_{12} - w_{22}}{2w_{12} - w_{11} - w_{22}} = \frac{1 - 0.8}{2 - 0.9 - 0.8} = 0.67$$

$\hat{p}$ = 0.67 (allele freq. of A1 at equilibrium determined by fitness components)

If selection is balanced - Advantageous for Heterozygous

<u>Simpler Way of Thinking</u>

We generally consider relative fitness (absolute fitness is hard to measure). We give one genotype a fitness of 1, and then give other 2 genotypes a fitness relative to this

Example - Fitness of A1 A1 genotype (as 1) and for A1A2 and A2A2 genotypes give relative fitness

Genotype:	A_1A_1	A_1A_2	A_2A_2
Viability:	w_{11}	w_{12}	w_{22}
Relative viability:	1	w_{12}/ w_{11}	w_{22}/ w_{11}
Relative fitness:	1	1-hs	1-s

(s = selection coefficient; h = heterozygous effect)

Selection coefficient - Selection against A2
1 - S (selection against A2)

Heterozygous Effect/Adv (H) - Heterozygote genotype has higher relative fitness than either homozygote dominant or recessive genotype. Heterozygote effect tells us relative fitness of heterozygote to the selective difference between both homozygotes (a measure of dominance)

Consider selection co-efficient (s) for each genotype - Selection against that genotype

- s and h are universal
- s value of 0.1 (10%) considered high (strong selection)

Explained:

s > 0	A2A2 less fit than A1A1 (s value of 0.1 considered strong effect)
h = 0	A1 dominant, A2 recessive (1 - 0)
h = 1	A2 dominant, A1 recessive (1 x s = s -> Same fitness as A2A2)
0 < h < 1	Co-dominance - Incomplete Dominance (0.5)
h < 0 (-ve)	Over-dominance (heterozygote favoured) - Balancing selection • 1 - (-xs) = Positive value +1 thus higher fighter than both A1A1 and A2A2
h > 1	Under-dominance (either homozygote favoured) • 1 - (xs) = Negative value, either A1A1 or A2A2 favoured

<u>Using relative fitness - Calculate change in freq. of A1 (p) due to selection</u>

$\Delta_s p = pqs\,[ph + q(1 - h)] \,/\, w$

$w = 1 - 2pqhs - q^2s$

Change of A1 freq. from 1 generation to next due to selection - determined by these equations

Means can be graphed - Model expectation

<u>Example 1 - Co-Dominance (h = 0.5) and (s = 0.1 - strong selection for p)</u>

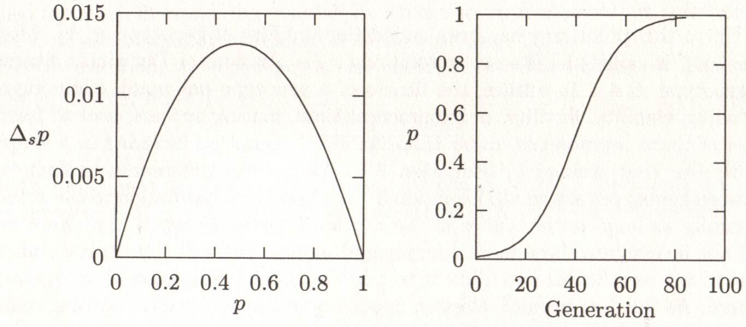


Figure 3.3: Properties of directional selection with $h = 0.5$ and $s = 0.1$. The left-hand graph shows the change in the allele frequency in a single generation. The right-hand graph shows the evolution of the allele frequency over 100 generations.

ΔsP - Shows change in allele freq. in a single generation
p - Shows evolution of allele frequency over 100 generations

Frequency of change highest at intermediate p values.

Lowest and highest values of P (A1 freq. in pop) - Slowest change in P due to selection
Fastest change when freq. of p is 50%

Over generations (right graph)
- Change of allele freq. is fastest at intermediate levels

Selection of P acts when it's at intermediate frequency level in pop

<u>Example 2 - Balancing Selection (over-dominance): h = -0.5, s = 0.1</u>

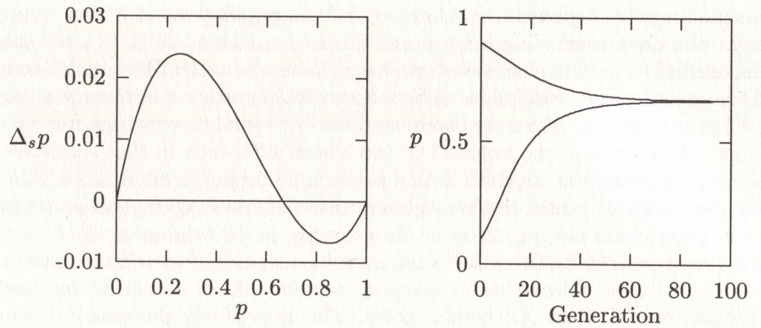


Figure 3.4: Properties of balancing selection with $h = -0.5$ and $s = 0.1$.

Heterozygous favoured

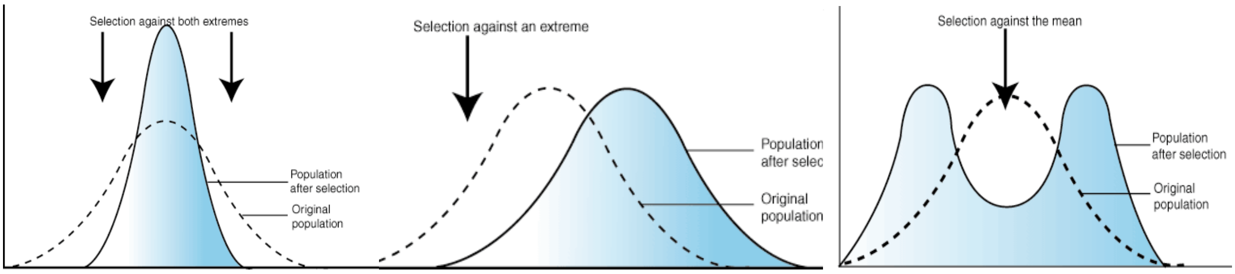
- p reaches equilibrium value

- Advancing generation time graph
- Starting from lower p value than equilibrium, over generations, p will increase
- Starting from higher p value than equilibrium, over generations, p will decrease
- Goest till reaches equilibrium freq. point = 0.67 value

Selection for a Single Gene at Level of Individual:

Balancing Directional Disruptive

Balancing Selection for a Trait - Selection for heterozygote, intermediate phenotypes, over-dominance (2pq)



Disruptive Selection for a Trait - Selection for both homozygotes, extreme phenotypes, co-dominance (p^2 and q^2)

Directional Section for a Trait - Selection for either homozygous, under-dominance (p^2 or q^2)

Selection can alter trait value distributions from original pop (dashed lines)

Selection and Drift:

1. ***Selection is a weak force when alleles are rare***

When new, favourable mutation enters pop, it's more subject to genetic drift, and may go to extinction just by chance esp. in finite pops

Strength of selection of favourable new mutation roughly s(1/2Ne) - likely to be less than 1/2Ne

Mutation freq. is half of Ne (effect of drift)

Ne - Num of genetically distinct individuals that contribute gametes to next generation

In finite pops, favourable new mutation usually lost due to genetic drift

2. ***Selection dominates over drift when allele becomes common***

Once established, selection will likely influence fate of an allele when selection coefficient for allele greater than effect of drift, this depends on Ne.

Ne = Effective pop size (genetic drift)

If Ne =1000, s needs to be greater than 0.0005
If Ne = 100, s need to be greater than 0.005

$$s > \frac{1}{2N_e}$$

If Ne = 10, s need to be greater than 0.05

So even if weak selection in sizeable pop, selection can have an effect
If pop is smaller, s (selection) must be stronger
As long as allele is established in pop

Summary:

1. Natural selection - Differential survival of phenotypes varying in fitness. Fitness - Measure of the relevant gene's representation in future generations

2. Selection only works on ***available*** variability - doesn't provide a species with whatever it needs

3. Frequency p' of an allele after selection is proportional to frequency of that allele among newborns, times their probability of survival (***viability = w***)

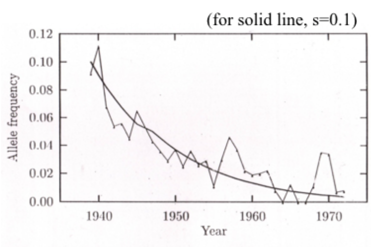
4. Directional selection is selection in favour of particular allele through homozygous genotype (with co-dominance). Balancing selection includes selection for heterozygote and frequency dependence. Disruptive selection against heterozygote

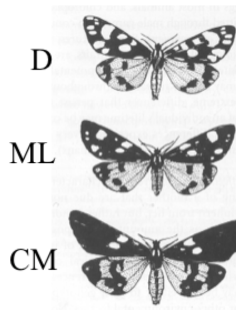
Natural Selection 2

Introduction

- Natural selection - Differential survival of phenotypes varying in fitness
- Phenotypes are determined in part by genotype
- Fitness - Measure of relevant gene's representation in future generations
- Balancing selection focuses on differential survival of individuals with heterozygous genotypes - multiple alleles maintained as overall fitness depends on allele freq. of alleles involved
- Alleles depends on their freq. in the pop

Theory of natural selection: Evidence via Domestic breeding. Selection works well in experiments, however empirical evidence in wild is hard to find





Directional Selection

Example - Medionigra Allele in Scarlet tiger moth

D: Typical form - Wildtype (dominula)

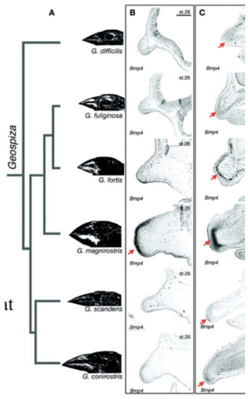
ML: Medium form (medonigra-like)

CM: Classic form (classical medionigra)

CM (Medionigara) allele declined in correlation with prediction line with selection of 0.1

<u>Due to selection of allele or temp ?</u>

In wild: D form was most common, CM and ML forms were rarer

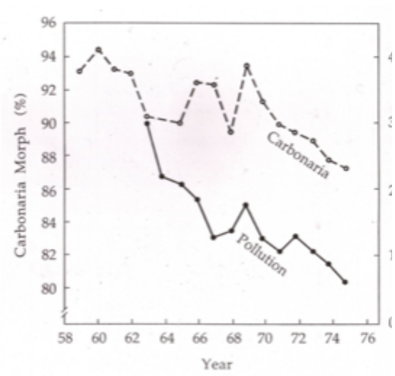


At higher temps: CM and ML more common

Thus, Could be due to temperature rather than selection

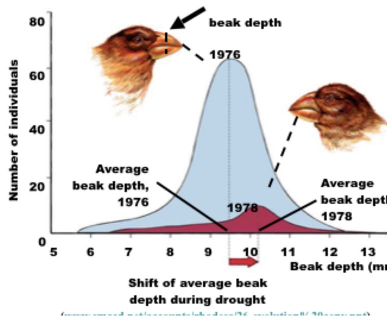
However, experiment was flawed

- Phenotypes of reared larvae were compared to wild-caught
- Temperatures were measured at the time and site of pupation whereas wild temperatures were measured in the air near the ground
- Temperatures cannot be related to one another
- Later variation was explained by drift



Example - Peppered Moth and Industrial Melanism

- Melanistic form (darker) rarer
- Common form (white)
- Melanistic form tracks pollution over time to hide from predators
- When melanistic form arises in non-polluted areas and vice versa, there is a higher risk of detection and predation and so selection is acting



Example - Galapagos Finches

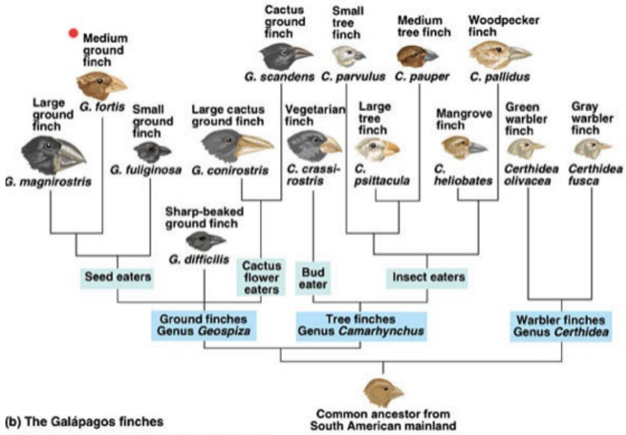
- Major drought affected beak depth in medium ground finch
- Shift in average beak depth during drought conditions
- Drought caused seeds (primary food source) become harder
- Thicker beaks selected for - More effective at obtaining harder seeds
- Selection in action over short period of time

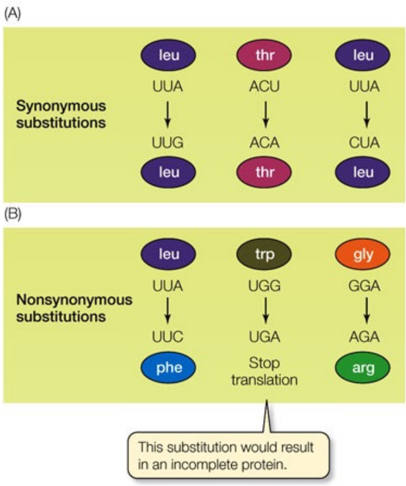
Change in Beak Thickness due to Change in Growth Factor Gene: Bmp4

- Strong expression of this locus - During larger beak formation

Further evidence for Natural Selection among Galapagos Finches

- Extensive morphological variation due to adaptation to local habitat
- Evolved in-spite of relatively lil differentiation in neutral genetic markers
- Much phenotypic variation -> Likely of strong selection occurring





Evidence of Selection at Individual Gene Level - Mutation

Consider rate of Non-Synonymous vs. Synonymous Change

Synonymous - Do not alter AA which is coded for in resulting protein

Non-Synonymous - Alters AA, alters resulting protein and may produce a stop codon

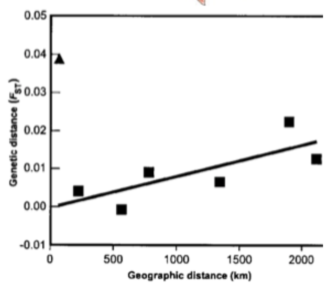
Ratio: d_n (rate of non-synonymous change) / d_s (rate of synonymous change)

$d_n / d_s < 1$ = Purifying selection - Deleterious non-synonymous changes being removed by selection

$d_n / d_s > 1$ = Positive Selection - Deleterious non-synonymous changes are selected for

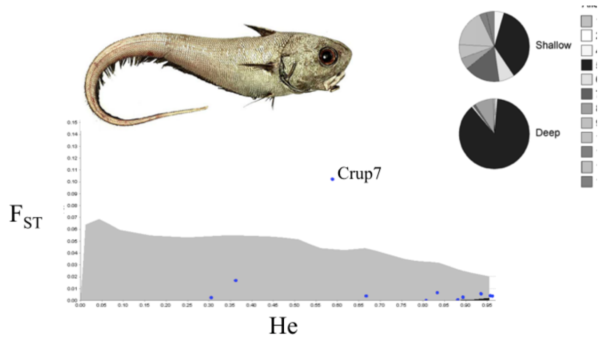
$d_n / d_s = 1$ = Neutral substitutions (or balance between positive and purifying selection)

<u>Example - Copper Rockfish</u>



- Evidence of local adaptation
- Measured how much diff exists between pops
- Genetic Distance (Fst) - Co-efficient in sub pops compared to pops, measure of differentiation between pops
- Comparing genetic distance to geographic distance
- Isolated (of copper rock pop) by geo distance - Pops genetical diffs drift more
- Due to isolation of copper rock pops has occurred due to distance
- Increasing distance decreases likelihood of dispersal and reproductive mixing
- However, triangle represents pops geo close but with high level of differentiation -> Selection is occurring

<u>Example - Round Nose Grenadier</u>



- Local selection and pop structure in deep sea fish
- Diffs within pop
- How much variation within this range may expect to see based on neutral expectations

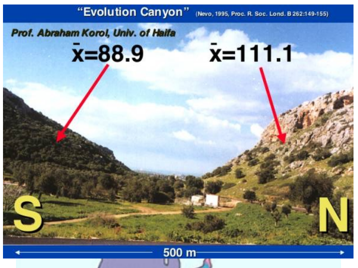
- Crup7 locus (allele 5) shows strong association with depth
- More frequent in deep water compared to shallow water
- Directional selection for this locus

- All other loci show balancing selection (in grey - below the line - more similar in individuals)

Possible to screen whole genomes, look for peaks of differentiation (F_{ST}) by comparing pops across genomes

Example - Drosophila melanogaster (more evidence of selection)

- Differential expression of HSP70 (heat shock protein) in 2 habitats with differing micro-climates geographically very close
- Evolution canyon (500m width)
- South side of valley: Cool and forested (x=88.9)
- North side of valley: Exposed, barren and hot (x=111.1)
- Very different levels of HSP70 expression
- North face pop under more stressful conditions -> Higher expression
- Small scale selective differential response to local envi



Balancing Selection:

2 main types of Balancing Selection - Over-dominance and Frequency Dependence

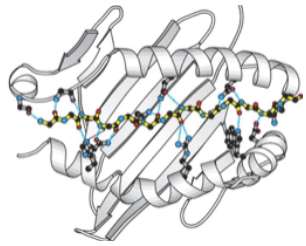
- Both - Strong selection for heterozygote

1. *Over-dominance:* Occurs when h<0 (heterozygote adv.)

Example - Sickle-Cell Anaemia

- Areas with high malarial risk (purple areas) and sickle cell anaemia (blue areas)
- Autosomal recessive disease caused by B-globin gene mutation from glutamic acid > valine substitution in one of the Hg chains that bind O2
- Homozygote suffers disease (crystal aggregations in blood that can block capillaries)
- Heterozygotes (carriers) has only mild form, and is at same time resistant to malaria (e.g. immune system prevention)

Example 2 - MHC Class 2 gene Polymorphism



- Immune system involves: MHC, class 2 alpha and beta form and alpha coils and beta sheets
- Peptide Binding Region: Alpha helices and beta sheets form cleft were peptides can bind
- Diversity in residues of PBR must be high
- Huge diversity of antigens to which MHC must bind
- Strong balancing selection in PBR
- dn/ds ratio very high -> Balancing selection, selection for heterozygosity to keep diversity high

- Purifying selection occurs outside PBR region (for conservation - identical)

Phylogenies based on neural markers (molecular clock)

Phylogenies constructed using MHC locus are very diff to those usually observed

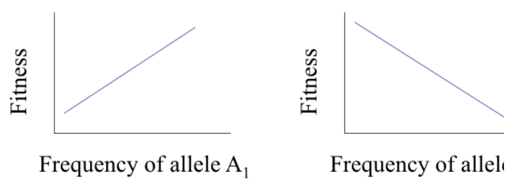
No connection to true evolutionary histories

Due to preservation of diversity at this locus over time - Heterozygosity strong selection, keep variety of alleles within pop over long time

Through balancing selection

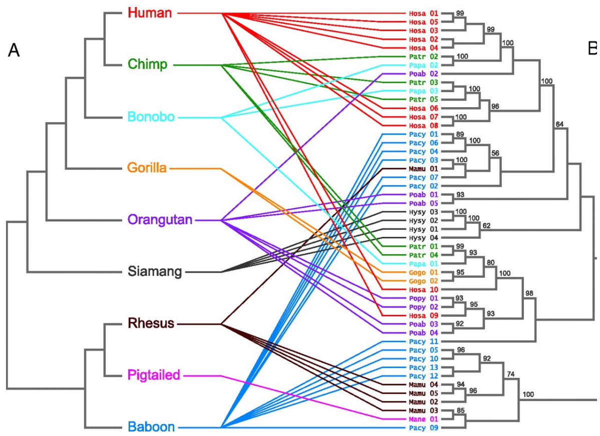
2. ***Frequency Dependent Selection***

Allele will be favoured when rare, but disfavoured when common (or vice versa) trending towards an equilibrium value



Positive - Fitness increases as allele becomes common, and decreases as allele becomes rare

Negative - Fitness increases as allele becomes rare, and decreases as allele becomes common



Example - Mullerian Mimicry

- Kind of positive frequency dependence in Heliconuis (honest signalling)
- Higher frequency of allele -> Greater fitness
- Unpalatable species mimic each other when in same geo range to reinforce aposematic signal to predators
- Avoid attack by predators, predators avoid distasteful prey
    - Aposematic - Coloration or markings serve to warn or repel predators

Example - Batesian Mimicry

- Negative frequency dependence in Papilo dardanus. (dishonest signalling)
- Mimicking species is palatable, but mimics distasteful model species
- Only effective if mimic species is rare compared to model species
- If great num of butterflies mimics -> predators will know they taste okay and signalling becomes futile
    - Negative freq. dependence (less the better - rarer)
- Achieved by adopting several diff model species to mimic -> Also promotes genetic polymorphism. (If mimic species is common, predators will realise that they are palatable)

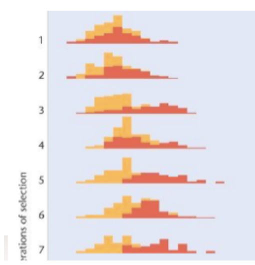
Other types of Freq. Dependence:

1. Temporal Patterns

    Characteristic may be an adv. part of the time (i.e in certain seasons), while another characteristic may be adv. at other times. If net benefit balances, the 2 characteristics may be preserved

2. Spatial Patterns

    Microhabitat variation can define separate niche space within same envi/geo area. In this case, individuals may adapt to different microhabitats - a potential path to speciation.



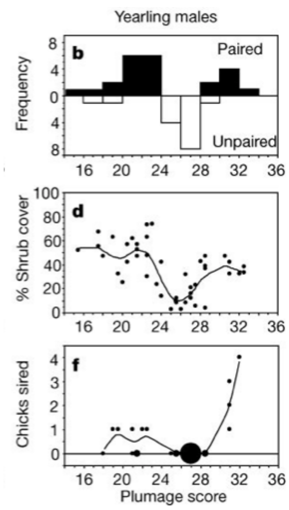
Disruptive Selection

Where either extremes are favoured - Works in principle, but is not generally seen in nature

Example - Fruit Fly

- Populations of fruit fly can be subjected to differential selection for 12 generations
- Red and orange represents 2 pops subjected to differential selection
- Lower and higher number of bristles (extremes) maintained in 12th generation

Example - Lazuli bunting

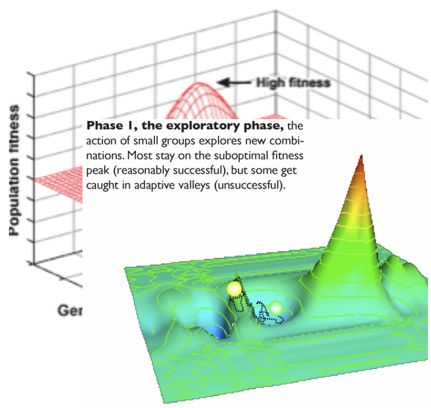


- Both dull and bright yearling males attract more females, maintained larger territories and had more successful broods than heterozygous phenotypes
- Intermediate coloured individuals didn't do very well

Shifting Balance Theory of Evolution

- Integrates directional selection and random genetic drift
- Importance of interaction between genes (epistasis)
- Gene combos would define a fitness landscape

- Traits which are controlled by many genes undergo epistatic interactions - Thus more complex situation with respect to fitness
- Landscape determined by gene interactions, with many diff adaptive peaks, with differing degrees of fitness



- Directional selection allows peak to be climbed (move towards an adaptive peak)

- Genetic drift can move pop around landscape: Off peak, through trough and onto other peaks (potentially)

Envisioned 3 Phases:

1. Exploratory Phase - Where pop may be on a peak, which is better than nearby options but not the best. Action of small groups explores new combinations, however majority stay on suboptimal fitness peak (which is reasonably successful) but some get caught in adaptive valleys (which are unsuccessful)

2. Selection Phase - Causes groups in adaptive valleys to move towards new, higher fitness peaks, genetic drift allows them to fall into trough whilst selection allows to climb another peak which cld be higher

3. Dispersal Phase - Groups at higher fitness peaks send off migrants, helping other groups to move to higher fitness peaks promoting success overall, influences everyone else. Dispersal of individuals from highest peak causes whole pop to move towards most fit state

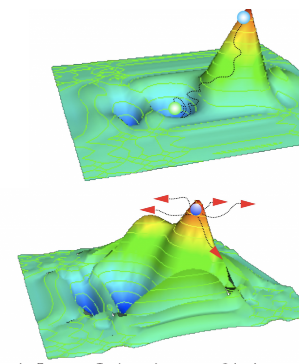
Process has been observed in evolution of diversity in warning colour and mimicry.

- Phase 1 and 3 are controversial
- Phase 2 is directional selection

Phenotypic Plasticity (Developmental):

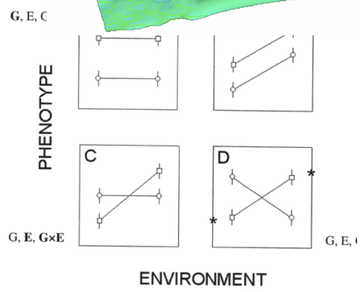
- Developmental plasticity potential for given genotype to develop diff phenotypes in diff envi
- Why wait for natural selection if you can do it yourself
- Ability to be phenotypically plastic will itself evolve

Example - Jeffrey Pines



- Grows upright or horizontal depending on wind strength (in high alpines)

- In normal habitat grows up vertically straight
- Phenotype heavily influenced by envi



Schematic "Reaction Norms"

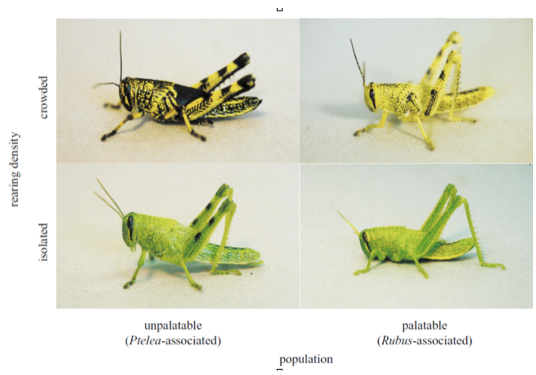
Defining diff types of interactions between genes and environment

A - No plasticity - No change from either locus

B - Similar plasticity - Similar change of each locus with changing envi

C - Genetic Variation for Plasticity - 1 allele remain static, 1 allele changes with envi

D - Gene-Envi interaction variance - 1 allele changes -ve, 1 allele changes +ve (envi has opp effects on loci



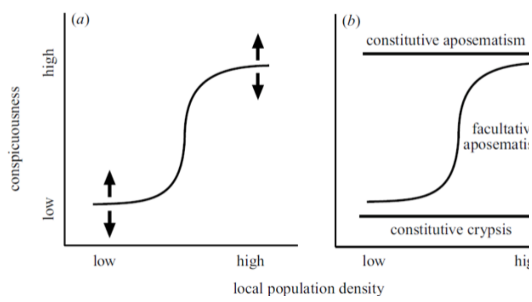
Cricket Aposematism:

- Relationship between pop density and palatability suggesting a role for phenotypic plasticity in evolution of aposematism
- Phenotypic plasticity gives natural selection a jump start

Depending on envi - Plasticity responds and takes adv.

- Colouration is very diff in isolated envi compared to a crowded envi
- In crowded envi - Boldly announces bad tastes

Genetic Assimilation:



- Process of how plasticity may facilitate evolution by natural selection
- Phenotype originally produced in response to envi condition, later becomes genetically encoded via artificial or natural selection

- Constitutive crypsis (avoid detection), crickets which are always cryptic

- Constitutive aposematism (declaring bad taste), crickets which are always mimicking

- A sigmoidal reaction norm is given, which may be affected by selection or drift in the cricket example.
- Facultative aposematism - Promotion by plasticity allows constitutive cryptic to become constitutive aposematic (in increasing conspicuousness)

Some features are just consequence of developmental process, and are present but not adapted nor exposed to natural selection. They are a consequence of DNA available.

Summary:

1. Many examples of directional selection, both for phenotype and at molecular level, though determining positive selection as motive force can be difficult

2. Evolution by balancing selection due to either selection for heterozygotes (i.e. sickle cell anaemia) or frequency dependent selection (i.e. positive, negative or related to temporal/spatial variation in habitat)

3. Evolution by disruptive selection due to positive selection of diff forms, or selection against heterozygote

4. Theory incorporating both natural selection and genetic drift is ***Shifting Balance Theory,*** whereby a fitness landscape can be explored by drift and peaks climbed by natural selection

5. ***Phenotypic plasticity*** allows for some phenotypic variation for given genotype, and may facilitate evolution of traits by natural selection. Ability to be plastic is also something can evolve

Sex

1. Why should I have Sex ? (evolutionary advg.)
2. How do I have sex ? (mating strategy, male/female, investment)
3. With who do I have sex ? (how closely related)
4. How can I continue to have sex ? (adaptive changes to genome to support continued sexual reproduction)

Evolutionary adv. of Sexual Reproduction vs. Asexual Reproduction

Mating strategies: Male or Female mating strategies

<u>Bedrid Rotifers - Rare Group of Orgs</u>

- Most eukaryotic species reproduce sexually - At some point in life cycle
- 50 million years - Asexual reproduction (cycled asexually for 50 MY)
- Very few species known to reproduce asexually
- Rotifers - Have as much variation in pop as sexually reproducing organism
- Sex doesn't always lead to greater genomic variation
- Driving mechanism for variation is mutation (cell divides)
- Same number of cell divisions wether asexual or sexual
- Reasons for asexual reproduction - why asexual doesn't dominate

<u>Evolutionary Equations</u>

Expression of this source

I = p + q

Separation of pop into 2 halves: p and q

Why doesn't asexual reproduction dominate

<u>Example</u>

I = C + (1 - C)

C = Males
(1-C) = Females

All sexually reproducing

Imagine pop where female pop is invaded by asexual mutant

Selection Co-efficient:

Asexual (1-S)
Sexual (1)

If s is small - Spread of asexual mutant will be fast (and if C is small)

Asexual variant introduced into pop, will spread through pop if there isn't much of selection disadvantage

<u>Results</u>

Results in 2-Fold Cost of Sex

Asexual mutant will spread through pop twice as fast than sexual mutant if not much pressure actively trying to stop the spreading

False to think sex increases genetic variation

<u>Why Do we Persist with Sex ?</u>

To answer calico cat question, we need to think about sex

Why does it persist in the face of what's called '2-fold cost of males'?

Asexual or self-fertilising females should be able to reproduce much faster than sexual females that need to find partner. Despite that, almost every eukaryote reproduces sexually at some point, so what's the advantage?

The evolution of sex, to some extent, remains unsolved problem, most theories focus on ability of meiosis to create genetic variation

<u>Main Theories:</u>

I. Leigh Van Valen's 'Red Queen' hypothesis
II. 'Muller's ratchet'

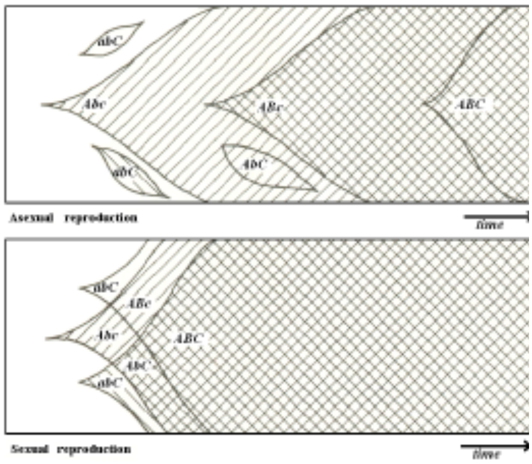
Commit to mixing genetic material with somebody else's - further questions:

1. How many parents should there be? Orgs have settled on 2, but reason for 2 over, say, 3 or 4 isn't immediately apparent!

2. What strategy should we adopt? It turns out that there are 2 stable strategies:

    A. Produce lots of gametes and invest energy in spreading them (= male)
    B. Produce fewer gametes and invest more energy in growing offspring (= female)

Sex Mixes Beneficial Alleles more Rapidly



Mixes variation more rapidly than asexual reproduction

Diagram:

Asex - Num of alleles, A B C sweeps to dominance, at a much slower rate

Sex - ABC (beneficial alleles) sweeps through pop at much faster rate

** Key diff, not total variety present, its about speed of change **

Sweep to fixation is much slower in asexual than sexual

For a responsive and adaptive population -> Sexual reproduction

What is pop responding to?
Selection pressures acting to favour rapid evolutionary change?

Movement, migration or change in envi?
Doesn't occur very often
So why maintain mechanism of rapid change if change in envi is slow

Answer = Disease

Red Queen Hypothesis

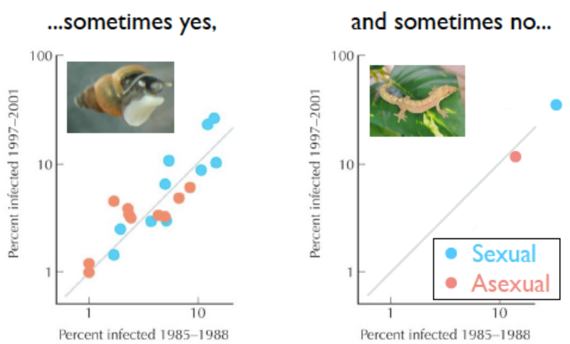
"Evolving as fast as you can to stay in the same place"

Selection pressure acting to favour rapid evol change?

- Envi doesn't change as often
- What is constantly varying = Disease
- Orgs are constantly effected by diseases
- If can rapidly evolve to fight off disease then more of sexual advg.
- Pop stays phenotypically same over period of time -> Require sex to continue reproduce
- Spread and allows genetic variation throughout pop
- Sexual reproduction produces a reservoir that can fight off evolving diseases (bacteria)
- Most stresses change over fairly long time spaces

<u>Evidence of Red Queen</u>

- Difficult to construct experiment
- Clean unaffected org



- On newly speciate orgs

<u>Muller Ratchet</u>

- Beneficial change sweeps quicker through sexually reproducing pop
- Unbeneficial changes retained over longer periods of time in a sexually reproducing pop
- Deleterious mutations build up solidly in asexual reproducing pop in irreversible manner

Selective advantage behind sexual reproduction
- Diff selective advg. hold in diff circumstances - Depends on pop
- Many disadvantage in sex - Some count more in specific pops

Sex - To spread your genes
- In comp - Spread own genes through pop more than anyone else
- Mixing genes with another individual = Trade-offs
- Thus, investment into reproductive cells

<u>What gives rise to Males and Females</u>

Diff investment into reproductive cells
Ever org produces equally sized, equal number of gametes

<u>Isogamous</u> (protosex orgs)
Previous primitive organisms both Male and Female - Equal sized gametes

<u>In Competition - Strategies</u>

Female - 1 Gamete larger with more nutrients, pay off

Male - Numerous, smaller gametes to reproduce with larger variety of partners

<u>Experiment</u>

1. Start with Isogamous pop -> Isogamous pops aren't evolutionary stable
2. Invaded by cheats - Move to evolutionary stable system (Anisogamous)

<u>Anisogamous Leads to:</u>

1. Diff in size of offspring

2. 2 diff types of comp (intra and inter sex comp) for survival of genes

   Intra - Male vs. Male
   Inter - Male vs. Female

Experiments - Looking at num of produced offspring against number of mates

Should I be Female or Male?

- First comp is between 2 sexes
- Who gets more out of sex reproduction: males or females?
- Evolution/frequency-dependent selection makes it about the same..

Anisogamy is Evolutionarily Stable Strategy

Assuming want to reproduce sexually, and with somebody else, what strategy should you adopt to maximise gene transmission for your investment?

2 Basic Strategies:

1. Males = Lil investment in each gamete, assuming equal total investments, means more gametes

2. Females = Large investment in each gamete, but fewer gametes

Early work by Bateman in Drosophila, male

- Fitness is proportional to num of matings
- Little extra benefit to females from > 1mating
- Either is an Evolutionarily Stable Strategy
- Isogamy tends to be invaded by cheaters (not always: some exceptions, usually algal and in marine systems)
- Stress, btw, both sexes are trying to 'cheat' the other.

Sex Ratio

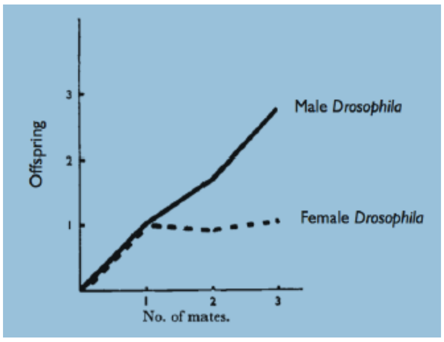
- Usually 1:1
- Why? = Because of Frequency-dependent selection
- Ratio of investment in offspring that matters, rather than numbers
- Females should invest about 0.5 in male production and 0.5 in female production
- Conover and Voorhees tested and provided evidence to support Fisher's Freq-dependent sex-ratio theory

Classic Paper on Diffs between Sexes

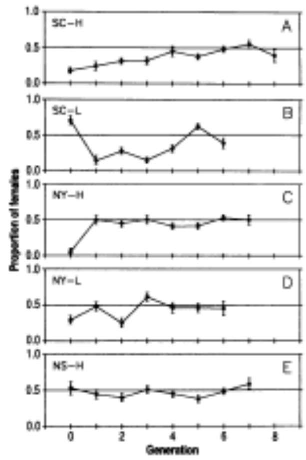
Females - Num of offspring produced didn't increase after certain num of matings, no advg. in females to reproduce with numerous mates

In Males - Advantage for males to mate numerous times, advantage above threshold

However - Findings are old/incorrect



Ronald Fisher - Evidence for freq. dependence of sex ratios



Major mathematical evolutionary biologist
Sexual rations are freq. dependent

Example - Stickleback

1 - All male (top)

0 - All female (bottom)

1. Start with skewed sex ratios
2. Over generations - Shifts back to equilibrated sexes to 50/50 even sex ratio
3. Pays to produce other sex

More females there are, pays more to be male
More males there are, pays more to be female

Competition During Mating

Male-Male Comp (Intrasexual)

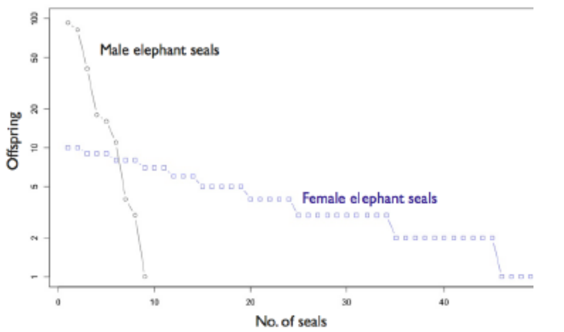
- Increased female investment -> Females are choosy
- Males compete for females (some exceptions: Phalarope, seahorses)
- Darwin explained secondary sexual characteristics this way: sexual selection
- Intrasexual ('Bateman's principle')
- Greater struggle for matings among males (males under greater sexual selection and so have higher variance in offspring num)
- Male fitness roughly linear with num of matings, female less so
- Bateman's findings supported in num of extreme cases
- e.g. Elephant seals have several-fold of sexual dimorphism: 90% of males have no offspring, but 1 had 93
- In contrast, >50% of females have one or more offspring1

Bateman's Idea - Elephant Seals Highly Sexually Dimorphic

- To equilibriate sex ratios
- Most visible/measurable comp often within sexes (intra-sex comp)
- More matings = More offpsring
- Males need to mate more often and find more females
- Males vs Males to compete for females
- Males have greater selective pressure -> They must find mates
- Results in Sexual dimorphism (due to strong comp)

- Males get larger, in order to compete for females (to compete with other males)

Evidence Supports Bateman's Ideas



- Female elephant seals - Tend to have have more offspring
- Male elephant seals - Most will not have offspring (small num of males produce offspring - dominant males)
- Broader num of females will have offspring
- Extreme sexual competition

How or when to have sex?

Which strategy to adopt to increase case of sexual reproduction - Male or Female?

- Choose sex (male or female)
- How to compete with other members of sex
- Can compete at num of stages
- Comp prior to reproduction - Fight and then if win, get to reproduce

Example - Competition in Kype - When?

1. Prior to reproduction - Fight, win then get to reproduce (develop kype hook temporarily allowing fighting with other males)

2. During mating

Example - Male Dimorphism in Dung Beetles

2 Male Types:

1. Major male
2. Minor Male

3 General Strategies in Dung beetle

1. Ultra-dominant strategy - Kill all and mate with all females
2. Monogamy strategy - Run off with 1 female, monogamous relationship
3. Sneaky Fucker Strategy - Minor male, pretends to be female, cheats on ultra-dominant strategy. Dimorphism within sexes, access to females and mates with females that major male hasn't mated with

Example - Damselfly

Comp occurring after competition

- Damselfly penises are hooked
- Can hook out sperm of previous male from female
- Removal of sperm from previous copulation
- Post-mating comp - Physical removal of sperm
- Then deposits own sperm

Sperm comp drives larger testicles

- Produce more sperm
- More production, more comp after fertilisation
- 2 matings in close succession
- More sperm = More likely to fertilise egg
- Requiring larger testicles
- Chimps with over 7 mating partners have largest testicle sizes
- Correlation between penis and testicle size - In primate family (humans relatively large)

To improve chances of Post-Fertilisation Competition

- Example - Argentinean lake duck
- Penis unravels inside female
- Greater penetration due to high comp

Competition Within Sexes (Intra-sex)

A. Before Mating

- Fighting/body size
- Sexual selection can raise matings at expense of survival (= sexual selection can override natural selection, so bright colours at the expense of camouflage)
- Selection for fighting can be to death (red deer, salmon have specialised fighting jaws = 'kype' grows before spawning)

B. During Mating

- 'Sneaky' males: dimorphism in male beetles (either large males or small males that sneak in)
- In many species, 3 general strategies (under negative freq-dependent selection):
    1. Ultradominant (= bull of a harem)
    2. Small, carefully guarded (~ monogamous)
    3. Sneaky on ultradominant ('sneaky fucker')

C. After Mating

- Sperm competition

- Sexual selection between sperm of rival males for fertilisation of eggs while in reproductive tract
- Remove competitors' sperm (damselfly penis has horn to remove others)
- Plug female, or hang on (dogs)
- Make more sperm (primates)
- Repeated matings, longer penises

D. **After birth (infanticide) -** 25% of lion cub deaths

Comp after Birth

- Kill offspring produced by competitors
- Common within harem system - Male lion takes over pride, kills all cubs left by predecessors
- Occurred within humans too

Female-Male Competition (Inter-sexual)

Sexually dimorphic traits are costly
- Why should they evolve?
- Only if females actively choose them
- Why should they choose them?

3 Main Theories:

I. Sensory Bias. Basically, supernormal stimulus: Exaggeration of a pre-existing stimulus to make it more distinctive and remove any doubt (e.g. yes, I really *do* want to mate - it saves wasting time for female)

II. Direct benefits to female. Males with silly sexual stuff healthier, as they have resources to produce them, so females less likely to catch diseases (uninfected males)

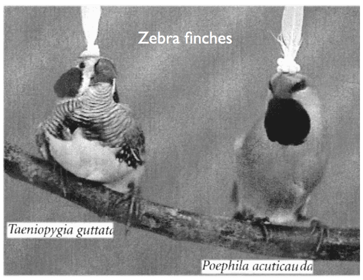
III. Indirect (fitter offspring)

A. Sexy sons (positive feedback: Lande and Kirkpatrick) runaway models of sexual selection. Coevolution between natural selection optimum (males) and sexual selection preference (females). If there's linkage disequilibrium, then runaway.

B. Or, just better genes.

Female Mate Choice

- In Zebra Finches - Males must be fit to support large appendages
- Sexy son - positive feedback
- Choosing mate with larger appendages will result in fitter offspring



Sexual Antagonism

- Sometimes a trait that's good for 1 sex is bad for other
- Called sexual antagonism
- Has been postulated as a driver for various traits, such as cheating females

Sexual Reproduction

Adv. to Sexual Reproduction

- Various processes it can occur
- Org adaptations adopted for sexual reproduction

1. How related should my mate be?

How much inbreeding vs. Outbreeding - How related/close should partner be?

Options:

A. Asexual Reproduction - Selfing (mate with self)

- Commonly seen in plants
- Selfing plants - Reproduce with self (Arabidopsis - Useful, grows quickly, small genome, model org)
- Fig Wasps -

Inbreeding vs. Outbreeding
- Closely related or distantly related - Spectrum between 2 extremes
- Mixed mating strategy - Preference will outcross but if need to, will inbreed

B. Inbreeding

- Fig wasps - Inbreed, lay eggs in figs, grow and reproduce within fig, only mates with siblings from within same fig

Adv. 1 - Preserves favourable gene complexes

- Example - Horse racing - Most race horses derive from 3 horses (godolphin arabian etc.)
- Extremely inbred
- Fast running preserved via inbreeding
- Inbred lineage from very long time ago
- Inbreeding selected on few gene complexes (very fex) and preserved in adv.
- Thus, racehorses are useless in wild as adaptability has been bred out

Advg. Number 2 - Reproductive Assurance

- Can always find a mate

Disadvg. - Genetic Load

- Royal Family - 2 branches
- Inbreeding will build up deleterious mutations
- Can reach asexual reproduction if too much inbreeding occurs
- Coefficient of kinship vs. number of marriages
- 0.25 = Share 25% of genes (siblings)
- In Sicily, people were marrying partners who share more genes than siblings due to high amount of inbreeding

Sea-well wright experimented on inbred pops of guinea pigs

- Found inbreeding for more than a certain number of generations, will accumulate deleterious genetic load and orgs will no longer be able to reproduce

Random vs. Assortative Mating

- Random - Choice of mate is random (chance)

- Assortative - Non-random choice in finding mates, choosing mate for particular property, factors going into mate choice

Regulation of Inbreeding? —> To Encourage Outcrossing

- What evolved for individuals to select mate
- What choices allow us to regulate amount of inbreeding
- Various adaptations evolved to regulate amount of inbreeding in plants
- Morphological and molecular adaptations can protect against inbreeding

1. Heterostyly

    Diff in height of stamen - Determines whether it can self-fertilise or not
    Morphological adaptations - Can give protection to inbreeding

2. Self-Incompatibility:

    If pollen from plant, falls onto stigma of same plant - Will not germinate = Self-incompatible plants
    Signal on pollen recognises signal on surface - No Self-fertilisation
    Male and female are not separated during mating - Must express compatible alleles
    SI Locus action - Molecular adaptation

    S-locus - single, multi-allele locus imparts to pollen a specific phenotype recognised by stigma and style of potential receptor plants
    2 SI locus - 1 in female and 1 in male - M and F express compatible alleles
    Must suppress recombination from occurring in these chromosomes
    No recombination at SI locus occurs, male and female loci no separated during reproduction - How mating systems are maintained

By changing histones and nucleic sequence at SI locus

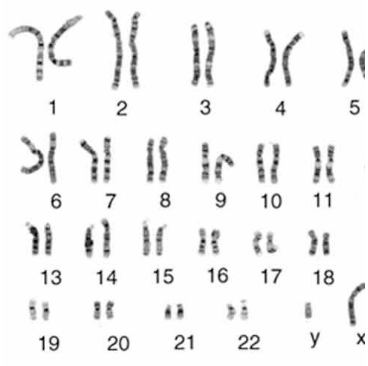
Issue in Plant Breeding - Can switch between inbreeding and outcrossing

- Switch from inbreeding —> outcrossing = Allowing more variability
- Switch from outbreeding —> Inbreeding = Species at extremes of geo range for reproductive assurance
  - Often seen in wild

Other genes at other loci can interact with SI locus - Still unidentified
- Mechanisms which can flip species between the 2 strategies
- Maintenance of trait, suppression of recombination of locus

Sex Chromosomes

Marchantia (liverwort)
- Gene org of liverwort Y chromosome reveals distinct sex chromosome evolution in haploid system
- Sex chromosomes are linked to sexual dimorphism
- Differences in female and male in species
- Greater diff in DNA needed to specify the phenotypic diffs



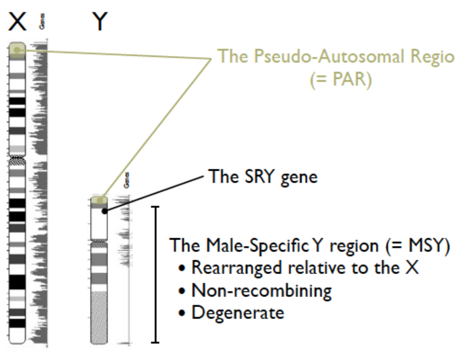
Distinct characteristic of sex chromosome = No Recombination

- Suppression of recombination - Linked to sexual dimorphism
- Greater the difference in chromosomes, greater the dimorphism = Why Y and X are diff sizes

Why X and Y are diff size

Pseudo Autosomal Region (PAR1 and PAR2) of human X and Y chromosome pair and recombine during meiosis - Genes not inherited in strictly sex-linked fashion

- Default developmental pathway is female
- No signal to become male
- Embryo develops as female (without signal)
- Male signal —> SRY gene or Testis Determine Factor (TDF)
- Responsible for initiation of male sex determination in humans



- Sex determining region on Y - MSY (Male Specific Y region) = Specifies male characteristics
- MSY - Rearranged relative to X, non recombinational, and degenerate
- Flips on and triggers transcription factors on Y to trigger male development/characteristic
- Important developmental process - Takes precedences over other info on Y

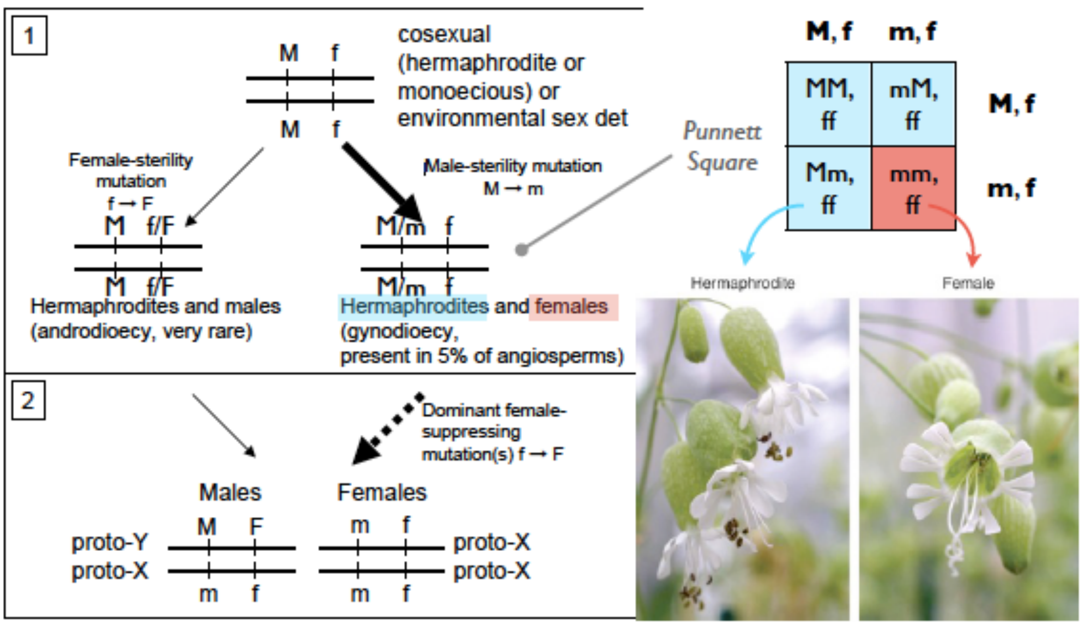
Due to lack of recombination - Mutations accumulate on Y chromosome

- Y can never repair itself through recombination (no YY found in org)
- Mutation on X chromosome -> recombination with other X to repair
- Y is therefore degenerate

Why Don't Sex Chromosome Recombine?

"If sex is determined by 2 or more genes, it's essential for these genes to be inherited together as a unit. This requires inhibition of recombination between differentiated segments of X (or Z) and Y (or W) chromosomes. The recombination in differentiated segments may be inhibited by an inversion or by a gene or genes controlling biophysical process of recombination."

Sex Chromosomes Suppressed Recombination as Sex Determination involves 2+ Genes



1. Co-sexual Species - Hermaphrodites (M - f)

Initial mutation gives rise to divergence of 2 sexes

Mutation causing Female-sterility and Mutation causing Male-sterility

2 Separate Populations:

A. Hermaphrodites and Males - (Very Rare)
B. Hermaphrodites and Females - Many more species select this pathway, favoured due to various selection pressures causing separate males and females

Deterioration of male - Male sterile mutation (i.e female) tends to be genetically stable, female-sterile mutation (male) male plants having to at some point will need to support self as single sex (hermaphordite and male) - Difficult to survive

2. Leads to Proto-Y and Proto-X chromosome

Simple 2 gene evolutionary model actually suggests sex determining loci must initially be linked for separate sexes to evolve

Male-sterility (adv. if females have higher fertility and/or if hermaphrodites produce inbred progeny suffering from strong inbreeding depression)

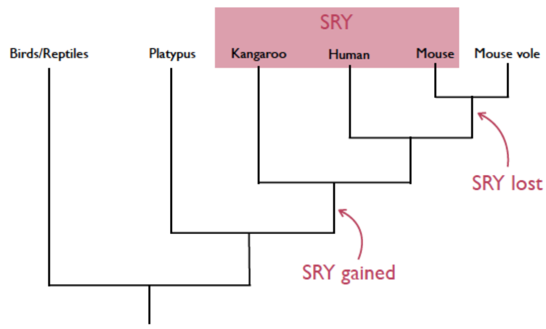
Female-suppression (adv. as males will pass on more genes)

Once females are present - Hermaphrodites selected to re-allocate more to male and less to female functions

Selection should then act to reduce recombination between initial 2 genes (proto-Y and proto-X)

Proto-Y = Slightly older with a MSY region

- Regions are no longer homologous thus no recombination occurs
- Large scale inversion/deletions, relative to X - Thus no longer homologous
- Leading to suppression of recombination -> Degenerate chromosome

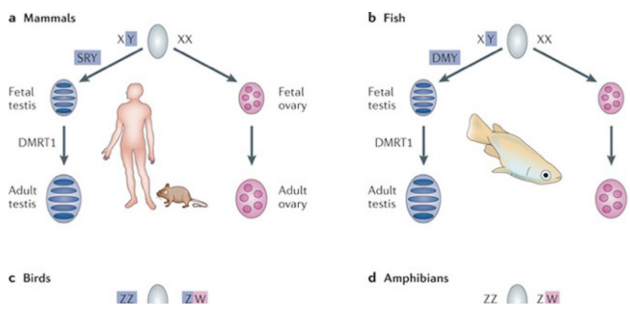


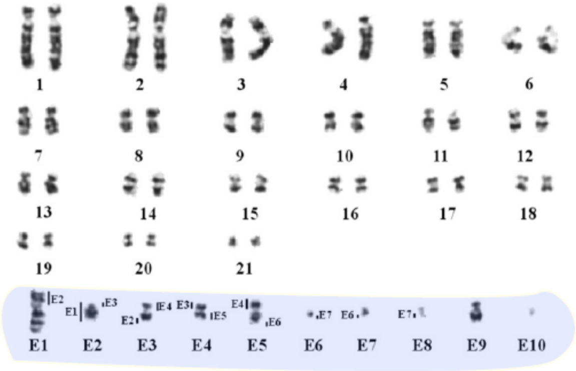
How effectively have species split sexes?

TWE is there homology between sex chromosomes

SRY - Back to phylogeny, gained long time ago

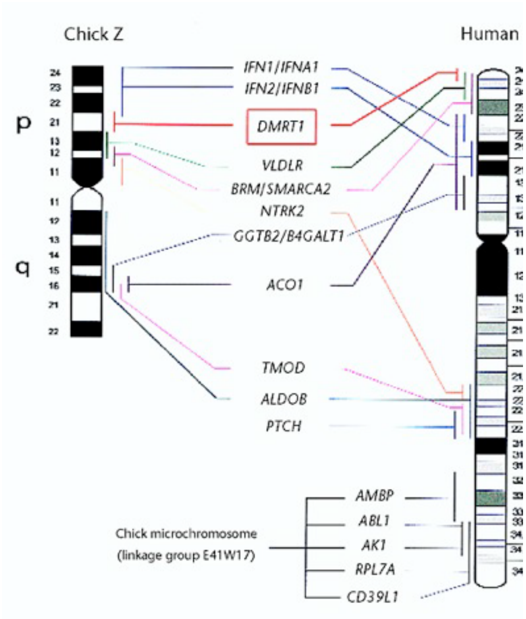
- SRY gene is same - Driving sex determination in numerous species





- In mammals related to DMY gene in fish, DMRT1 gene in chickens
- Humans, fish, chickens etc. all have sexes
- Gene determining male is the same however sex chromosome is different

<u>Sex Chromosomes are Constantly Evolving…</u>



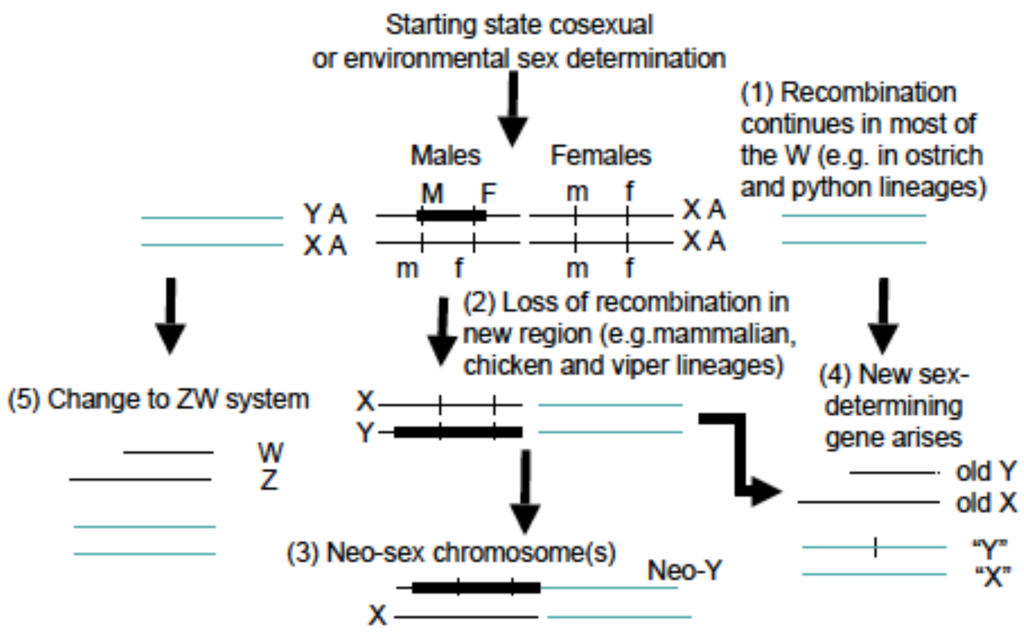
- Gradual genome rearrangements create "evolutionary strata"
- Human Y chromosome will disappear over time
- Continually degenerate to point where no longer visible
- Male chromosome (10,000 more years)
- Important thing about y chromosome is SRY gene determining sex-switch
- SRY gene moves around
- In 10,000 years - Y chromosome will degenerate and SRY will move onto a new autosome
- SRY moves onto autosome -> Becomes new y chromosome
- Sex determination function passed on to another chromosome - Giving a new-sex chromosome or even to a new gene

Diagram - 300 million years of conserved synteny between chicken Z and humans

<u>Seen in Platypus</u>

- 26 pairs of chromosome in total
- Platypus sex chromosome - 2 groups, 5 sets of chromosomes
- 5 sets - Act as X
- 5 sets - Act as Y
- Inherited as a unit
- Various patterns of assembly
- Will gradually assemble over time to produce single X and single Y
- Suggests that evolution of sex chromosomes is a more dynamic process than previously expected

<u>Summary of some Evolutionary Changes that can Occur after small sex determining region evolves</u>



ZW Sex Determination System
- Determines sex of offspring in birds, some fish and some insects etc.
- Ovum determines sex of offspring (opposed to sperm determining sex)
- Males are homogametic sex ZZ
- Females are heterogametic sex ZW
- Z chromosome larger than W containing more genes

- Mate choice:
- How breeding should be - Leads to question how inbred should i Be
- TWE do i need to mess around my genome, to determine method of reproduction
- Large scale genome evolution - i.e. genome behaviour evolution
- Extreme - How sex chromes evolve (large-scale changes, SRY gene moving on chromosome depending on how mating systems are evolved)

neo

Problem of evolution - A lot of selection occurs due to tiny selection adv. if an alley has 100th of a percent fitness advatnge, eventually it'll spread
Cant spot fitness advg. unless

Small fitness adv in female (proto-x chromosome)

Cant be tested effect is so small

Sexual Selection

Sexual Selection - Outline

- Sexual Selection:
  - what is it?
  - how does it operate?
  - why is it present?
  - why is it important?
- Mating patterns:
  - main types
  - determinants
- Sexual conflict

LO:

- Understand operation and evolutionary importance of sexual selection
- How did sexual selection originate?
- What determines strength of sexual selection?

Darwin - Sexual Selection

Individuals in sexually reproducing species can improve their chances of reproducing in 2 ways:

1. ***Natural Selection -*** Compete successfully to survive and acquire resources allowing reproduction (struggle for existence)
   - Selecting traits aiding individual in survival
   - Adaptations that aid survival

2. ***Sexual Selection*** - Compete successfully for mating opportunities
   - Monopolise access in terms of mating opps

   Characters that:

   A. Aid competition within one sex for access to other (intra-sexual selection), males compete amongst themselves to get to females

   B. Enhance attractiveness of individuals of one sex (again, usually males) to members of other (inter-sexual or epigamic selection) - Exhibit genetic, physical quality, condition and access to resources

   Epigamic Selection - Comp for mates, attracting other sex, females accept males (or occasionally reverse) with certain traits

At a cost to other components of reproductive success, e.g. adult survival (bright plumage or large antlers etc. - risk of predation or energetically costly)

Males generally compete for access to females and usually aim to increase their attractiveness

Sexual Selection - Potent evolutionary force:

- Lies behind elaborate morphological, physiological, behavioural traits, behavioural displays, sexual dimorphism, elaboration of weaponry, communication mechanisms - photogenic material in firefly

Mating Success vs. Reproductive Success

Mating - Number of copulation individuals achieve with opp sex

Reproductive - How many produced (offspring)

Females will mate with multiple males or vice versa etc.
Struggle between males for possession of females - Conflict of interest within males

Darwin - Sexual Selection

Darwin - "Sex Selection depends not on struggle for existence, but on struggle between males for possession of females - Results isn't death to unsuccessful competitor but few or no offspring, therefore sex selection is less rigorous than natural selection"

Intra-Sexual Selection:

- Competition between males
- Traits denote dominance
- Access to fertilisation opportunities
- Involves post-copulatory competition
- Sperm competition in female reproductive tract - Healthier sperm will reach eggs
- Far more intense than pre-copulatory comp

Inter-Sexual Selection:

- Females select males
    - Female birds by selecting mate with elaborate qualities
- Not purely for attraction
- Usually indicates quality of males that attracts females
- Good condition - Allows maintenance

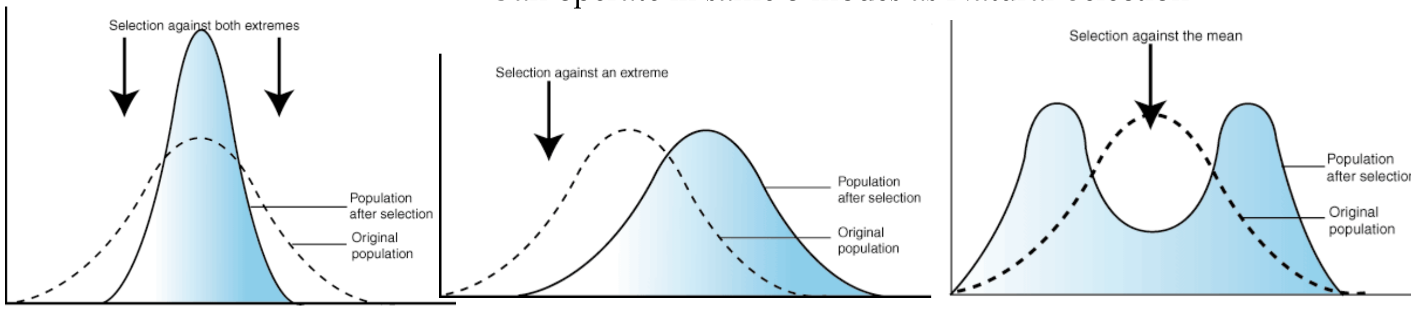
- Good energy expenditure - allows displays
- Males that have access to high energy sources -> results in their morphological attractive traits

Same Characteristics can serve in both or either of the functions:

i.e. Antlers or Body Mass

- Indicator of male quality
- Involve in male-male comp - Agnostic behaviour

Can operate in same 3 modes as Natural Selection



Sexual selection is most often directional

- Drives formation of ever more elaborate traits
- For more extreme traits
- Until costs associated become so high there is a balance between survival and attraction
- Balance between cost of natural selection and benefits in terms of gaining mating opps

Secondary Sexual Characteristics - Impact on Survival

Antlers - Energetically expensive
Bright Plumage - Conspicuous to predators etc.
Displays - Energy and risk to predation

Sexually selected traits becoming even more costly -> Leads to extinction

Sexual Selection and Natural Selection - Interwoven processes

- Some view these as diff processes
- But survival is valuable only if individual reproduces
- Traits which aid survival will only be passed on through reproduction - passed onto subsequent generations

- Both processes act through differential reproductive success

- How much to invest in struggle for existence vs. struggle to mate - Trade off

- Trade off between sexually selective traits and naturally selective traits
- Depends on relative contribution each makes to individuals lifetime reproductive output

<u>Sexual Selection:</u>

- Can influence morphology, physiology and behaviour
- Caution - Easy to assume a trait is sexually selected
- Difficult to demonstrate empirically what traits have arisen from and why

- Which traits due to intra- or inter-sexual selection?

Example - Male pheasants

- Once assumed male ornate tails associated with female choice and spurs associated with comp between males
- More detailed and phylogenetic studies were carried out
- Elaborate tail is for support in aerial combat with other males (intra-sexual)
- Spurs were inter-sexual - Females prefer larger spurs

<u>Sexual Dimorphism - How Do Sexes Differ</u>

How do Sexes Differ?

- Sexes differ in behaviour, genetics, morphology etc.

Mammals: Seems obvious, however more complex in other taxa (not only morphology)

What is the basic distinction between males and females?

Evolution of Anisogamy

- Differential investment in gametes (diff gamete size)
- Fundamental driving force behind evolution of many sex differences and is basis of sexual selection

Males - Large numbers of small motile gametes, unlimited (sperm production)

Females - Limited, large and well provisioned gametes (eggs)

<u>Evolution of Anisogamy - Arisen from Isogamy</u>

- Similar sized gametes
- Isogamy is less costly (e.g. microorganisms, fungi, algae - anatomically similar)
- Natural variation - Disruptive selection -> Less motile gametes or More motile gametes

Isogamous vs. Anisogamous - Dependent on 2 factors:

1. Size At Adulthood

   Example - *Volvox* spp. (green algae)

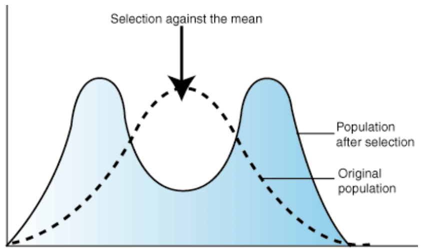
   - Forms multi-cell colonies
   - Diff sized colonies (small -> large)
   - Variation in gamete size depends upon colony size

   - In small colonies - Mainly isogamous
   - In medium colonies - More variation but similar
   - In large colonies - Anisogamous

2. Need to Provision Developing Offspring

   - Better provisioning = Better chance of survival

   - Ancestral state isogamous but natural variation in gamete size
   - Large gametes (containing more resources) - Better provision for developing offspring
   - BUT - Large gametes are less mobile - Less encountering freq.



   - Smaller gametes - Are mobile, faster, but less resources

   - Diff strategies/sizes have diff advg.

   - 2 small gametes fuse: Not enough provisioning for offspring
   - 2 large gametes fuse: Low probability of meeting due to immobility

   - Leads to disruptive selection —> Anisogamous

Anisogamy and Sexual Selection

Profound implications for subsequent evolution of 2 sexes.......
Comp/Conflict within and between sexes

Most evident in Male and Female Behaviour:

A. Why females are choosy?

- Typically females invest most in offspring - Esp. if internal fertilisation

- Produce large provisioned gamete
- Invest more in reproductive opportunities
- Mammals - Internal gestation and females lactate to provide nutrition - Heavily investing in offspring

- Egg production (fecundity) is finite - Limited num of mating opps
- Females want best genetic input
- Must choose good quality males -> To determine success of their offspring

- High investment & limited matings = Females prefer 'good quality' males to maximise success = Female choice

B. Why males monopolise mates?

- Males typically don't invest so heavily in individual (offspring) or reproductive opp

- Sperm production - Unlimited and cheap -> Unlimited potential matings
- Individual male could fertilise all females within pop
- Males are in excess due to unlimited production of sperm
- Thus males must compete for limited reproductive opportunities (females)

- Also - Uncertainty of paternity, males unknown if females offspring is theirs or not (multiple matings with female, so may not be father)

- Max Success: Mate with as many females as possible -> Male-male (intra-sexual) comp -> Secondary sexual characteristics

- Thus males less choosy about mates

Anisogamy:

- Males don't act as a parasite on female investment
- Male strategy has associated costs
    - Costs of comp - energy, injury etc
    - Developmental costs - weaponry, secondary characteristics.

- Females are limiting and males are in excess

Key Point (Bateman's Principle)

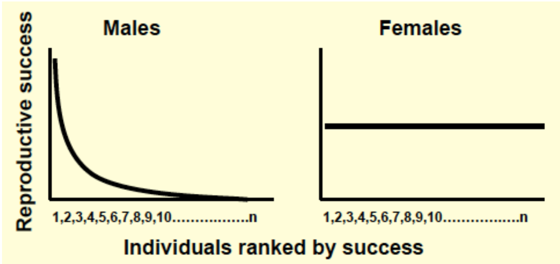
- Limiting sex - Sex with lower max reproductive rate - Females (limited num of eggs,)
- Acts as resource males of which unlimited sex (males) compete over

Sex with higher potential reproductive rate (males):
- Invest less in each reproductive attempt
- Experience greater comp for mates

-> Strong sex selection

Determinants of potential reproductive rate: Pattern of parental care and mating pattern

<u>Variation in Reproductive Success</u>
Classically high variation in males and low variation in females



Greater variation in success amongst males (males can achieve no reproductive success)

Females always achieving high success - Limiting resources, mated by 1 male atleast, most achieve same reproductive success

Affects individual strategies

Sex Dimorphism and Secondary Sex Characteristics

Sexual selection is a powerful selective force
- Driving morphology, physiology and behaviour
- Potential force in driving evolution

BUT - <u>Not all dimorphism is product of sexual selection</u>

Other Selective Pressures:

Fecundity - Females tend to be larger than males (in amphibians)

Feeding Ecology - Morphology (mosquitos - females only take blood, males have shorter-lifespan

Primary Sex Diffs - Bird species: females larger than males, females must carry eggs around (flying around) in reproductive period require mechanically larger wings

Sexual Selection: Mating Patterns

Mating Pattern or Mating System

Sexual Selection:

- Intra-sexual comp: Within one sex (usually males)

- Inter-sexual or epigamic selection: Mate choice (usually females choosing males)

What is Mating Pattern?

Mating Pattern - Describes pattern of matings between individuals (males and females) in a pop (matings vs. reproduction) - composed of individual mating strategies (may differ)

Mating patterns is a pop wide composite of individual strategies, and does not refer to individual strategies adopted to enhance individual fitness

Why study/classify these patterns?

- Classification allows identification of patterns - Categorise and makes easier for us
- Compare pops or species - Find general pattern within and between
- Mating patterns can shift over time - Observe the shifts
- Identify underlying causes of variation in success, strength of sexual selection and evolutionary outcomes
- Find main fundamental drives

Matin patterns - Only focusing on sex reproducing species (within 2 sexes)

How do we classify mating patterns?

Numerous Parameters:

- How many mates mates individuals have per breeding episode (within 1 or lifespan)
  - Variation in mating success (degree of polygamy)

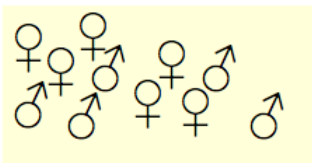
- How the mates are acquired ? (Intra-Inter sexual selection?)

- Duration of “pair” bond (Brief or prolonged?)

- Patterns of parental care (male or female care?)

Main types of Mating Patterns: Definitions

Promiscuity - Brief “Meet and Mate”



- Individuals aggregate, randomly
- Scramble competition to mate - Grab whoever they can (random)
- No structure to this

- Short temporal time-scale
- Neither male or female invest in offspring post-fertilisation
- Favourable envi conditions i.e. temperate pond emerging in wet season

<u>Monogamy</u>

♂ ♀

- Male and female long duration of pair bond
- Both involved in providing care for offspring
- Envi where offspring requires care post-birth - Resources difficult to acquire etc.
- Parents must work together
- Males limited in ability to abandon female (otherwise she cant help) - “Pit of monogamy”

<u>Polygamy</u>

Polygyny: ♂ ♀ ♀ ♀ ♀
Polyandry: ♀ ♂ ♂ ♂ ♂
Polygynandry: ♂ ♀ ♂ ♀ ♂

- Broad term: Individual of 1 sex monopolise numerous mating partners
- Female or male monopoly, or mix of 2

Polygyny - Individual male with multiple females

Polyandry - Individual female with multiple males

Polygynandry - Mix of two, complex interactions, bit more structure than promiscuity, some kind of protection or care for offspring, alliances between males and females

<u>Diff Forms of Polygyny</u>

A. Resource Defence Polygyny
    - Monopolise resource rich habitat/territory
    - Male able to control access to key resources, large territory etc. and dominate access to females due to resources available
    - Based on territoriality

B. Female Defence Polygyny
    - Hareem defence
    - Physically, herding and controlling females in tight groups (forcefully)
    - Example - Pinniped species

C. Male Dominance Polygyny - Hierarchy, dominant individual has access to females in envi, females select based on dominance hierarchy (through male-male comp)

D. Lek Polygyny - Males establish hierarchy dominance, via displays, formalised structure, males gather at site to perform display, females visit and then choose based on quality of males

E. Uni-Male Polygyny - Single male defends territory or hareem

F. Multi-male Polygyny - Male alliances, alpha and beta - (Beta - gains some copulation but protection, can inherit territory if alpha male dies etc.)

Diff Forms of Polyandry

Species which show sexual reversal, females larger and dominant

A. Resource Defence polyandry
   - "Territoriality"
   - Females larger than males and dominate them
   - Resource envi is very rich
   - Female will lay eggs with particular male, give to male to look after - Male looks after own "brood"
   - Move onto next male
   - Simultaneous or sequential polyandry

B. Female Access Polyandry
   - Like harem
   - Dominant large females will monopolise, establish hierarchy
   - Males who look after own brood

C. Cooperative polyandry
   - Males all care for all offspring in 1 "brood"
   - Females have multiple males in territory
   - Rather than leaving separate brood eggs are all laid in 1 clutch
   - Mixed paternity

D. Non-Parental Polyandry
   - Neither sex invest in offspring after birth
   - Females larger and mate with numerous males

Polygynandry

- Both sex have multiple mates and either sex can invest in offspring
- i.e. both sexes mat polygamously - both sexes have multiple mates
- Several males form pair bonds with several females simultaneously
- Elaborate bonding between individuals
- Example - Lions and various primates
- long term social groupings

Sexual Selection 2

Determinants of Mating Patterns

Example of Mating Pattern - Grey Seals (M) makes sounds around breeding colonies
Why?

2 Main Themes:

1. Parental Care - Main giver of care (f or m)

2. Dispersion in Space and Time of key resources, food, mates themselves etc. (Socio-ecological)

Mating Patterns composed of Individual Strategies:

- Individuals adopt mating strategies that maximise their own fitness under given ecological conditions
- Emergent properties within pop, comprising all individuals within pop, trying to max their own survival/fitness
- However conflict of interest -> Within and between sexes = Key forces behind Sexual Selection

Mating patterns originate from Anisogamy

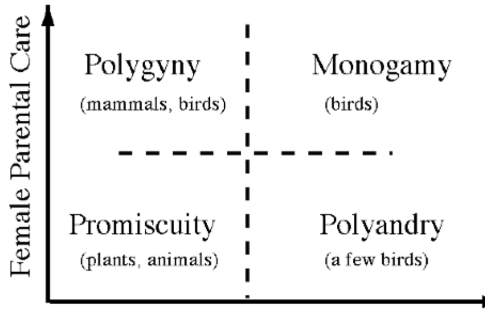
Main strategic division in mating patterns between Males and Females

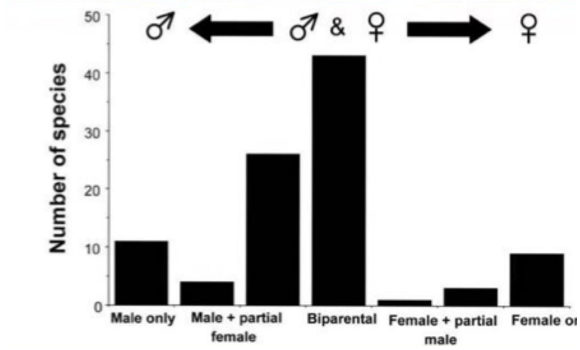
Females -> Heavily invest in offspring, limited mating, invest in eggs, get choosy for HQ males

Males -> Generally invest less and have unlimited num of potential matings, uncertainty in paternity - so males generally less selective, must compete for access to mates. less choosy

Broad Strategic Division between Sexes - Both trying to max their reproductive success
- Females are limiting resource
- Males - More sexual comp, more aggression (dominant alpha males, fight and monopolising to find mates)
- Or subordinate males (satellite)
- Conflict within sexes

Parental Care and Mating Patterns





Promiscuity - Brief meet and mate (Common amongst plants and animals), 0 parental care of male and female, some don't need to meet to produce offspring - e.g. aquatic animals

Polygyny: High female parental investment/care, males free from burden of offspring care, monopolising numerous groups of females (mammals, birds)

Polyandry: Male provide most care for offspring, females go find more reproductive opportunities (few birds)

Monogamy: Both sexes required to provide offspring care (Birds)

Example - Distribution of Parental Care in Shorebirds

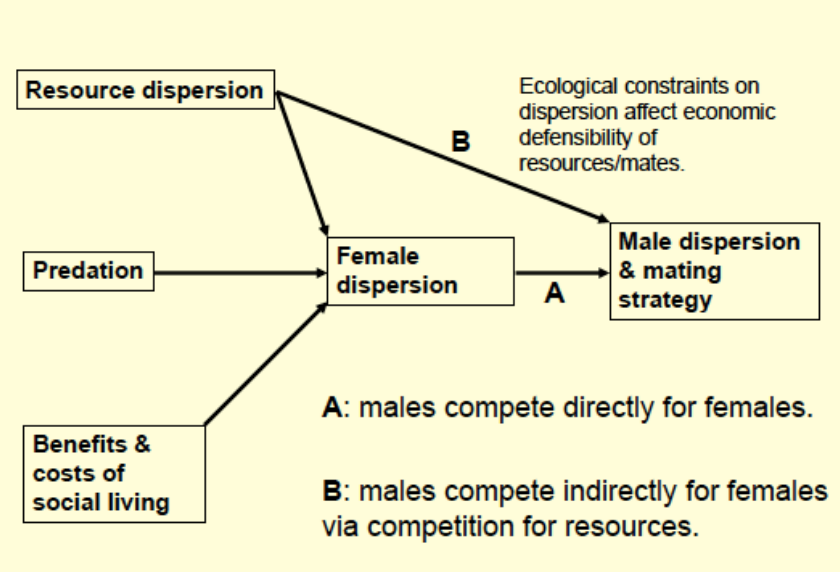
- Most species Bi-parental: Male or female primary caregiver in raising chicks
- 1 incubates chick and other is off foraging
- Lengthy period of investment from hatching to fledging
- Generally speaking - Females invest more

Socio-Ecological Model

- Distribution of resources and or mates in space and time
- Stems from differential parental investment

- Female reproductive success limited by access to resources, not by access to males
- Females need access to resources to provision high investment in offspring, influenced by predation i.e. shelter from threats (impact on foraging) and benefits/costs of social living

- Female distribution is determined by key resources
- Male reproductive success is limited by access to mates
- Males distribution is driven by female distribution, to maximise access to females



(Generally)
Female Dispersion Dependent upon:
A. Resource dispersion
B. Costs and benefit of social living
C. Predation

Female dispersion main driver of male dispersion and mating strategy (access to females):

Either:

A. Males compete directly for females (hareem defence system - aggregating groups of females)

B. Males compete indirectly for females via comp for resources, monopolise resources which females are dependent upon, envi potential for polygyny (then can monopolise females)

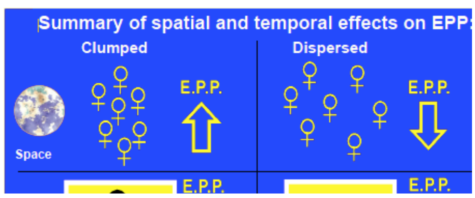
Potential for polygyny to occur depends on driving factors of limiting sex
Dispersion factors of limiting sex, determined by resources -> Spatial clustering of females

<u>**Socio-Ecological Model - Spatial and Temporal Dispersion and EPP**</u>

EPP = Envi potential for Polygamy

- Dispersion patterns of limiting sex are determined by envi (resources)
- Spatial clustering of females in resource-rich areas
- Temporal clustering of females due to synchrony
- Affects potential for individual males to monopolise groups of females (EPP)

If EPP High and if Individual males can Monopolise —> Polygyny



If Low EPP —> Monogamy

Spacial

Females clumped in space - Makes easier for males to monopolise - High EPP

More dispersed pops - Harder for males to monopolise - Low EPP

Temporal

High synchrony in sexual receptivity makes it harder for 1 male to mate with all females - Low EPP

Low synchrony males may be unable to maintain their territory for sufficient time to mate with all females

Moderate synchrony level required to maximise EPP - Allowing sequential access to females that are highly clumped and moderately synchronised -> High EPP

Grey Seal Example - Resources/habitat, Female distribution and Male behaviour

- Males play no role in terms of parental care (free from this)
- Females are sole care givers in seal species
- Grey and Weddel seals are both exactly alike however differences in mating calls - What differs?

Grey Seals

- Reasonably spatially clustered, females gathering around pools of water
- Easily patrolled by individual male, and monopolised by single male
- High potential for polygamy amongst grey seals (high EPP)
- Balance more in favour to males
- Less opp for females to express mate choice

Weddel Seals

- Female distribution -> Max groups of 3
- Locate in cracks near ice flows (in and out of water)
- Widely disturbed in space
- Impossible for males to control large groups of females
- Thus wedded seal must perform elaborate courtship song (mating call) to attract females to them
- Evolved courtship song - Attract females to them to gain mating opportunities

Spatial distribution driven by envi, determines mating pattern in envi for females and males

In Pinnipd species - Dominant males monopolise great number of females

Types of Mating Patterns - Why They Occur and Examples

Promiscuity - Why?

- Common in marine invertebrates and plant species
- Example: Shedding gametes into open ocean
- Example: Scramble comp in frogs and toads

Parental Care: Neither sex invests in offspring after fertilisation, not much selective pressure to choose mate - thus occurs largely indiscriminately

Dispersion: No predictable pattern in dispersion, solitary or unstable and temporary groupings

- Within unpredictable envi system: Temporally unpredictable and unstable -> Mate with whoever
- Not common in birds and mammals due to requirement for care of young until independence

Polygyny - Why?

Parental Care: High female investment in offspring and low male investment

Dispersion: Females aggregated in space and moderately aggregated in time -> High EPP

- Successful males monopolise females
- Intense male-male comp
- Many unsuccessful males - Adopt alternate strategies (sneaky etc.)

Resource-Defence Polygyny:

- Males defend areas of resource vital to females
- Territory quality rather than male quality important in female's decision to mate
- Generally correlation between male and territory quality - Fitter males can gain access to resources

Either: Uni-male or Multi-male:

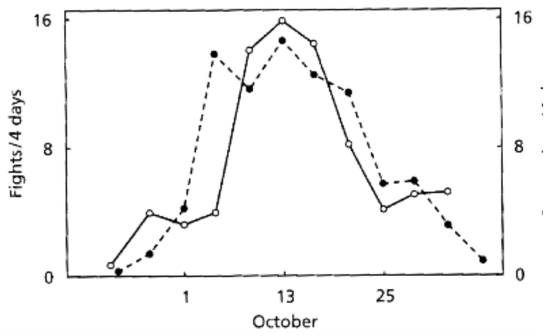
Uni-male (Alpha) e.g. Black prairie dogs

Multi-male (Alpha and beta) e.g. African lions - beta male helps to defend territory and has limited num of mating opps

Examples: Organe Rumped Honeyguides:
- Primary foods source for females is beeswax
- Beeswax essential food but has very patchy distribution
- Males with territories encompassing large numbers of beehives gain access to more females
- Mating success is high for territory owners

<u>Female Defence Polygyny - Why?</u>

- Tend to occur in EPP
- When females are naturally aggregated on site - Like breeding site
- Males able to gain 'possession' of several females directly & defend them against rivals
- Males enhance clustering by actively herding females
- More likely to occur if females are gregarious (living in flocks)
- Seen in many ungulates and pinnipeds



Example - Red Deer:
- Temporally determined - Conception period of females
- Red deer stags compete via display and physical conflict for available females (harem) during rut
- Solid line - Number of females
- Dashed line - Level of male-male comp
- Physical conflict for access to females, with intensity of aggressive interactions related to number of females which are sexually receptive

Example - Baboons gelada
- Breeding seasons in baboons much longer - So harems must be defended all year
- Females are spatially clustered in social system
- Live in resource-rich envi so males can provision themselves, allowing maintenance of territories and agonistic interactions
- Males able to both defend harem, feed themselves throughout year

- Whilst in deers, seasonal envi, poor foraging conditions, resources limited in autumn and winter, males can't maintain territories/defend females and and gaining resources for self - Break on male ability to keep hold of females

<u>Male Dominance Polygyny - Why?</u>

- Males aggregate, establish dominance relationships and hierarchy through displays and competitions
- Males do this among themselves
- Females chose males depending on their status within hierarchy
- Form depends largely on degree of synchrony of female sexual activity

Explosive Breeding - Temporary ponds forming
- All females enter breeding condition simultaneously and arrive at male aggregation together
- Males then display at ponds, females will choose based on relative dominance status

Occurs in Many frog and toad species (e.g. European frog - mating can occur on only 1 night)

Difference from Promiscuity?
- Female choice element
- Choosing based on male dominance status

Females not synchronised:
- Don't come into sex receptivity at same time - In terms of temporal organisation
- Few females (small pop) sexually available (even more of a limiting resource)
- Visit a male aggregation (lek) at any one time, leading to greater intense male-male comp for these females
- Through displays and aggression to establish relative dominance status
- Individuals in centre of lekking arena - Most dominant
- Females choosing males based on status

<u>Lek Polygyny - Why?</u>
- Males provide no parental care - Focus on display/aggression
- Due to dispersal of females in envi, males don't control resources or females
- Females choose mates solely on physical characteristics
- This leads to extreme epigamic (mate attraction) characteristics
- Cannot herd or monopolise females economically nor defend them
- Advertise and try to attract females to them

    e.g. Bright plumage, attention-grabbing behaviour

Parental Care: Males provide no care, females can raise offspring alone

Dispersion: Female range is not defendable & female groups unstable but at high density - unpredictable resources

<u>Polyandry - Why?</u>

Parental Care:
- Females monopolise access to males
- Male care for offspring beyond fertilisation high
- Female investment is low
- Frees female from care and gives her chance to increase reproductive output through multiple matings

Resources - Abundant:
- Females can max reproductive success by producing several clutches
- But only limited num of eggs can be laid in any 1 clutch (morpholigcally/physically constrained)
- Males are often left to incubate eggs and care for offspring while female seeks other mates
- Rare occurrence - When resources are available

Often have complete sex role reversal:
- Females are larger, more showy and defend territories containing males and nests
- Males become limiting resource and females compete for access to them
- Females sometimes kill eggs of another female to induce her male to copulate again (female-female intra-sexual comp)
- Polyandry rare: Rare for females to invest little in their offspring and males to invest highly

Example - Spotted Sandpiper

- Short duration of breeding, high abundance of resources
- Multiple clutches of egg leaving with diff male partner each time
- Simultaneous or Sequential polyandry
    - *Simultaneous - Each female holds large territory containing smaller nesting territories of 2 or more males who care for eggs and tend young*
    - *Sequential - Female mates with male, lays eggs, then terminates relationship with that male, leaving him to incubate eggs while she goes off to repeat this sequence with another male*

Example - Phalarope

- Sequential polyandry
- Females compete access to males directly (reverse of male dominance polygyny)
- Female dominance hierarchy established

Polygynandry

- Neither sex can secure power
- Some systems thought to be polyandrous may in fact be polygynandrous

- Results from inability of either sex to control access to mates through holding resources
- Leads to sexual conflict between sexes

Monogamy - Why?

Parental Care:
- Offspring require extensive investment
- More offspring survive if both sexes provide parental care
- = Mate Assistance Hypothesis

Resources:
- Are often limited such both parents are required to forage and provision offspring
- = Mate Assistance Hypothesis

Dispersion:
- Few females relative to males, or females very widely dispersed in space and/or time (females receptive for short time), often linked to resource dispersion
- Spatially and temporally
- Male - Best to guard any female comes along, wait till she becomes sexually receptive rather than going to search for another one
- Mate-Guarding Hypothesis

"Pitfall of Monogamy" - Both individuals entrapped, neither can exhibit control and place burden of parental care on other

Example - Raptors/Sea birds etc. - Common in Birds

- Both sex care for young
- Social monogamy
- Long development to fledging age
- In Sea Birds - Must fly far to find unpredictable resources (vary in location)
- In Raptors - Predatory, food source scarce and unpredictable in location

In mammals monogamy is rare:
- Uncertainty of paternity issue
- Both sexes usually cant care for young equally

Mate Assistance - Monogamy

- Spotless starlings
- Males given more testosterone -> More aggressive
- Resulted in less parental care and trying to copulate with more females
- Males with reduced testosterone - Gave more parental care
- Fledging success altered accordingly - Higher in males that give more parental care

Mate-Guarding - Monogamy

- Clown Shrimp
- Female receptive for short time (when shedding exoskeleton) and widely dispersed, and temporal receptivity
- Therefore finding receptive females difficult
- Males guard mate until they become sexually responsive
- Females - Sedentary
- Males - Move around looking for females and once found, guard till receptive

Female-Enforced - Monogamy

- Burying beetles
- Females will lay eggs, provide a lot of care
- Clean and regurgitate food for them
- Both female and male work together - Male & female bury carrion for larvae to feed on.
- Males still try to increase reproductive success by sneak off
- Release pheromones to attract more females
- When males do this, females will prevent male from doing this

Sexual conflict

Preferred Mating Patterns:

Example - Dunnock Mating Patterns