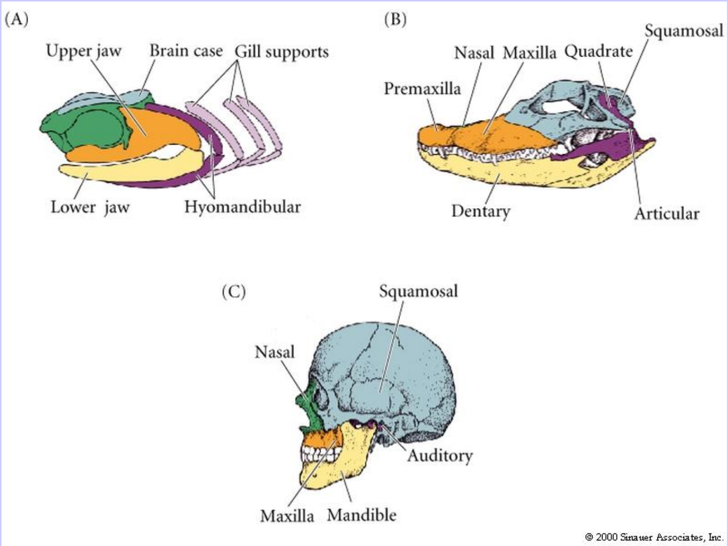
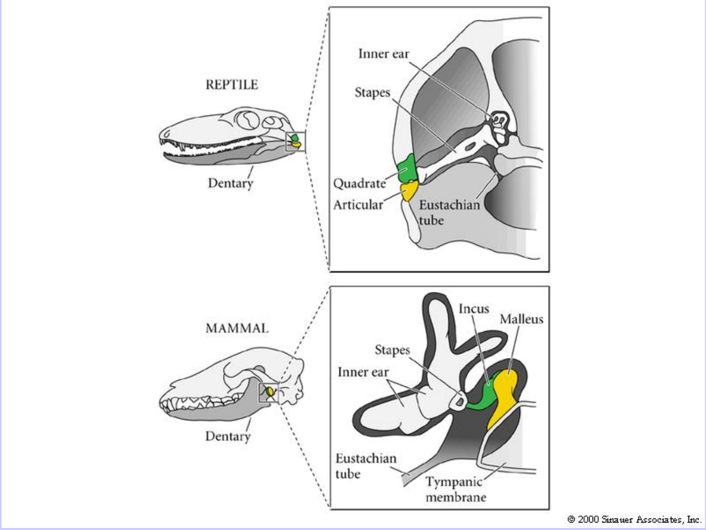
B. Duplication and Divergence

- Genes
  - Hox genes: multiple; duplications in vertebrates
  - Myo D genes: family for different stages of muscle
  - Globin genes: expressed at different times with different oxygen affinities
- Freeing of constraints allows divergence for new function

C. Co-option

- jaw to mammalian ear
  - jawless fish form jaw from first gill arch
  - then next gill forms hyomandibular bone to connect skull to jaw
  - this also transmits sound to ear and becomes part of middle ear in terrestrial vertebrates
- the quadrate and articular bones are not needed in mammals so become also part of middle and inner ear





Co-option of a Structural Gene Product

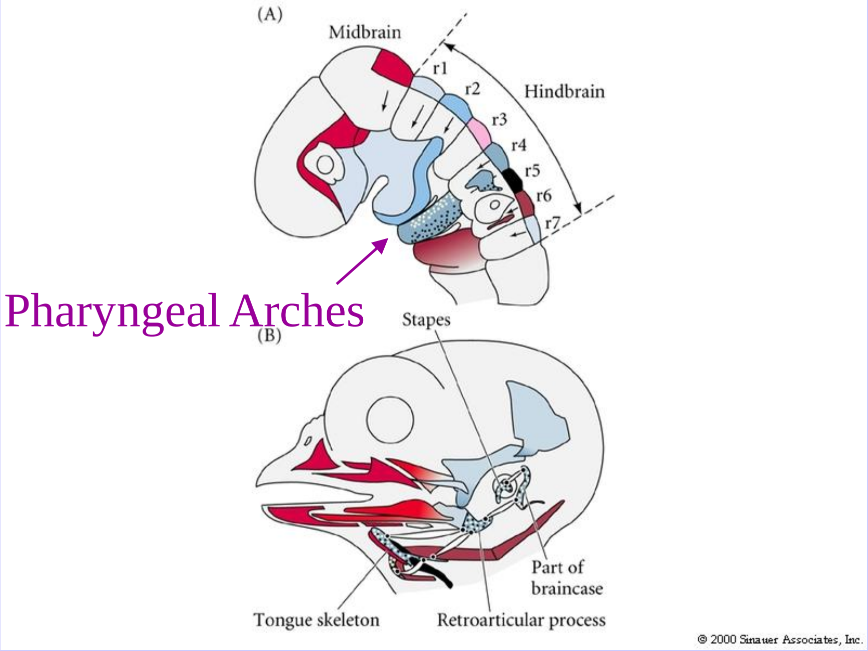
- lens crystallins
  - small soluble proteins at very high concentrations
  - some of them are identical to various *metabolic enzymes* in vertebrates and invertebrates
- explanation: what is a good lens protein?
  - high solubility and no aggregation
  - so use what you have and concentrate it
  - economy

Correlation

- Coordination when one part changes and induces a second to follow
  - one (or more than one) module changes
    - *morphological*: to integrate anatomical change
    - *biochemical*: as in ligand-receptor interactions

Morphological Correlation

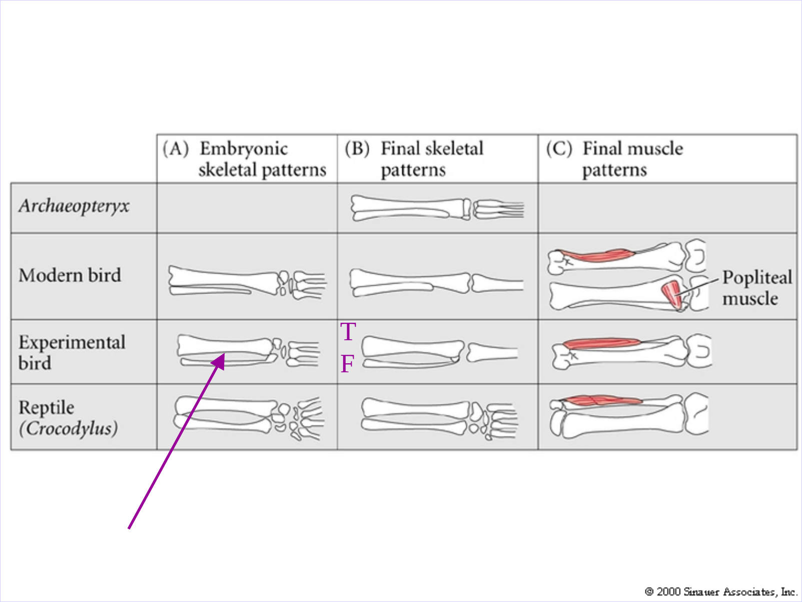
- Neural crest → pharyngeal arches and facial bone and muscle
- Neural crest of *each* rhombomere (1,2,4,6)→ each particular set of bones and muscle connecting them (one module)
- Facilitates coordination of changes in each module



chick N.C. cranial structures

Experiment to Change Module

- Gold foil in early chick hindlimb to separate regions producing tibia and fibula
  - tibia is shorter, curved fibula connects to tibia at both ends
    - bones look like reptilian pattern
  - *but* muscle also changes to reptilian (coordinated change)

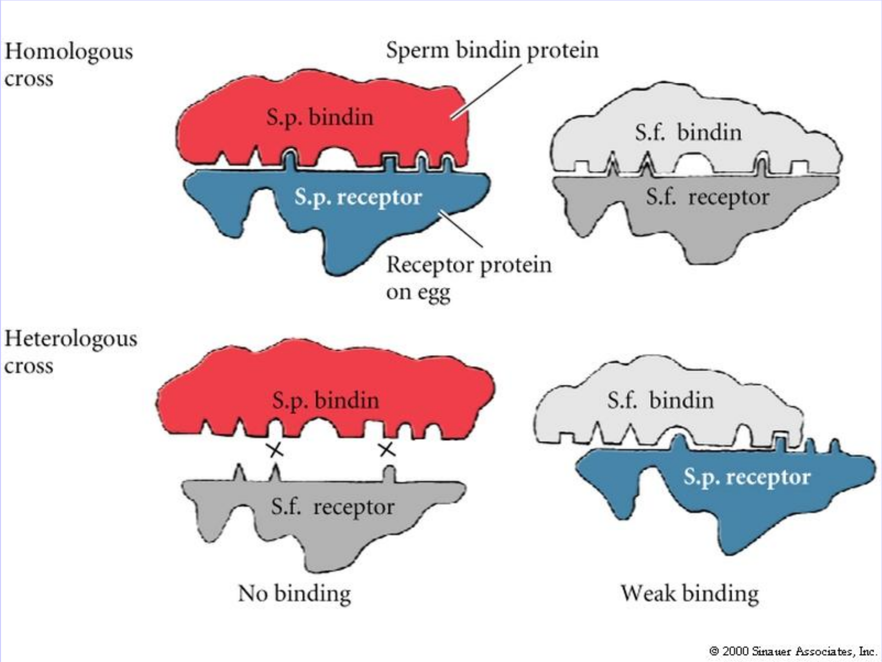


How Will Nerves and Blood Vessels Respond?

- Fine grain patterning
- Use selection based on functional properties
  - neurons dies unless in the right region so need not specify all outgrowth in detail
  - similar with blood vessels
- Generates complexity (given environmental and physiological variability)
  - no need to have exact patterns programmed if for example a new limb anatomy is made

Biochemical Co-evolution of Bindin and Its Receptor

- Ligands and receptors have to "fit"
- Bindin and bindin receptors can co-evolve and contribute to speciation
  - weak binding through some sites allows enough interaction to lead to selection for other sites
- Co-evolve



Constraints

What Are Developmental (Evolutionary) Constraints?

- Not all phenotypes are equally possible because of constraints of structures already evolved
  - so some paths of evolution are more likely than others
- Types
  - A. physical
  - B. morphogenetic
  - C. phyletic

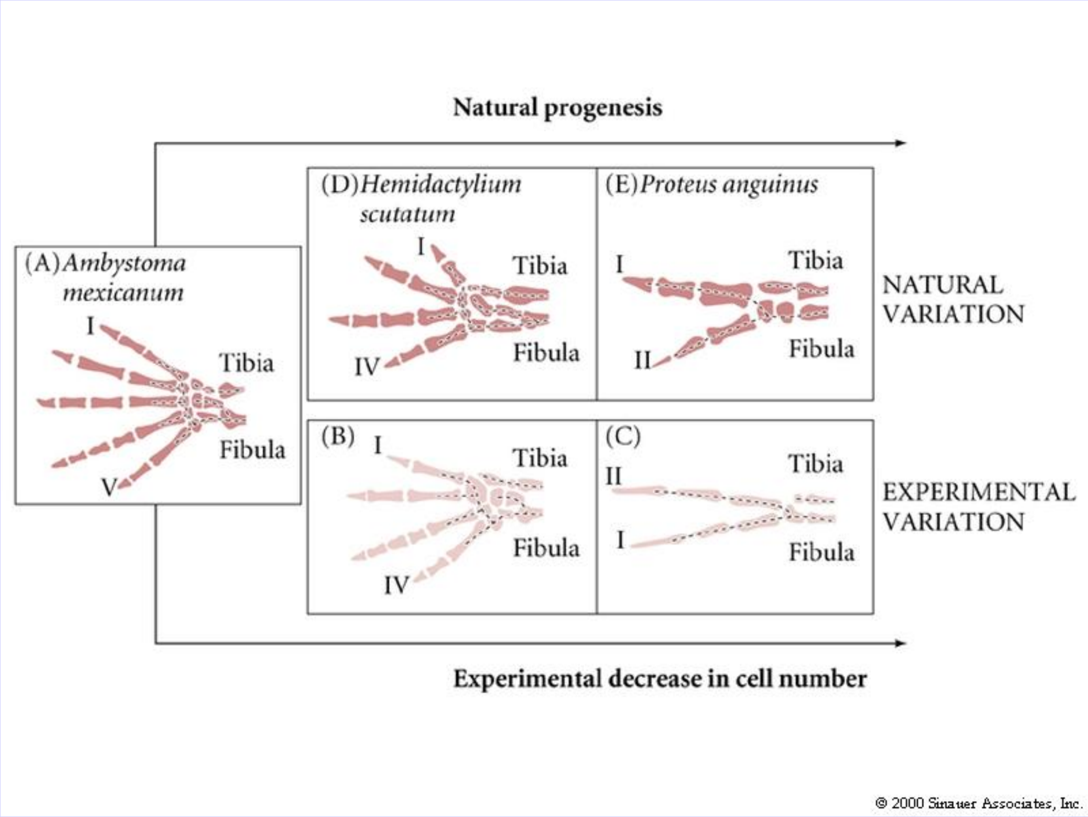
A. Physical Constraints

- Laws of physics
  - hydrodynamics, diffusion, physical support
- Limits types of living organisms in earth environment
  - need to circulate fluid, keep weight from crushing organism
  - fundamental cellular processes underlying morphogenesis have limits

B. Morphogenetic Constraints

- Rules of construction may limit
  - don’t see autopods with short middle digits
  - don’t see long limbs with humeri in series, only longer humeri
- Reaction diffusion models can’t generate some patterns, favor others
- Expt: if you limit cell division
  - fewer cells in bud
  - some structures disappear in predictable order mimicking pattern of organisms with smaller limb buds

Cell Number and Digit Number



Real salamanders

Colchicine treatment of *Ambystoma*

C. Phyletic Constraints

- Historical limts
- Once a structure is invented it may be needed for one stage but not another
  - e.g. notochord dispensed with in adult vertebrates
  - e.g. pronephric kidney no adult function but makes ureteric bud inducing the real kidney
  - both must be retained (for neural or kidney induction)
- Likewise, genes used in more than one stage or module become more constrained
  - change may affect multiple modules
  - like hox genes

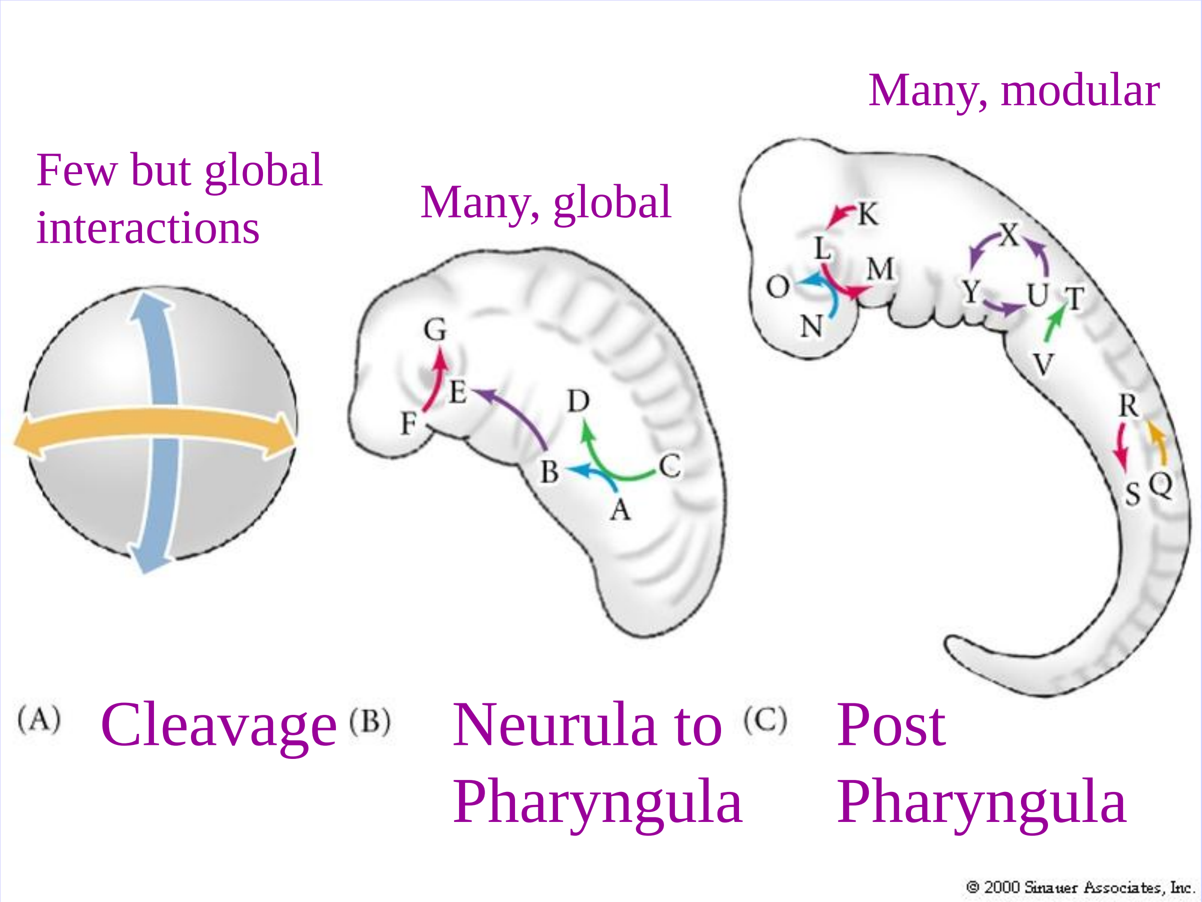
Phyletic Constraints

- Early and late development are more open to change than middle
  - Early cytoplasmic changes in mollusc embryos that make many different types of larvae later still form similar molluscan adults
  - Early alterations in some sea urchins species skip larval stages but still become similar adult sea urchins
  - So early devo is not very constrained

Phyletic Constraints

- Many different late adult adaptations distinguish vertebrates bodies
  - middle of devo (like neurula less variable)
  - why?

Pharyngula Bottleneck



Pharyngula is the *phylotypic* stage (characterizes phylum)

Bottleneck Hypothesis

- Early development: few inductions
  - But axis formation, gastrulation
- Late development: isolated modules of inductions
  - Alterations tolerated because independence
- Middle has global and multiple inductions
  - mis-induction is serious and globally disrupts organization (so more constrained)
  - these constraints lead to the phylum type after which, for example, a vertebrate can only be a vertebrate

"Old Evo"

- Modern Synthesis (1940s)
  - merged populations genetics with evolution
  - diversity from random mutations selected by environment for highest fitness
  - genetically inherited
  - isolation of populations with different accumulated mutations produced species
  - macro (between species) and micro-evolution (within species) same explanations
  - population genetics explains all

“Old Evo”

- Population genetics
  - gradual evolutionary change
  - accumulated small genetic changes result in large changes in species
  - genetic change produces one (or no) corresponding change in phenotype
  - predict very different organisms should have very different genotypes
  - emphasizes differences in adults leading to differential reproductive success

New Ideas

- But
  - periods of stability interrupted by rapid change
  - minor genetic changes in different species (like chimps and humans)
  - regulatory gene changes result in major alterations of phenotype
  - same gene can produce different phenotypes in different genetic background
  - conserved homologous genes include transcription factors and signaling pathway genes
  - important changes occur in embryos not adults

“Evo-Devo”

- So need both population and developmental genetics approaches
- Need to know more about
  - regulatory genes in populations
  - evolution of signaling pathways
  - implications for body plan, morphology, form, speciation