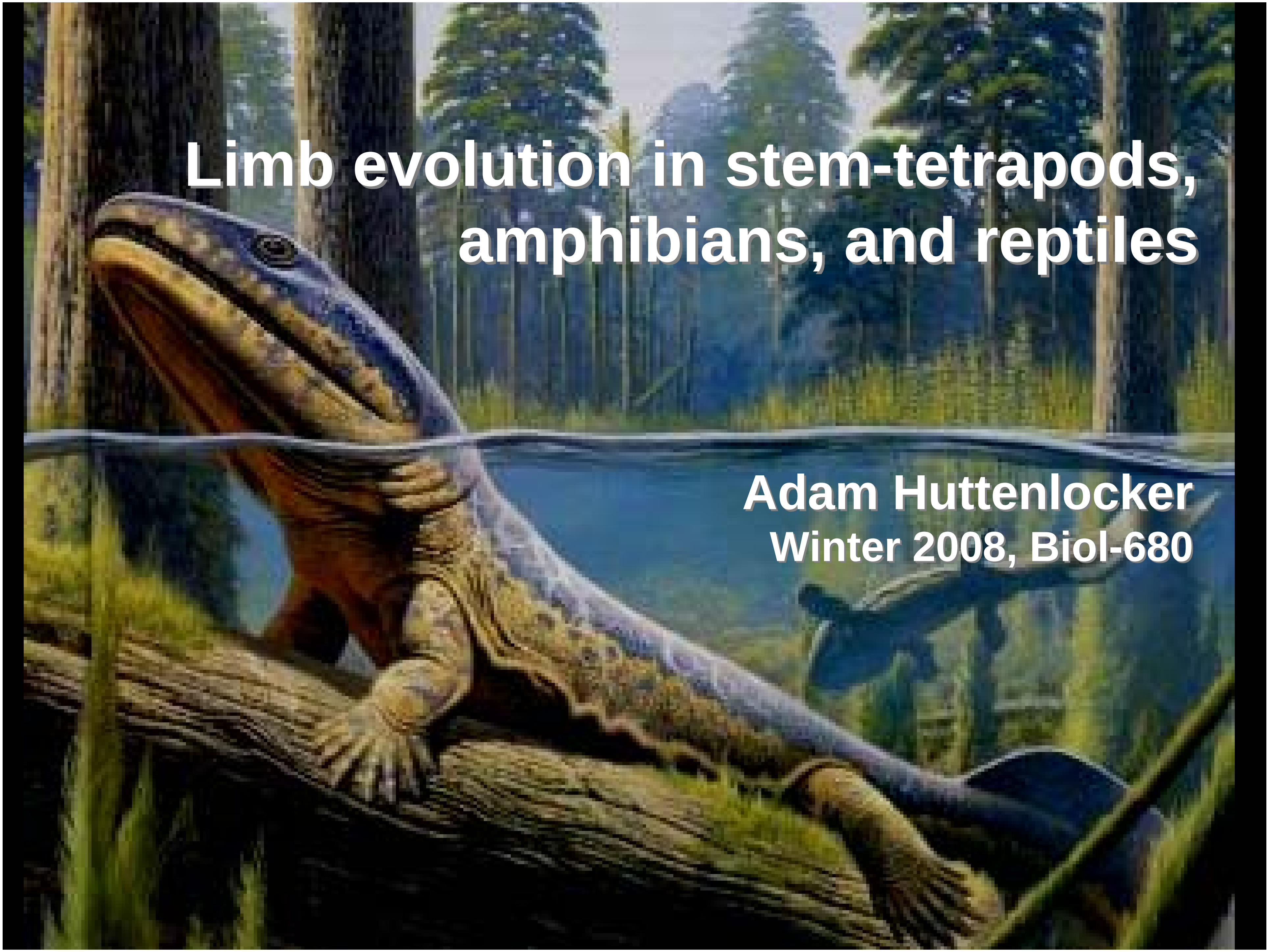


Limb evolution in stem-tetrapods, amphibians, and reptiles

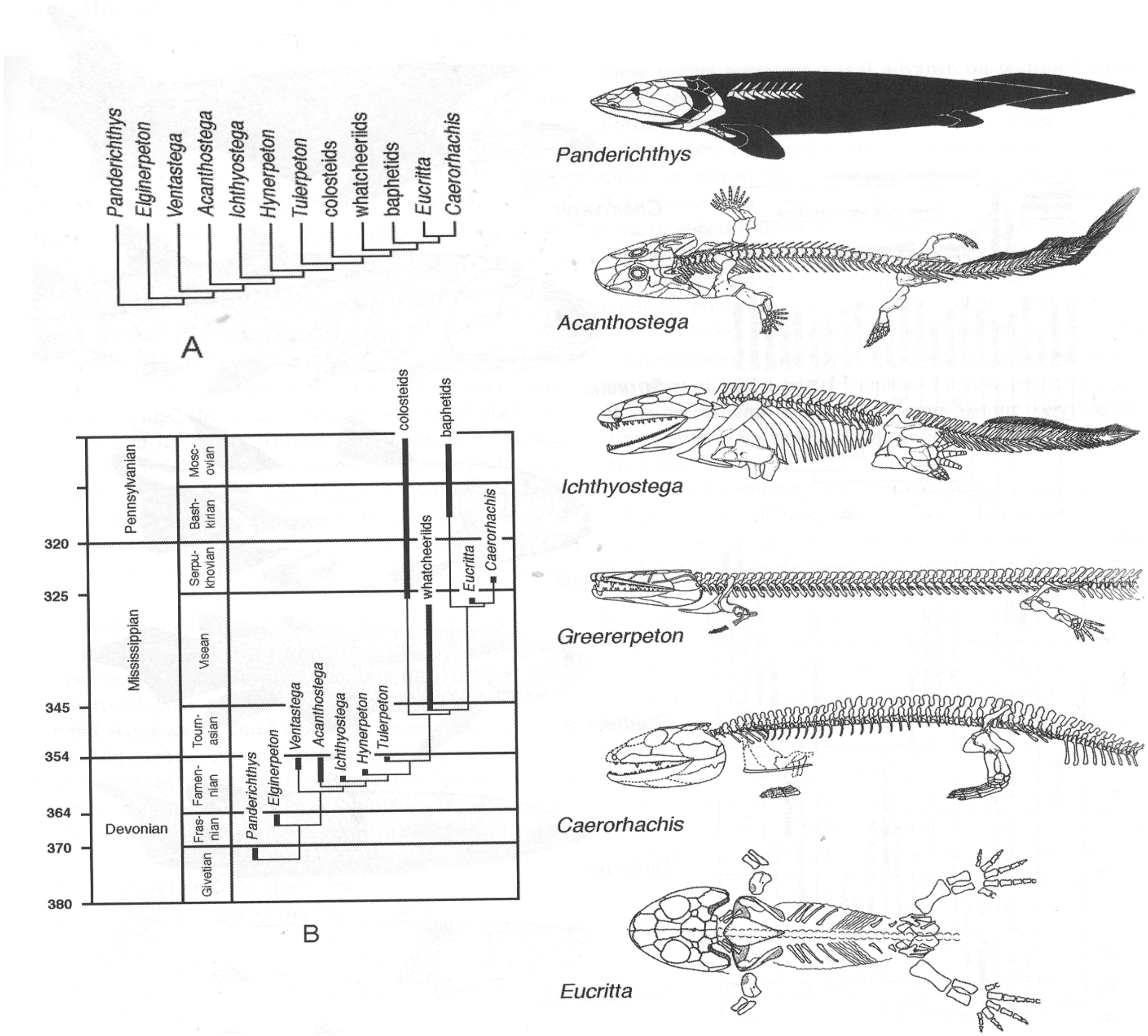
Adam Huttenlocker

Winter 2008, Biol-680

Chapter 13: Evolution of the Appendicular Skeleton of 'Amphibians'

R. L. Carroll & R. B. Holmes

1. What is meant by 'amphibians'?



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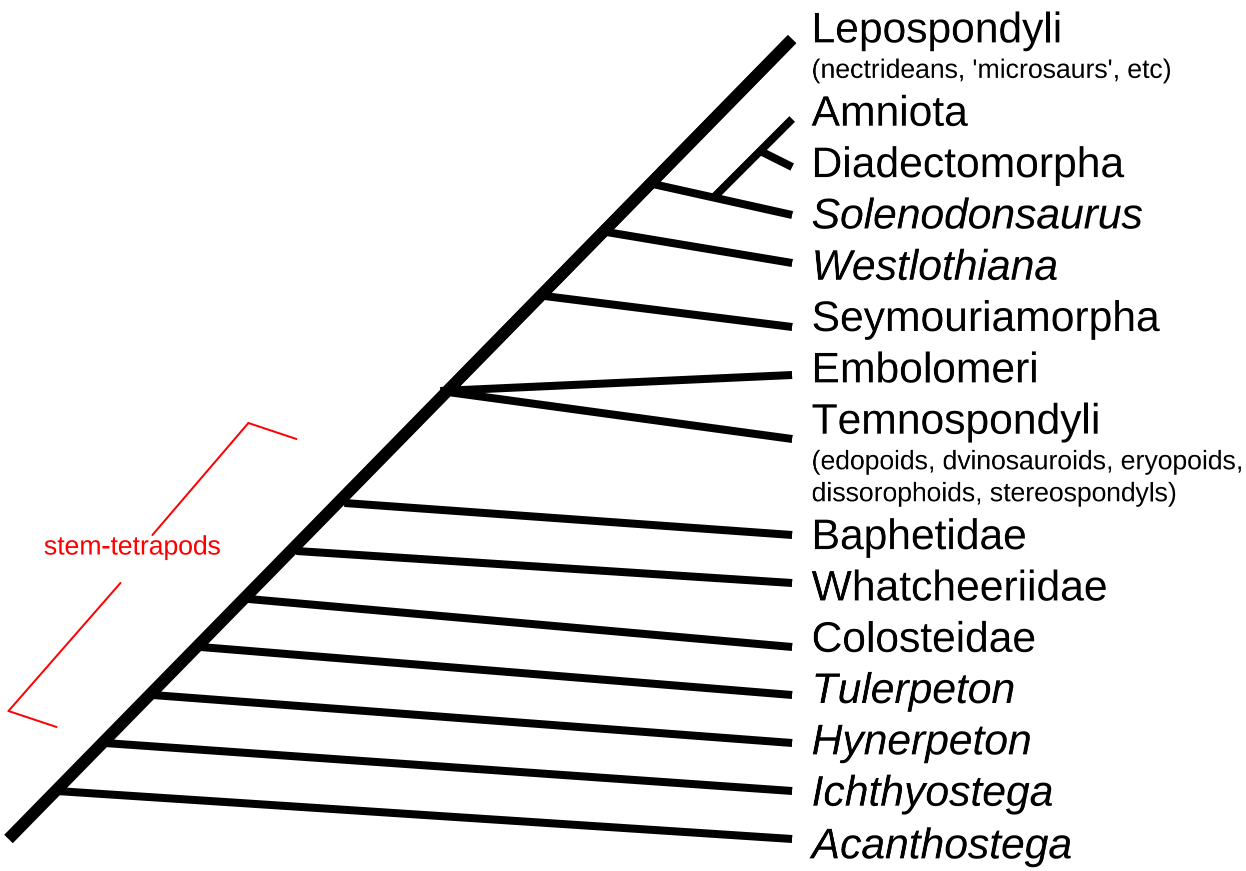
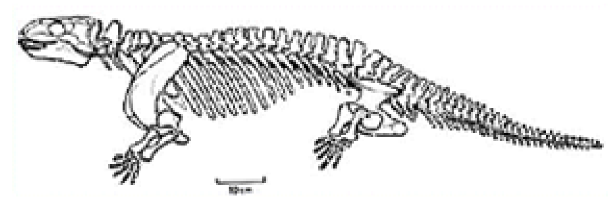
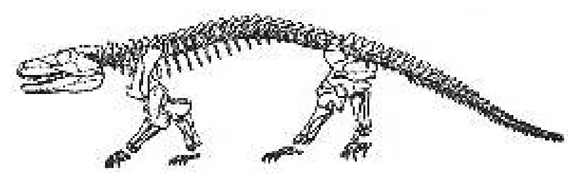
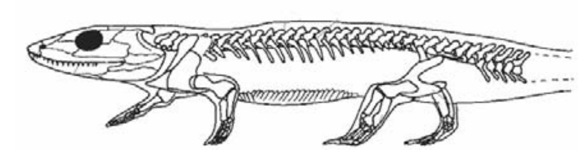




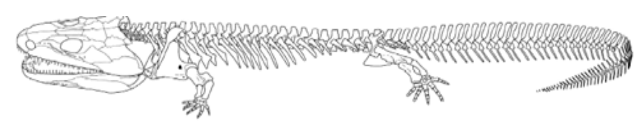
Diadectes (diadectomorpha)



Seymouria (seymouriamorph)



Dendrerpeton (temnospondyl)



Ossinodus (whatcheeriid)

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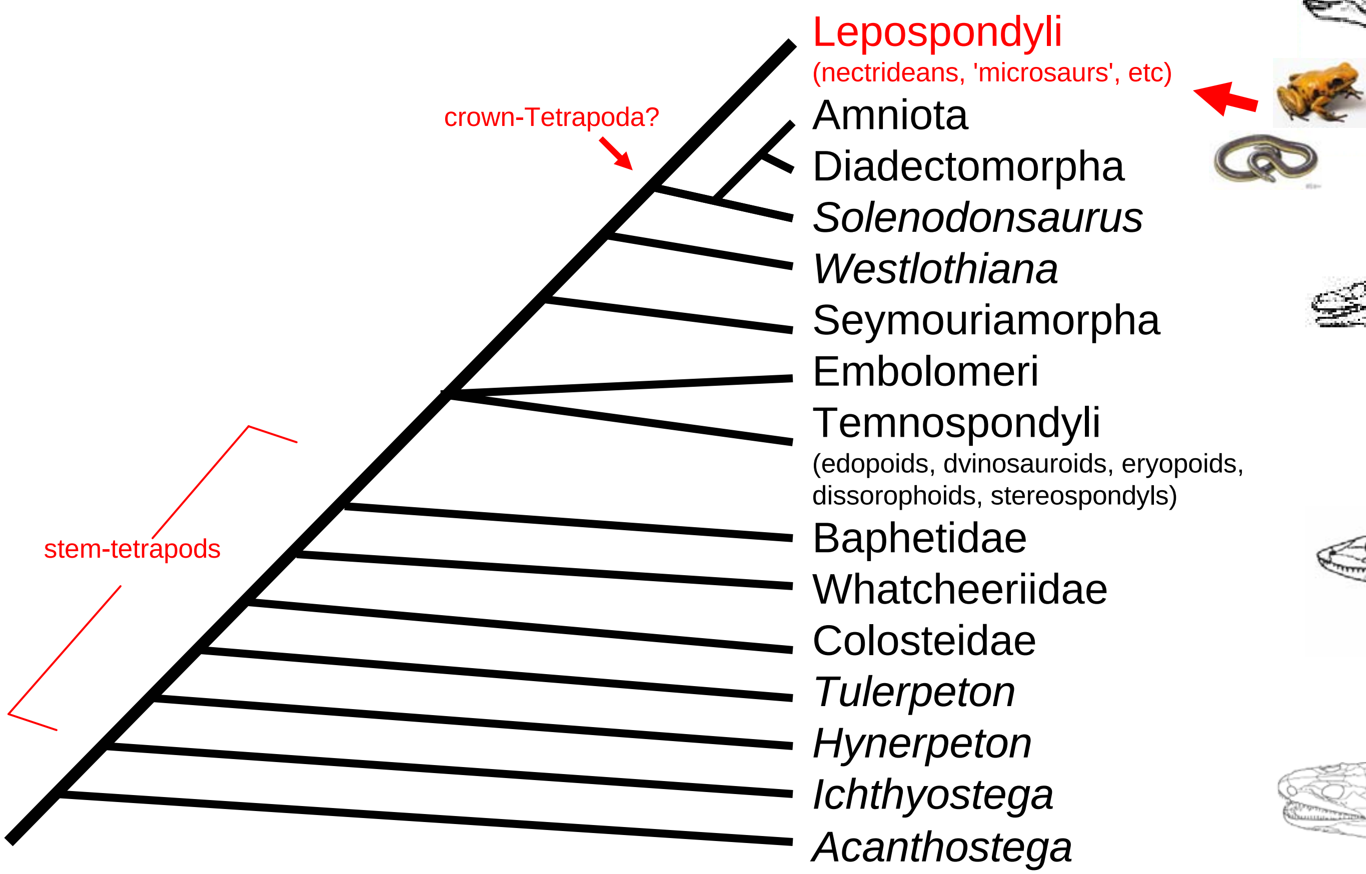

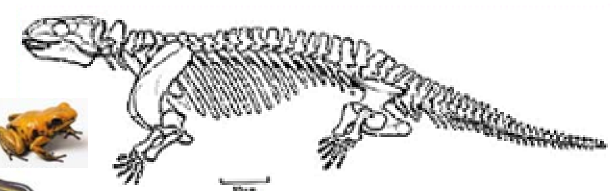

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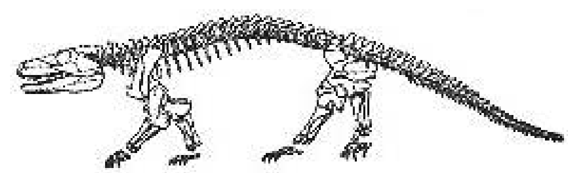

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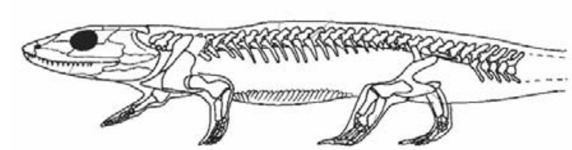

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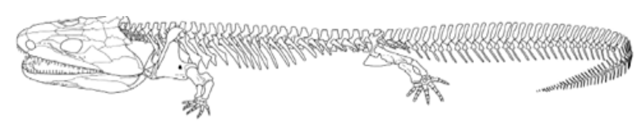

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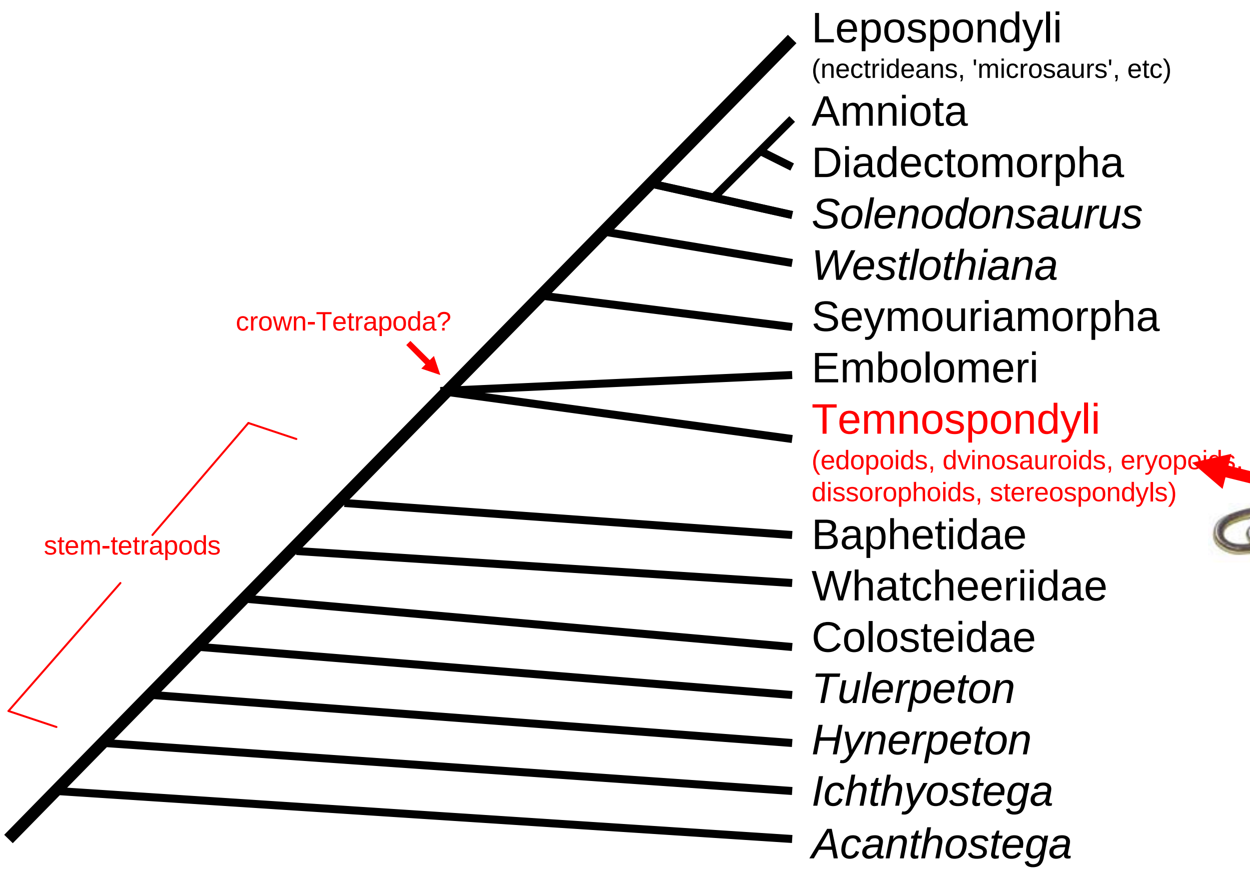

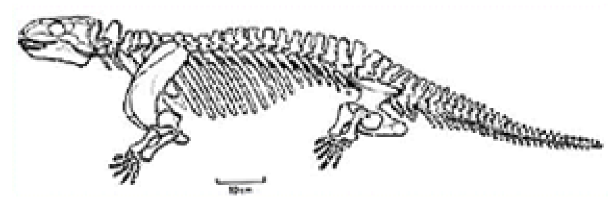

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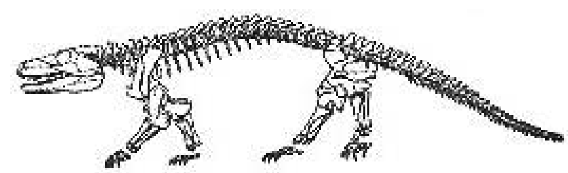

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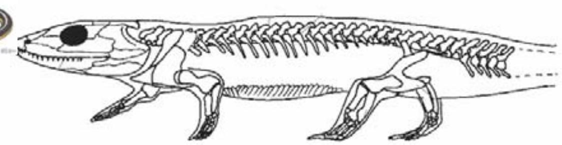

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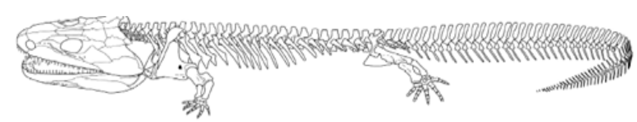

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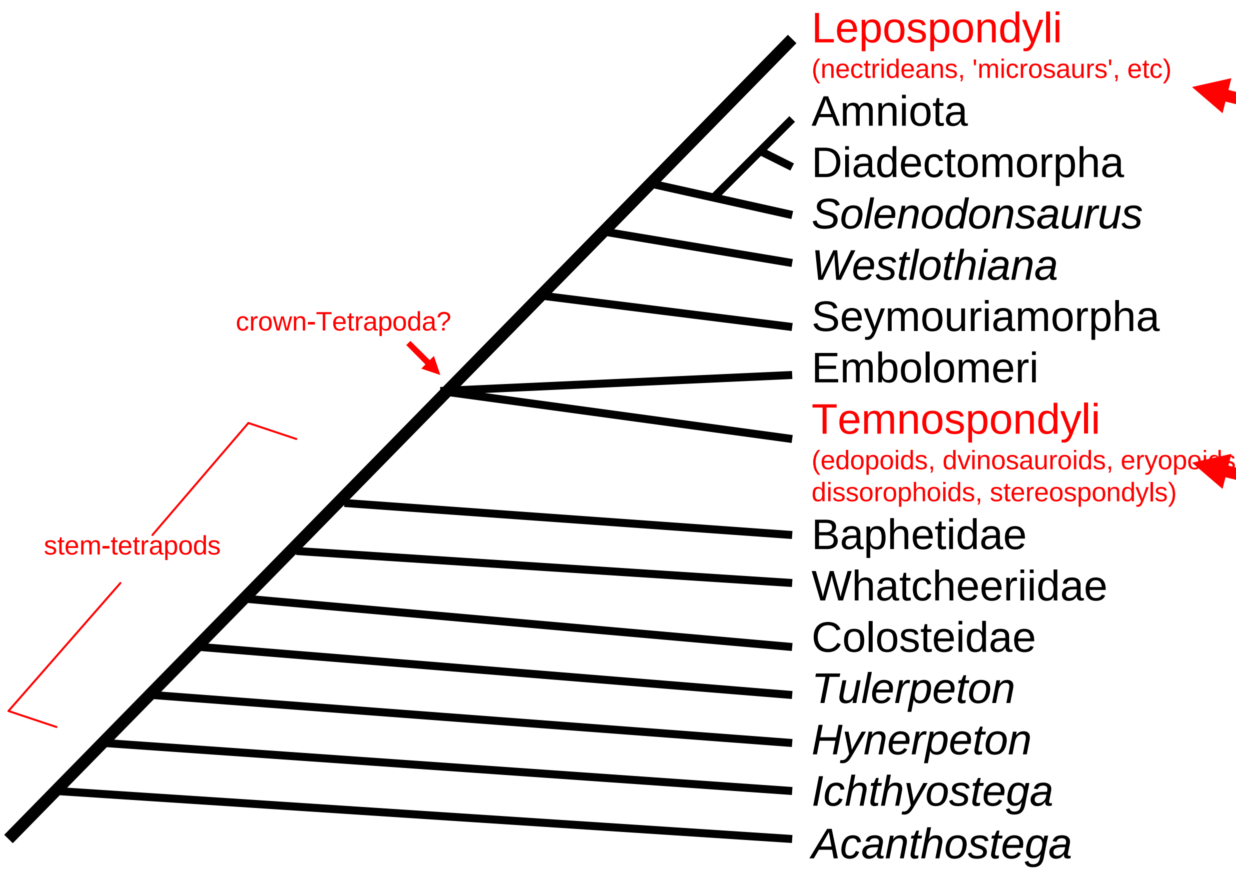

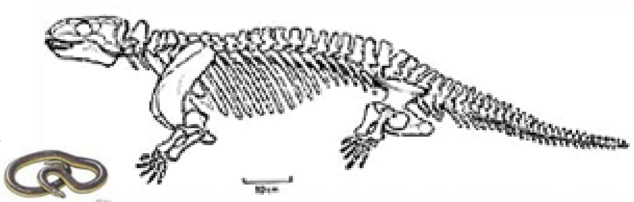

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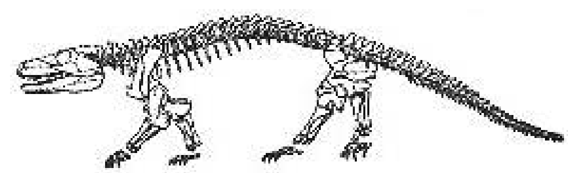

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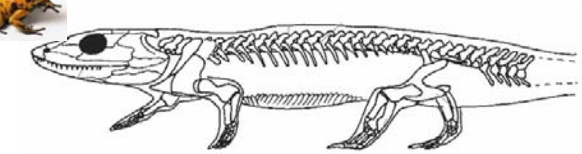

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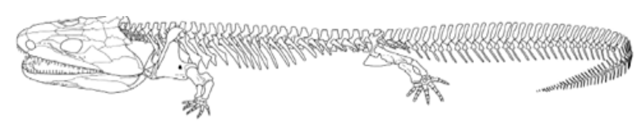

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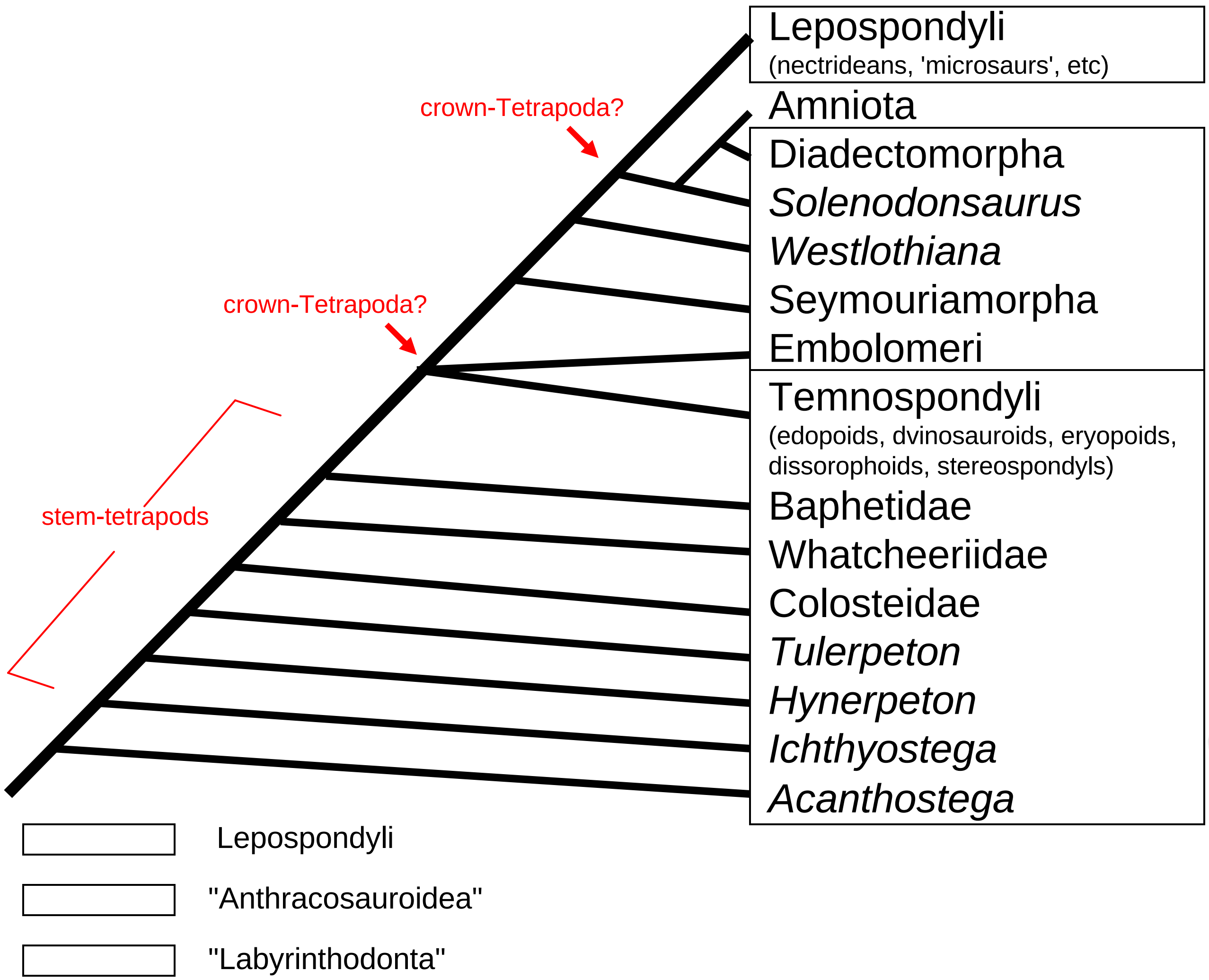

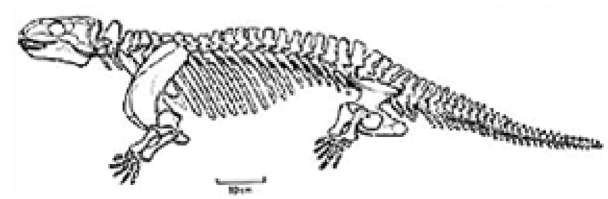

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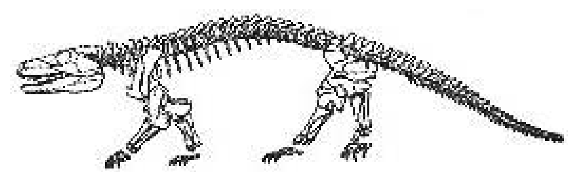

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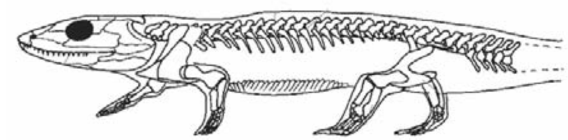

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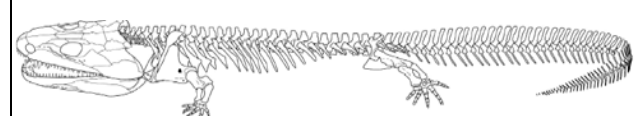
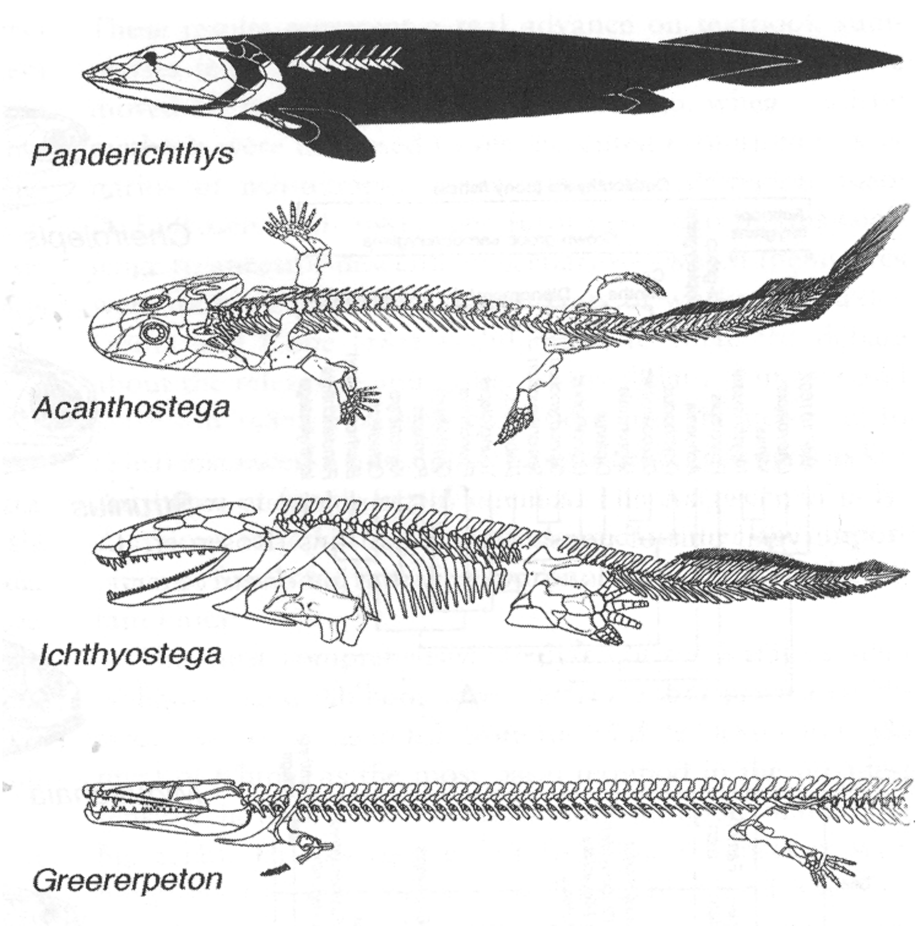


Ossinodus (whatcheeriid)

2. Limbs and girdles of stem-tetrapods



- Major trends discussed by Andrews & Westoll (1970) and more recently by Clack (1996, 2002)

- Early stem-tetrapods (Stegocephalia) characterized by reduction of dermal elements; pelvic girdle anchored to vertebral column; zeugopod and autopod distinct, with wrist bones and clear "ankle" bones (tibiale, interm, fibulare); distinct digits with loss of dermal fin rays

- Examples include: *Acanthostega*, *Ichthyostega*, *Hynerpeton*, & *Tulerpeton*

2. Limbs and girdles of stem-tetrapods

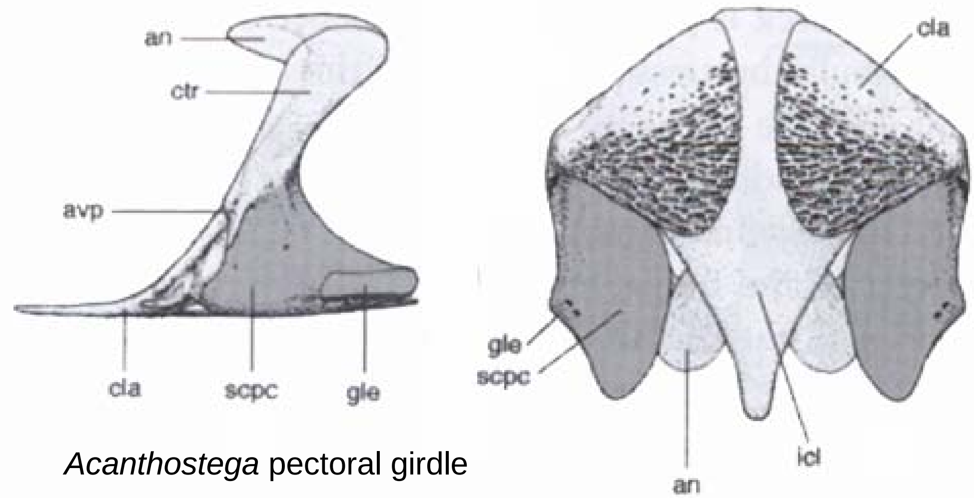
Trends in early limb girdle structure:

- Parallel changes in girdle ossification (i.e., ossification centers)

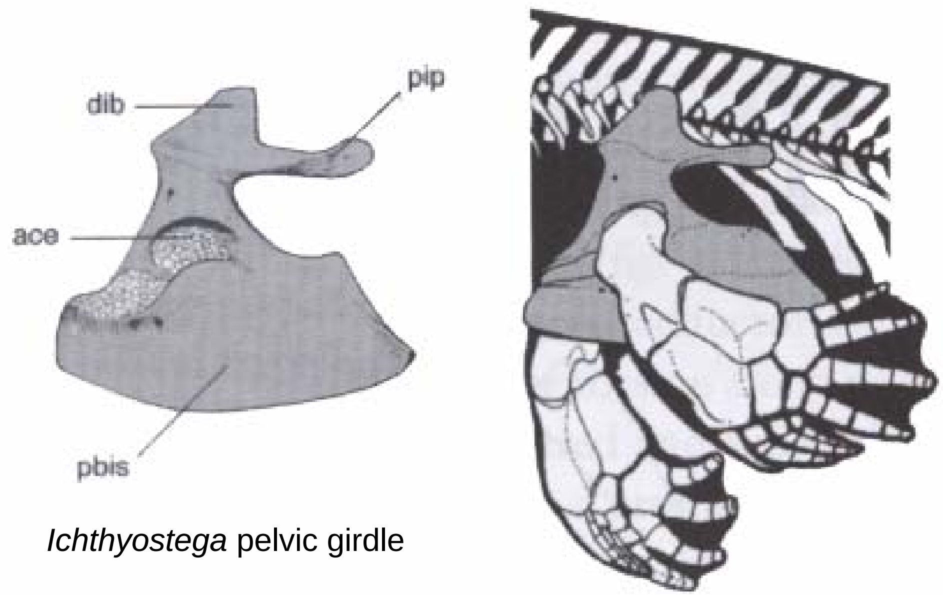
- •Expansion of endochondral "core" / reduction of dermal components

- •Glenoid is "strap-like"

- •Pelvic girdle attaches to vertebral column



Acanthostega pectoral girdle



Ichthyostega pelvic girdle

2. Limbs and girdles of stem-tetrapods

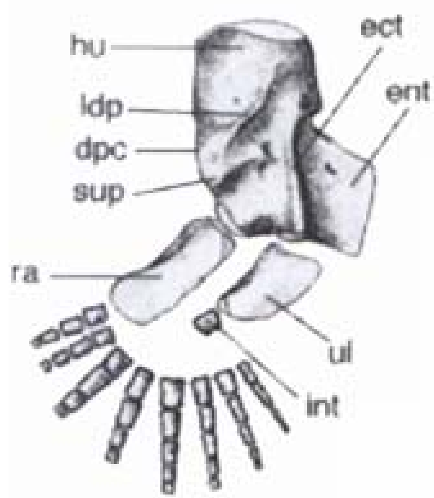
Fore- and hindlimbs of early stem-tetrapods:

•Humerus "L-shaped"

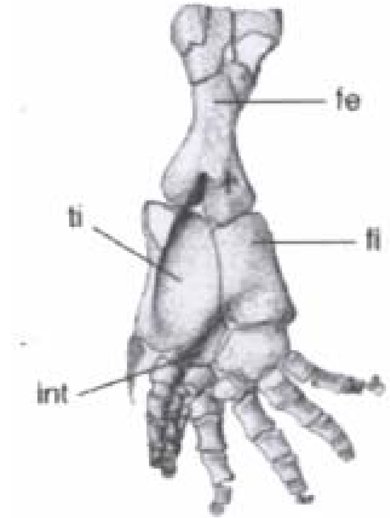
•Ulna forms a distinct olecranon process (e.g., Ichthyostega)

•Hindlimb elements become progressively longer and cylindrical in cross-section

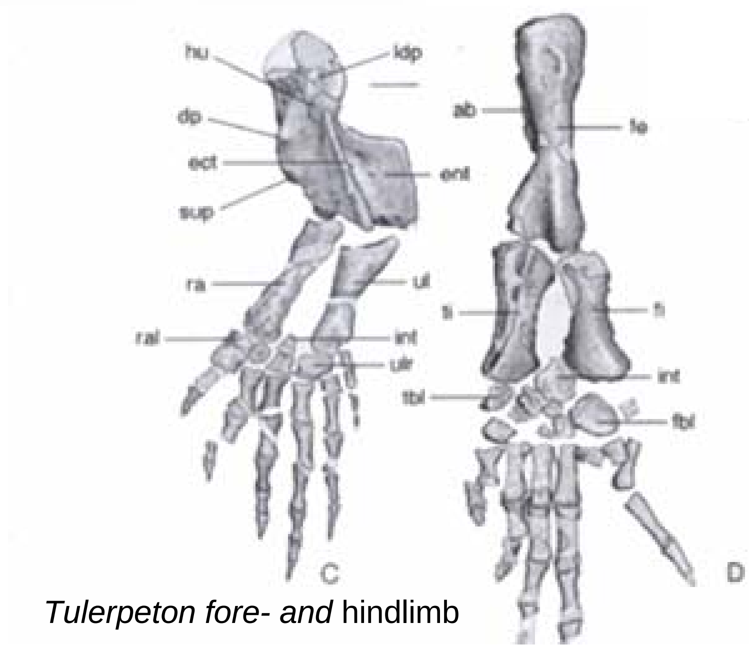
•Podium bears distinct digits (8 or less) and absence of dermal fin rays



Acanthostega forelimb

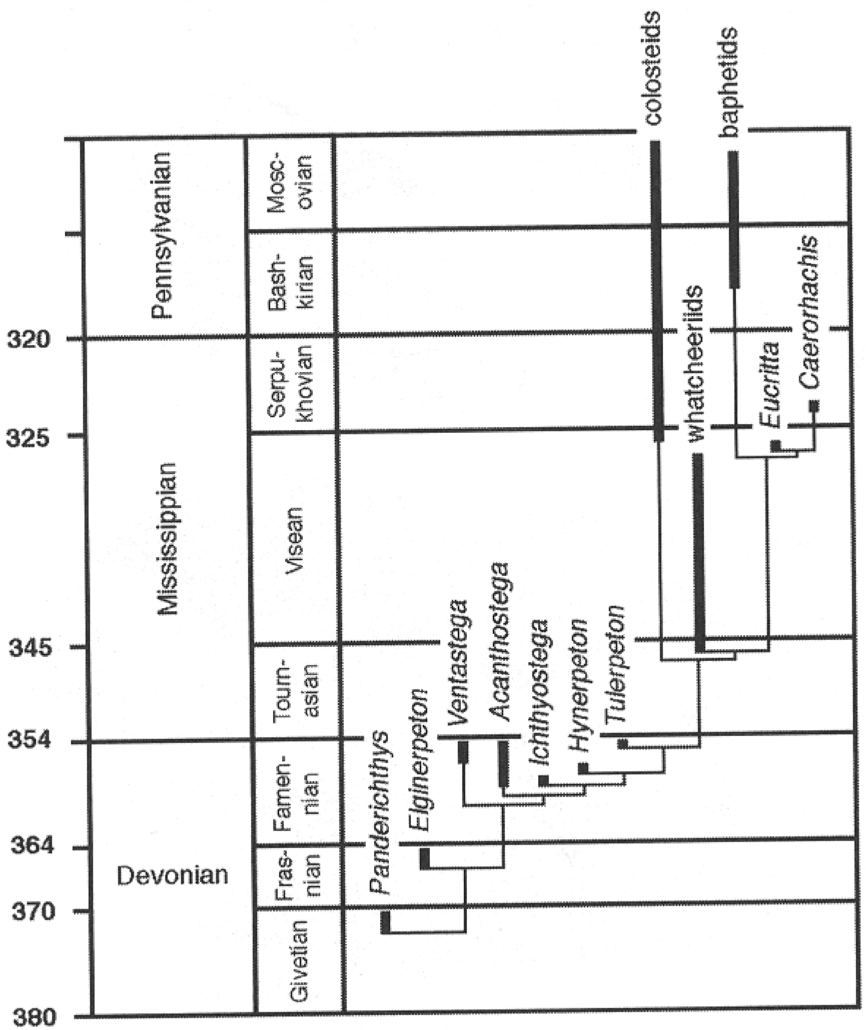


Ichthyostega hindlimb



Tulerpeton fore- and hindlimb

3. Carboniferous-Jurassic 'labyrinthodonts'

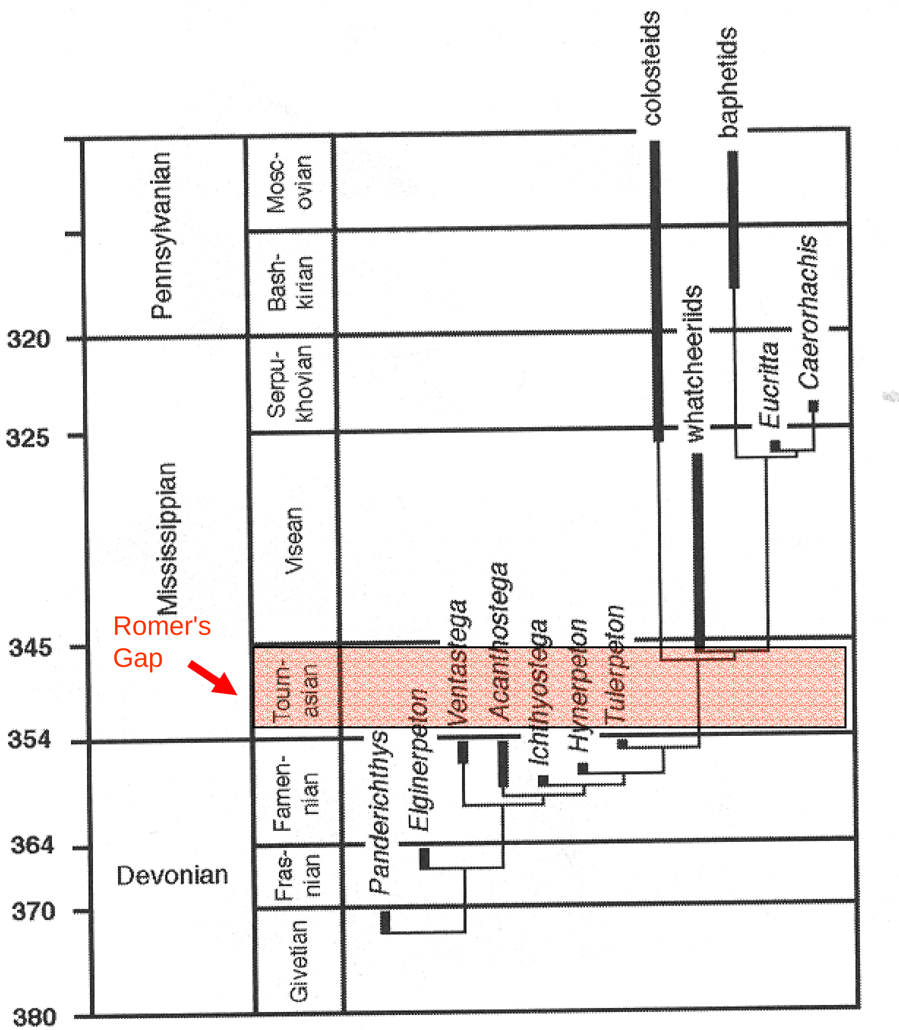


Later 'labyrinthodonts' (general):

•Gap between Upper Devonian & Visean (Mississippian) records (Tournasian or "Romer's" Gap)

•Intermediate forms abundant by end-Visean, including: Colosteidae, Whatcheeriidae, Baphetidae, Crassigyrinidae, and *Caerorhachis*

3. Carboniferous-Jurassic 'labyrinthodonts'



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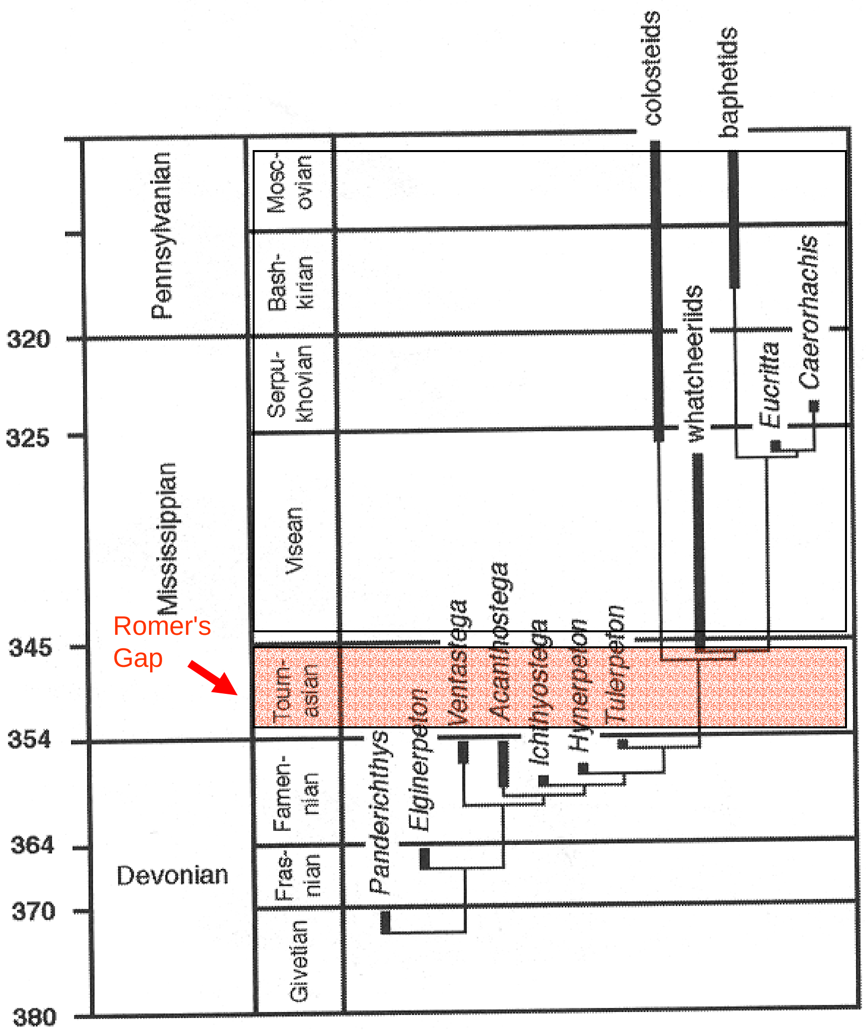

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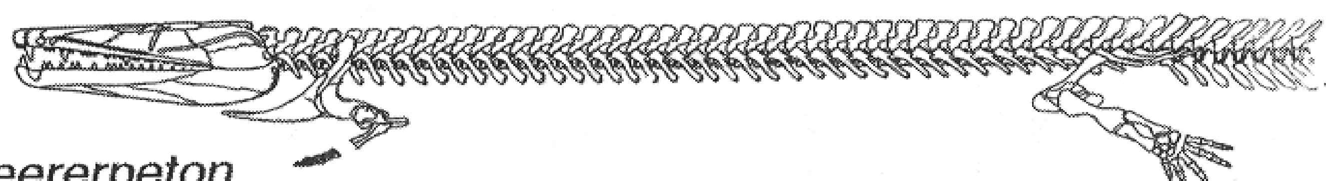
3. Carboniferous-Jurassic 'labyrinthodonts'

Colosteidae (e.g., *Colosteus*, *Greererpeton*)

• Pectoral limb & girdle: loss of anocleithrum; scapulocoracoid expanded; reduction of manual digits to five (characteristic of "higher" tetrapods); manual phalangeal formula 2-3-3-4-3

• Pelvic limb & girdle: distinct pubis, ischium, and ilium; pentadactyly; pedal phalangeal formula 2-2-3-4-2+



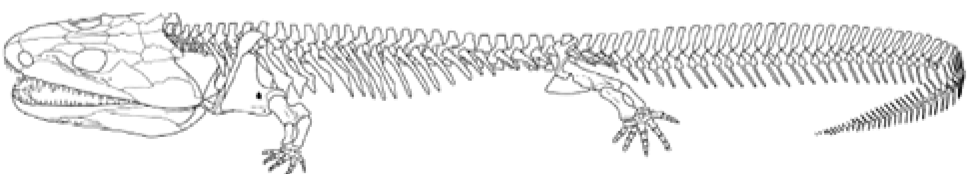
Greererpeton

3. Carboniferous-Jurassic 'labyrinthodonts'

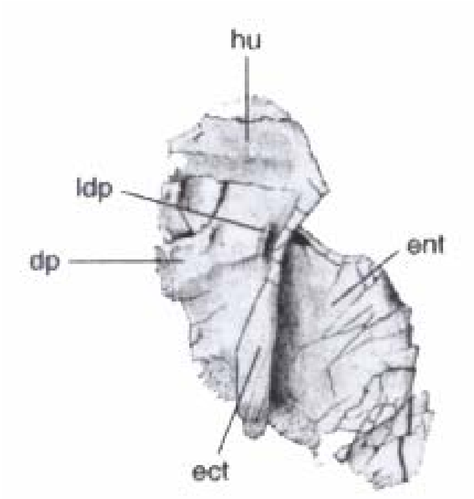
Whatcheeriidae (e.g., *Whatcheeria*, *Ossinodus*)

• Pectoral limb & girdle: interclavicle retains long stem; enlarged humerus with more torsion

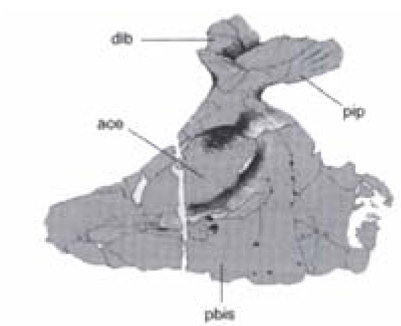
• Pelvic limb & girdle: distinct pubis, ischium, and ilium (as in colosteids); robust hindlimb elements



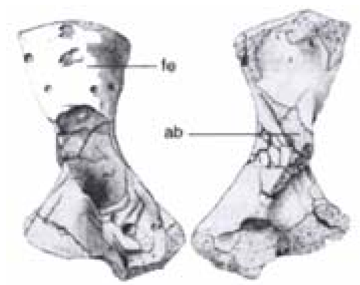
Ossinodus (whatcheeriid)



Whatcheeria humerus



Whatcheeria pelvic girdle



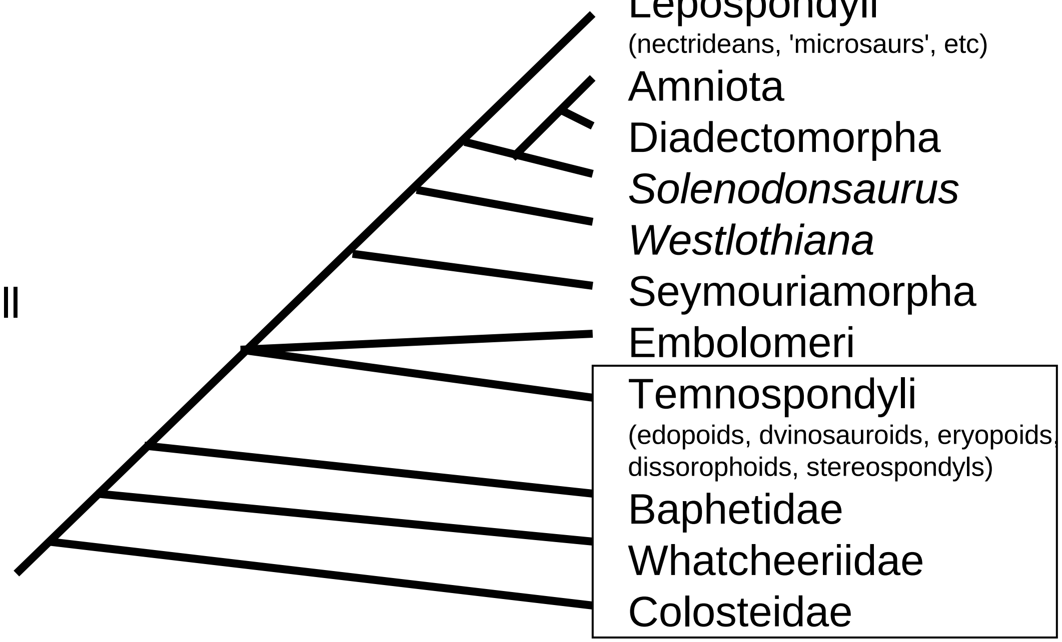
Whatcheeria femur

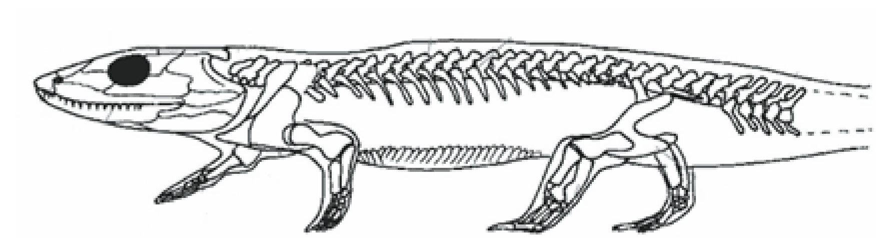
3. Carboniferous-Jurassic 'labyrinthodonts'

Temnospondyli (e.g., *Denderpeton*, *Balanerpeton, Eryops*)

- General characteristics:
  - "firm attachment of cheek to skull table"
  - Enlargement of interpterygoid vacuities
  - Retain contact between postparietal & supratemporal
  - Intercentrum usually dominant central element of vertebra

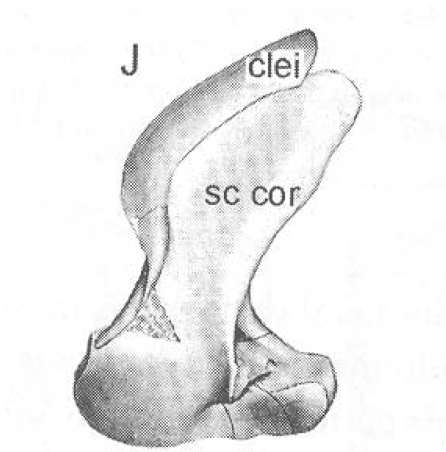
- 2 major radiations:
  - Basal temnospondyl radiation
  - Stereospondyl radiation



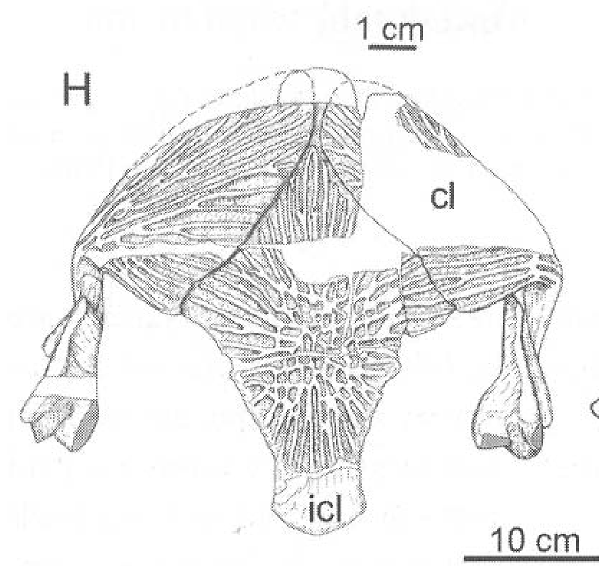


Dendrerpeton (temnospondyl)

3. Carboniferous-Jurassic 'labyrinthodonts'



pectoral girdle of dissorophoid, *Dissorophus*

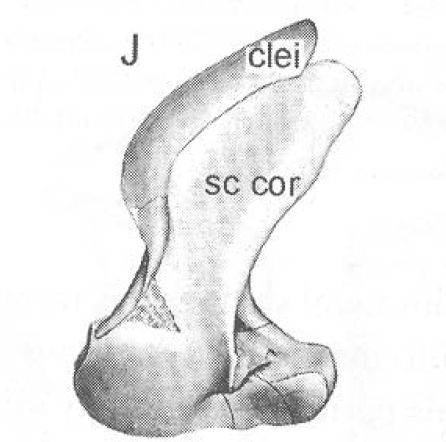


pectoral girdle of stereospondyl *Siderops* (ventral view)

Temnospondyl pectoral & pelvic girdles:

- pectoral girdle directly behind skull w/ interclavicle projecting between jaws
- interclavicle forms broad, ventral plate, but posterior stem reduced
- dorsal cleithrum spoon-shaped plate that forms much of dorsal margin of girdle
- fused scapulocoracoid, although highly reduced in derived stereospondyls where coracoid may be poorly ossified

3. Carboniferous-Jurassic 'labyrinthodonts'



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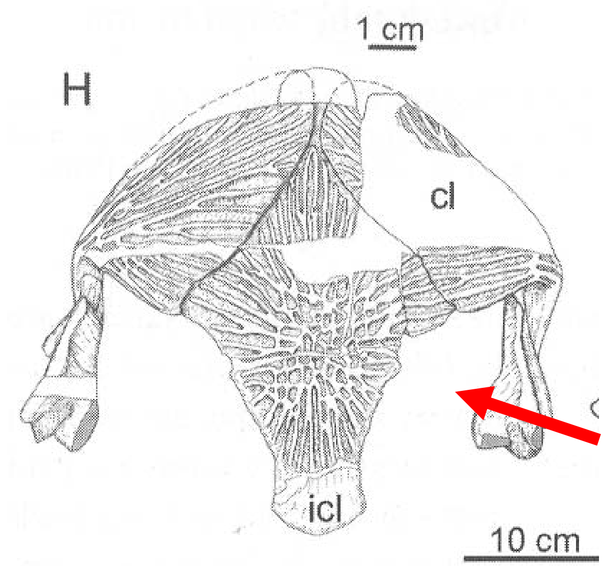

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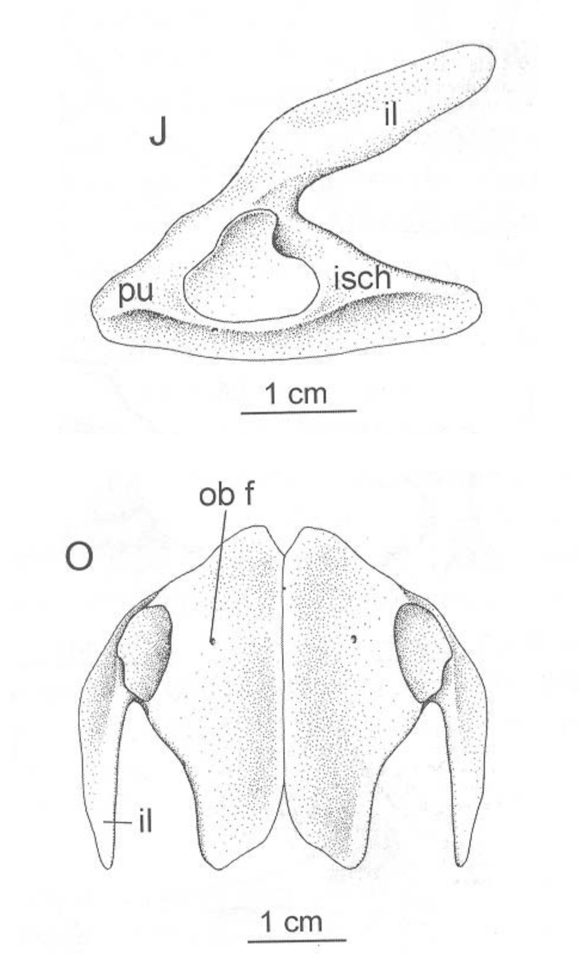


Dendrerpeton pelvis in lateral (above) and ventral (below) views

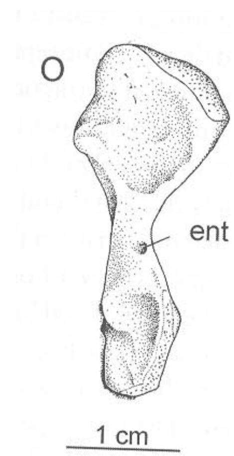
Temnospondyl pectoral & pelvic girdles:

- iliac blade typically tall/elongate, but lacking anterior dorsal process
- triangular, plate-like ischium w/ apex directed posteriorly
- pubis w/ small obdurator foramen; late ossification (possibly cartilaginous in stereospondyls - Milner & Sequeira 1994)

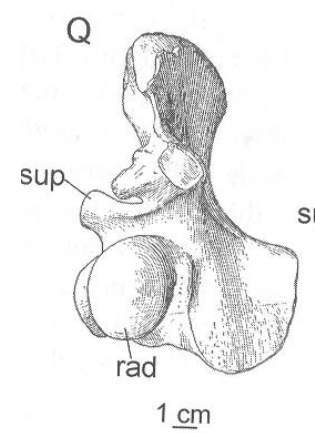
3. Carboniferous-Jurassic 'labyrinthodonts'

Temnospondyl fore- and hindlimbs:

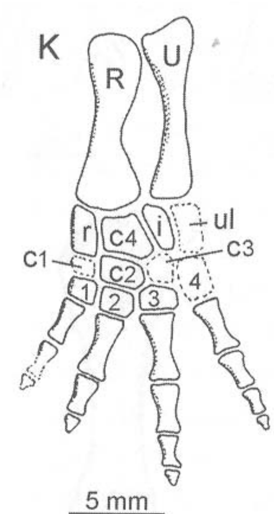
- L-shaped humerus modified by absence of ant. crest and realignment of ectepicondyle
- proximal deltopectoral crest
- increased flexibility of elbow
- entepicondylar foramen lost
- zeugopod highly variable
- carpus often poorly ossified
- 2-2-3-3 phalangeal count (*Balanerpeton*, *Amphibamus*, *Micromelerpeton*)



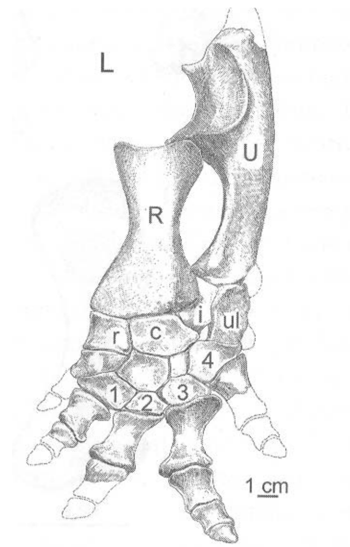
Dendrerpeton humerus



Eryops humerus



Balanerpeton distal forelimb



Eryops distal forelimb

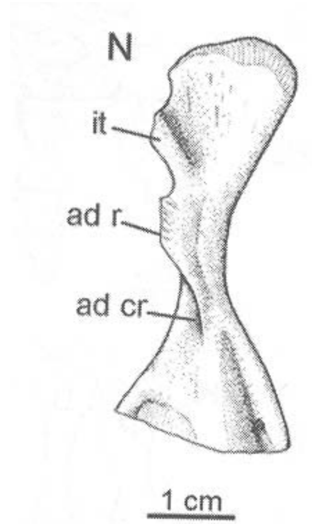
3. Carboniferous-Jurassic 'labyrinthodonts'

Temnospondyl fore- and hindlimbs:

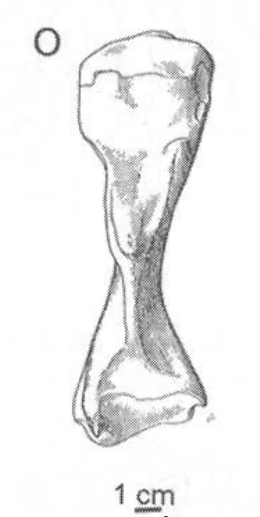
• femur similar to Devonian tetrapods, but w/ fourth trochanter prox. in more terrestrial forms

• zeugopod variable as in the forelimb

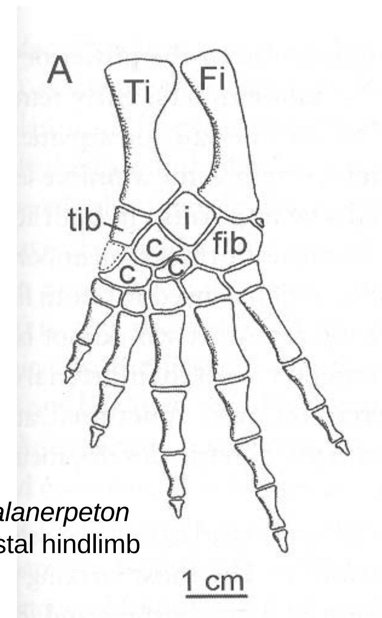
• pedal phalangeal count often 2-2-3-4-3 (*Balanerpeton, Dissorophus, Eoscopus, Amphibamus, Tambachia?)*



Dendrerpeton femur



Eryops femur



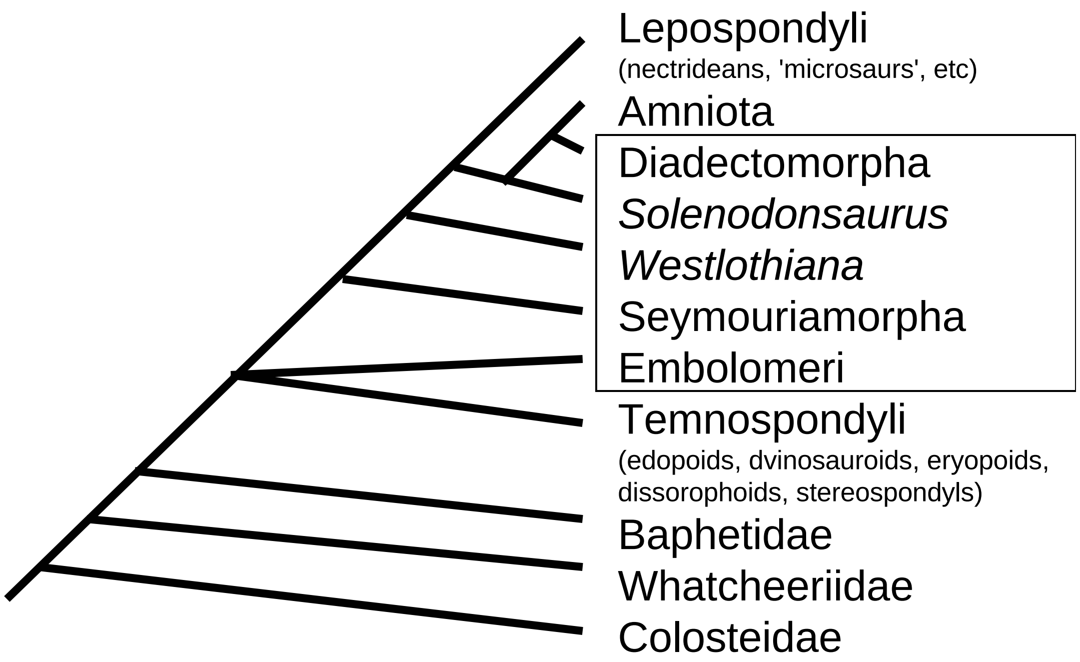
Balanerpeton
distal hindlimb

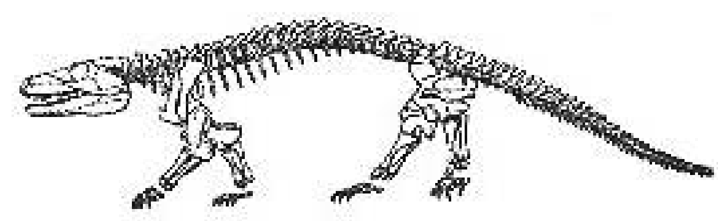
4. 'Anthracosauroids'

'Anthracosauroids'

•General characteristics:

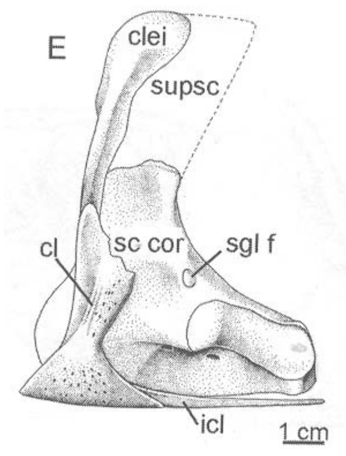
- posterolateral extension of the parietal to reach the tabular
- retention of closed palate and mobility between skull roof and cheek
- pleurocentra may fuse ventrally and become cylindrical



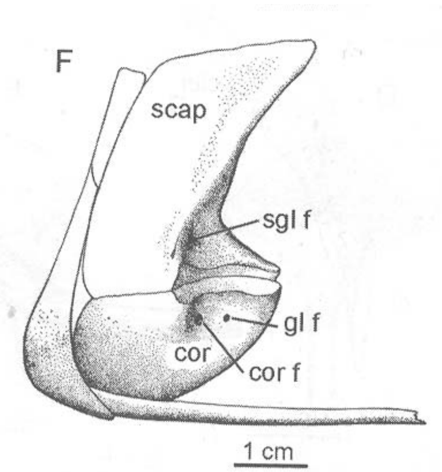


Seymouria (seymouriamorph)

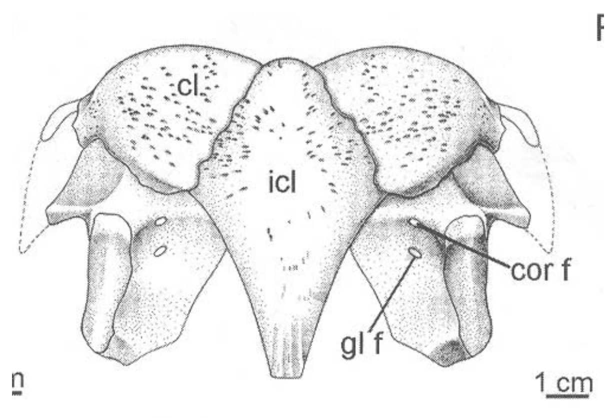
4. 'Anthracosauroids'



Proterogyrinus pectoral girdle



Seymouria pectoral girdle

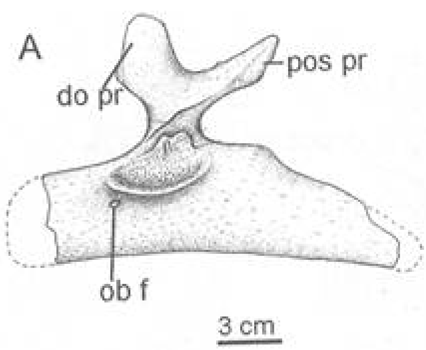


Proterogyrinus pectoral girdle (ventral view)

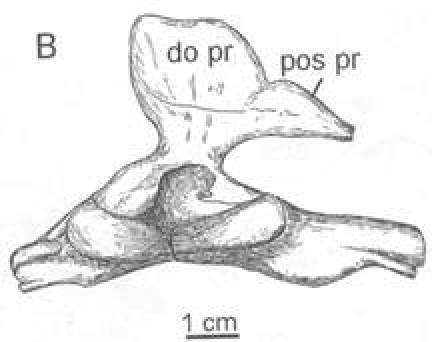
Pectoral & pelvic girdles:

- anocleithrum of Devonian tetrapods largely absent, but retained in *Pholiderpeton* and *Discosauriscus*, suggesting multiple losses
- scapula & coracoid distinct ossifications in seymouriamorphs
- "strap-shaped" glenoid, suggesting little rotation
- small cleithrum in seymouriamorphs w/ no dorsal expansion (as in amniotes)

4. 'Anthracosauroids'



Eoherpeton pelvis



Seymouria pelvis

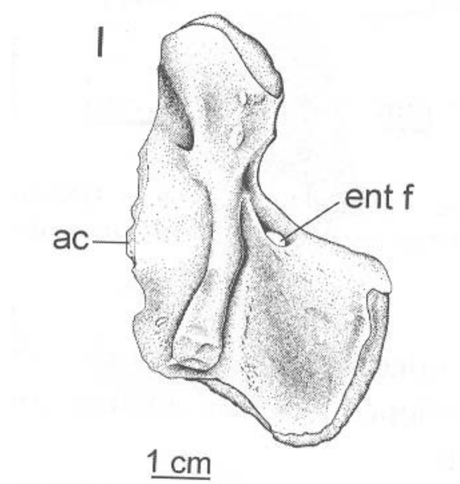
Pectoral & pelvic girdles:

• ilium retains bifurcation in early 'anthracosaurs'
• pubis often unossified; may be pierced by more than one foramen (e.g., *Proterogyrinus*)
• pubis well-ossified in *Seymouria* and *Discosauriscus*

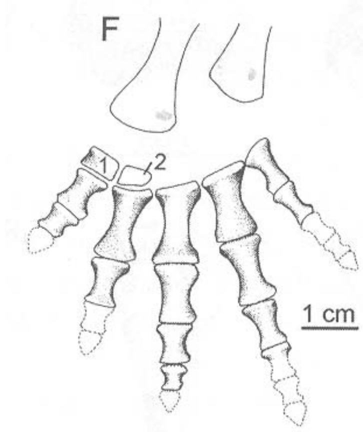
4. 'Anthracosauroids'

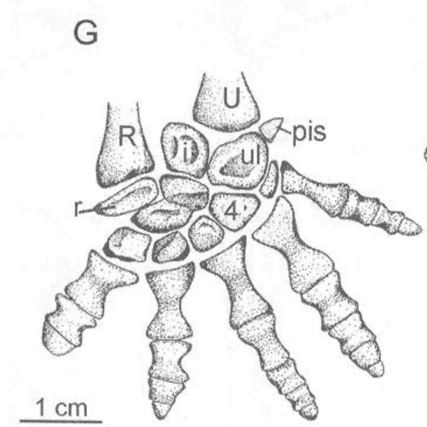
Fore- and hindlimbs:

• Humerus generally retains primitive L-shape; prominent anterior crest precludes presence of distinct shaft
• limited flexion at the elbow, due to orientation of ulnar & radial facets
• generally retain a short zeugopod
• carpus is poorly known; well-ossified in *Seymouria* (ulnare, int., rad., pis., and two centralia as in primitive amniotes)
• phalangeal formula 2-3-4-5-3 as in early amniotes



Proterogyrinus humerus





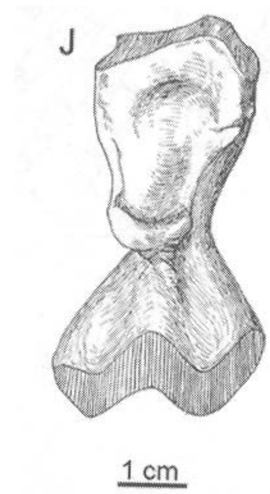
Proterogyrinus distal forelimb

Seymouria distal forelimb

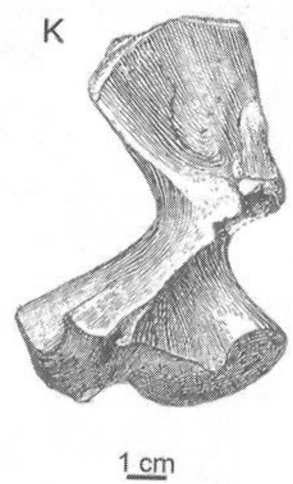
4. 'Anthracosauroids'

Fore- and hindlimbs:

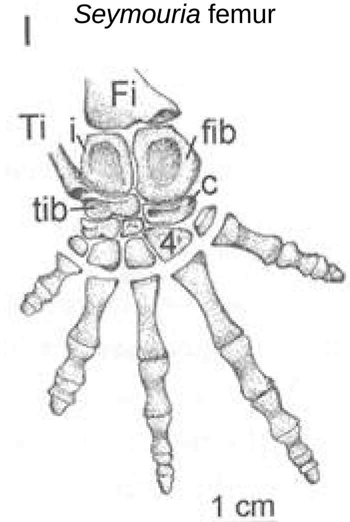
• femur generally primitive in structure
• short zeugopod (55-60% length of femur)
• tarsus highly variable among groups
• phalangeal count usually 2-3-4-5-4 as in diadectomorphs & early amniotes



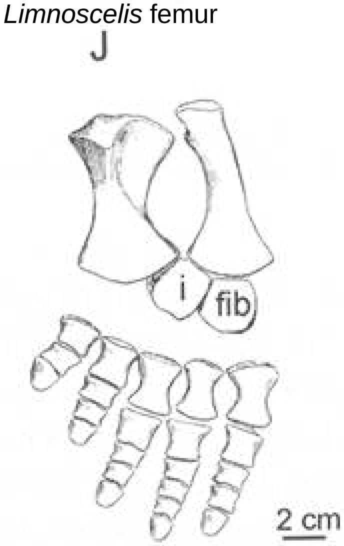
Seymouria femur



Limnoscelis femur



Seymouria distal hindlimb



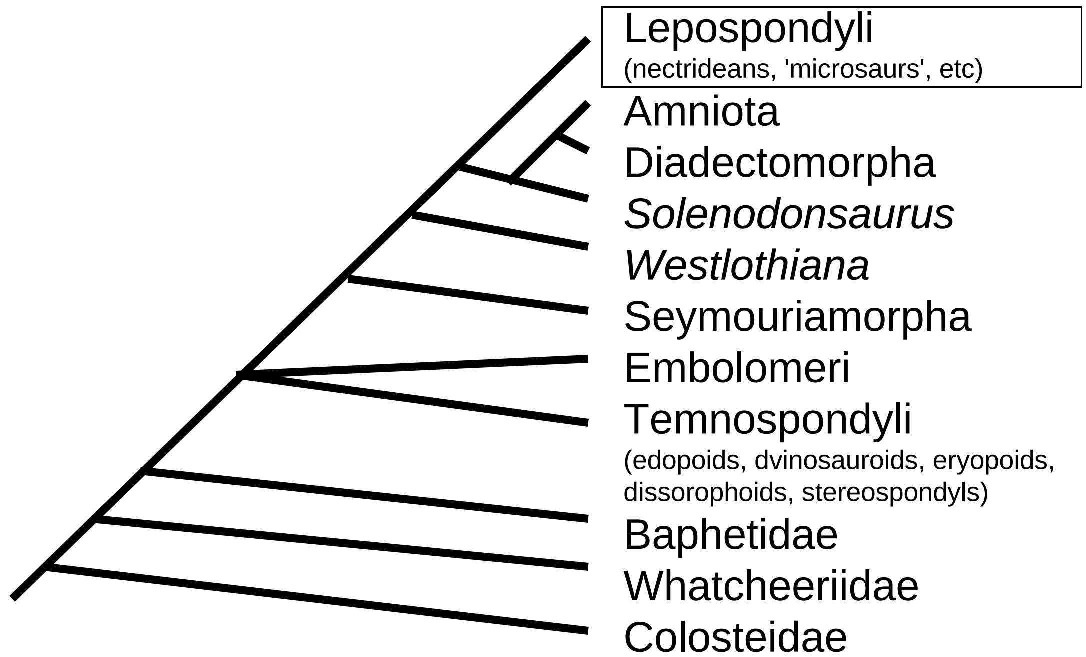
Limnoscelis distal hindlimb

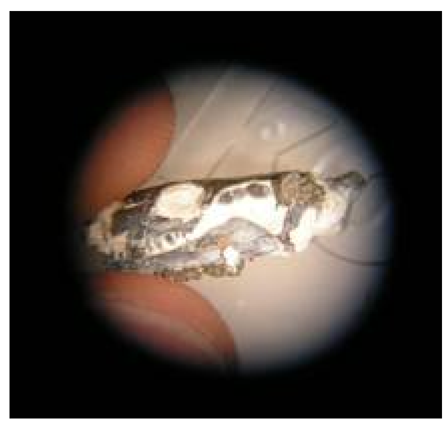
5. Lepospondyls

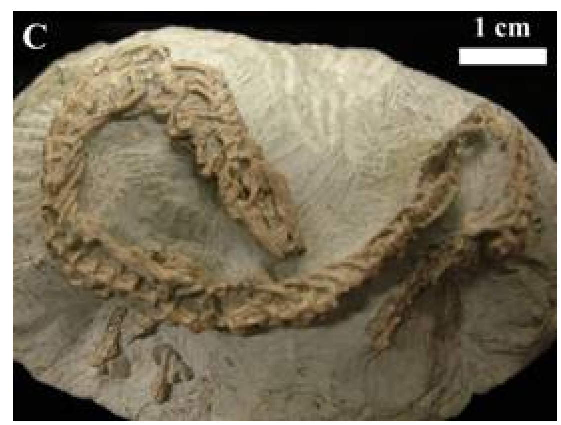
Lepospondyls

•General characteristics:
- relatively small body sizes
- holospondylous vertebrae as in lissamphibians & amniotes
- tendency for limb reduction/loss

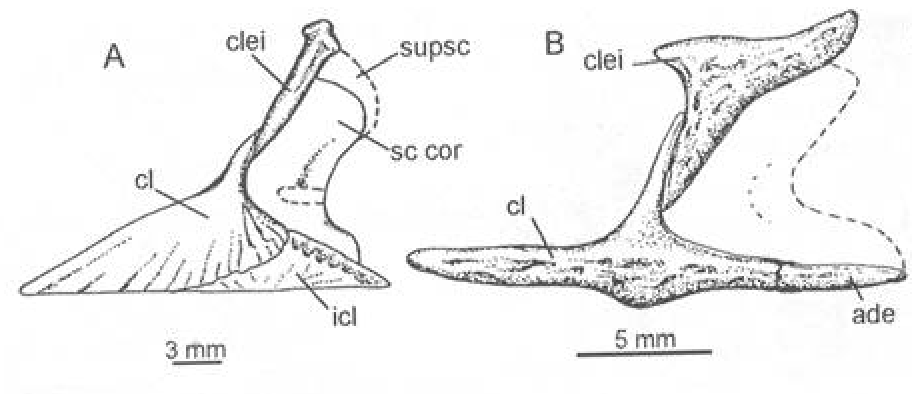
•Taxa include:
- "microsaurs"
- Nectridea
- Lysorophia
- Adelospondyli
- Aïstopoda







5. Lepospondyls



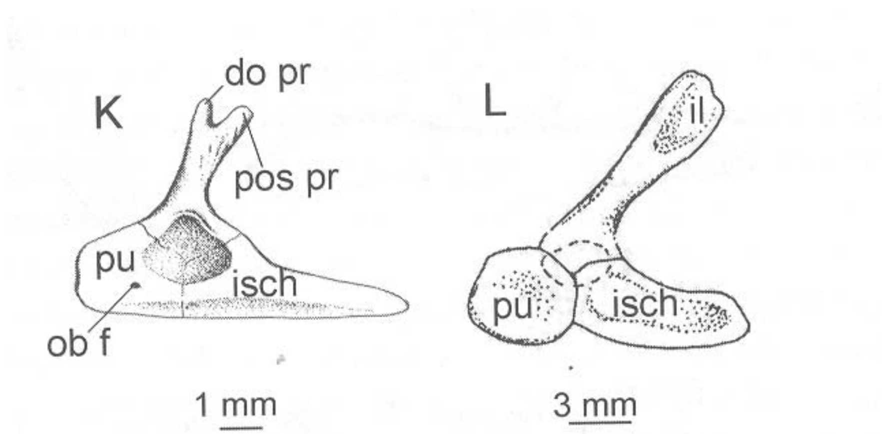
nectridean *Urocordylus* shoulder girdle

nectridean *Diceratosaurus* shoulder girdle

Pectoral & pelvic girdles:

• dermal elements of shoulder girdle extensive; often fimbriated margins; large clavicular blades and wide, diamond-shaped interclavicle; smooth surface in "microsaurs," but deeply sculptured in nectrideans
• scapulocoracoid fused but coracoid fails to ossify in some small species
• helical glenoid as in temnospondyls
• possible cartilaginous suprascapula as in "labyrinthodonts"

5. Lepospondyls



microsaur *Tuditanus* pelvic girdle

nectridean *Urocordylus* pelvic girdle

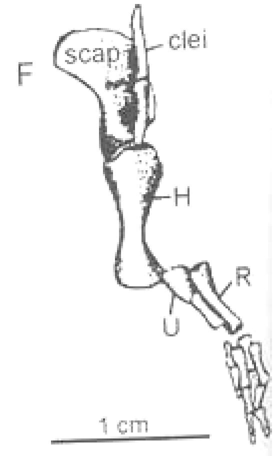
Pectoral & pelvic girdles:

- pelvis lightly built and separated into 3 ossifications; pubis unossified in small species
- iliac processes tend to reduce distinction independently

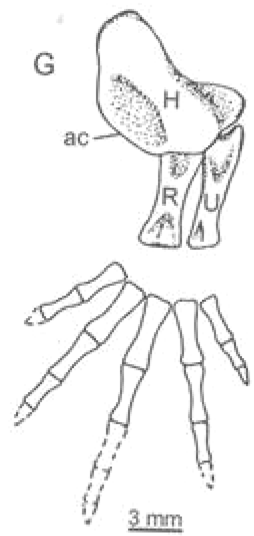
5. Lepospondyls

Fore- and hindlimb of lepospondyls:

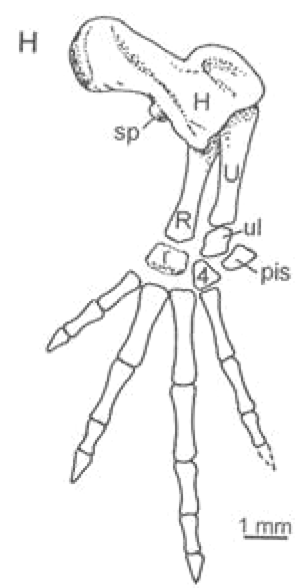
• highly variable
• humerus ant. crest absent in "microsaurs"; entepicondylar foramen lost in species w/ small humeri; extremely reduced in lysorophians, adelospondyls, & aïstopods
• stylopod & zeugopod tend to be slender and the olecranon of the ulna is lost in small forms
• carpal ossifications are known in only a few "microsaurs"; absent in lysorophians, adelospondyls, & aïstopods
• no more than 4 manual digits in "microsaurs"



lysorophian *Brachydectes* forelimb



Urocordylus forelimb

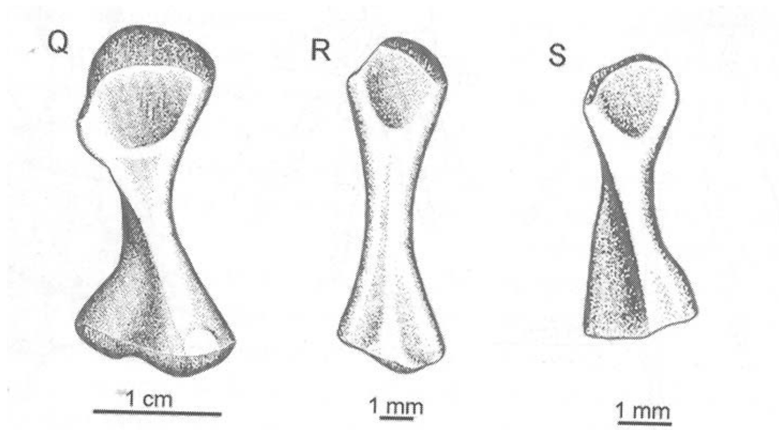


Sauropleura forelimb

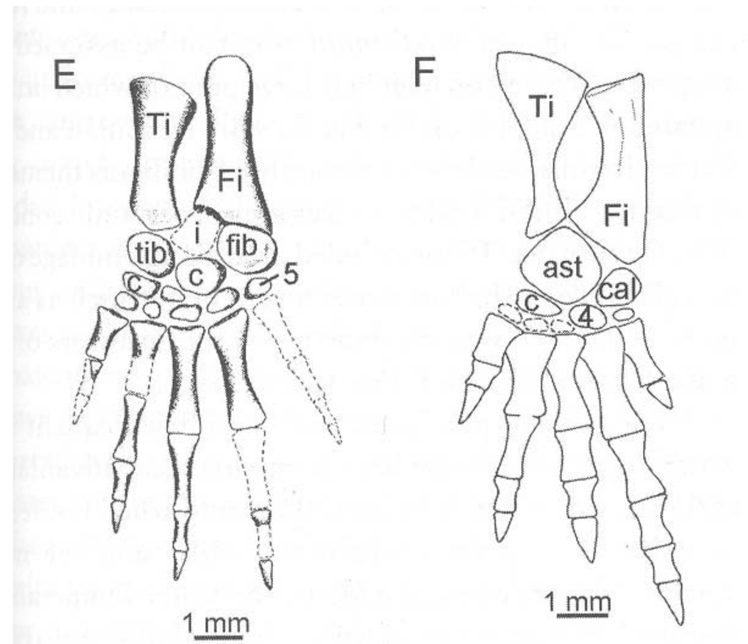
5. Lepospondyls

Fore- and hindlimb of lepospondyls:

• femora tend to resemble small to medium-sized temnospondyls
• ends of femora tend to be incompletely ossified in small, aquatic forms
• zeugopod very short
• pedal phalangeal count highly variable



Microsaurs *Trachystegos*, *Rhynchonkos,* and *Microbrachis* (femora)



Microsaurs *Rhynchonkos* and *Batropetes* (distal hindlimbs)

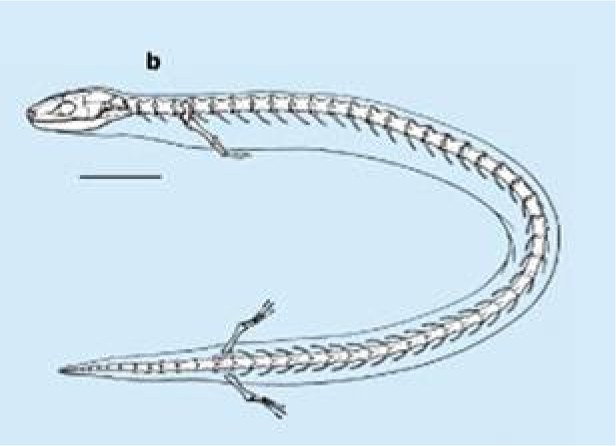
6. Modern lissamphibian orders

Caecilians (Gymnophiona)

• General: 175 spp., 6 families; Jurassic-present; modern forms are limbless; extinct *Eocaecilia* reveals affinities to the microsaur *Rhynchonkos*

• *Eocaecilia* (Jurassic of Arizona) - scapulocoracoids, humeri, radii, ulnae, femora, tibiae, and fibulae; spiral-shaped glenoid; femur has prominent trochanter & resembles salamanders; 3 digits associated w/ hindlimbs

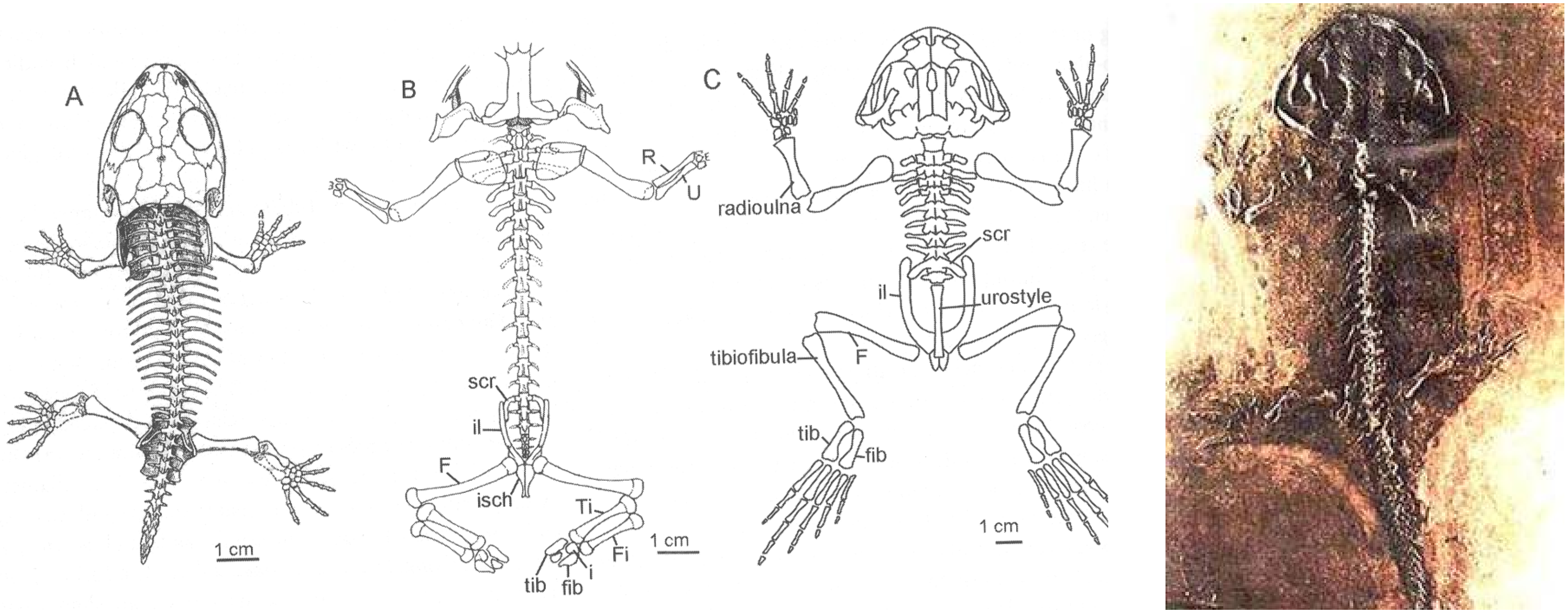




6. Modern lissamphibian orders

Salamanders (Batrachia: Caudata)

• General: strong evidence for temnospondyl origins of batrachians: pronounced metamorphosis and aquatic larvae w/ external gills



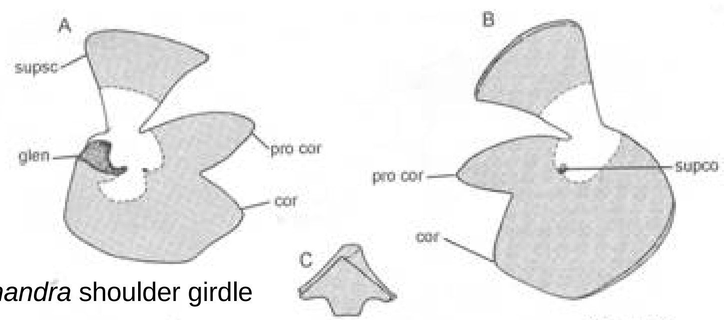
Micropholis (A), *Triadobatrachus* (B), *Notobatrachus* (C), and *Karaurus* skeletons in dorsal view.

6. Modern lissamphibian orders

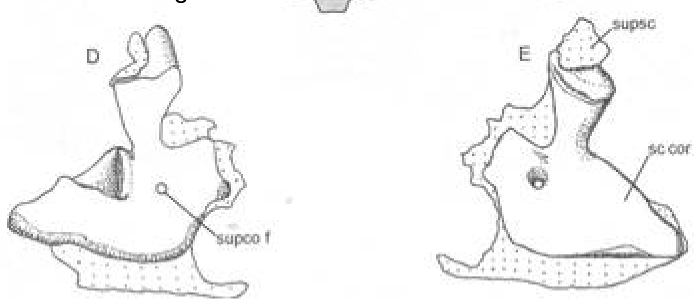
Salamanders (Batrachia: Caudata)

• General: strong evidence for temnospondyl origins of batrachians: pronounced metamorphosis and aquatic larvae w/ external gills

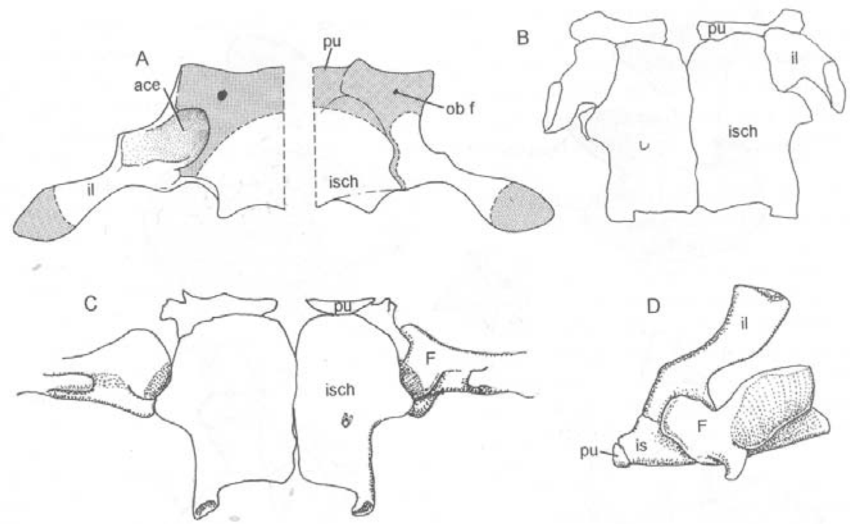
• Pectoral & pelvic girdles - loss of all 3 dermal bones of shoulder girdle; endochondral girdle is well-ossified in hynobiids; 3 elements of pelvis retained, but highly cartilaginous



Salamandra shoulder girdle



Hynobius shoulder girdle



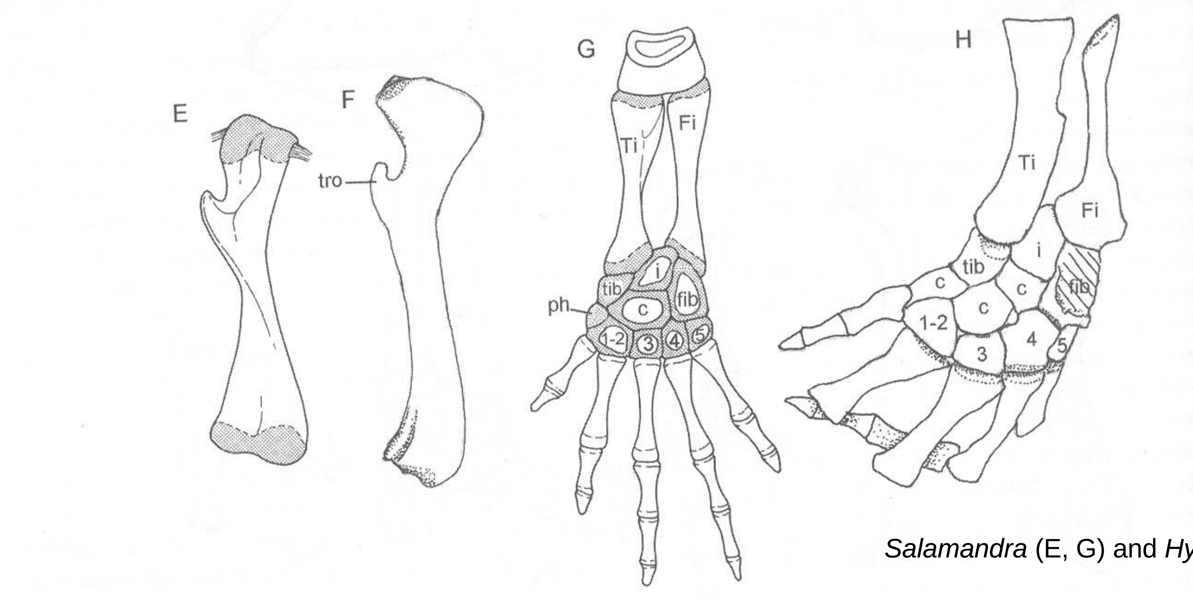
Salamandra (A) and *Hynobius* (B-D) pelvic girdles

6. Modern lissamphibian orders

Salamanders (Batrachia: Caudata)

• General: strong evidence for temnospondyl origins of batrachians: pronounced metamorphosis and aquatic larvae w/ external gills

• Forelimb & hindlimb - humerus & femur often w/ long, slender shaft; entepicondylar foramen lost; very short zeugopods; 2-2-3-3-2 common pedal phalangeal formula (but highly variable); complete loss of hindlimbs in sirenids; reduction of fore- and hindlimbs in amphiumids



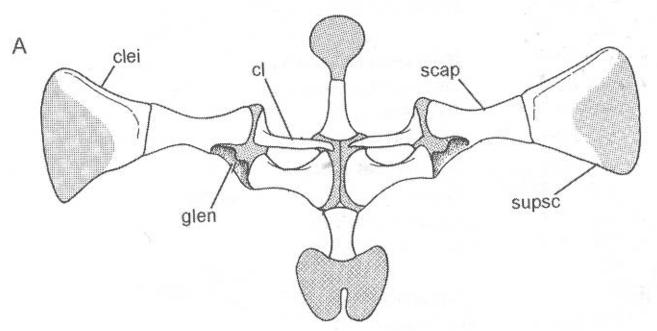
Salamandra (E, G) and *Hynobius* (F, H) hindlimbs

6. Modern lissamphibian orders

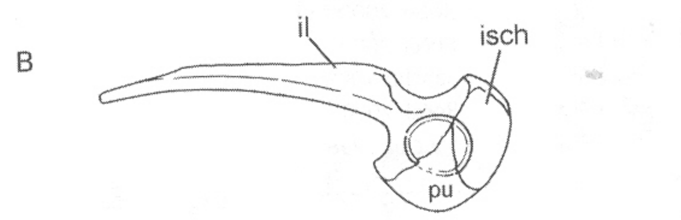
Frogs (Batrachia: Anura)

• General: Most highly derived hindlimb & girdle (saltatory locomotion); modifications involved elongation of hindlimb, strengthening of zeugopod; reduction of trunk vertebrae, and consolidation of anterior caudal vertebrae into rod-like urostyle

• Pectoral & pelvic girdles - scapula and coracoid distinct; cleithrum and clavicle present, but interclavicle lost; elongate iliac blade; pubis (often cartilaginous) and ischium positioned posterior, rather than ventral



Rana shoulder girdle (ventral view)



Rana pelvic girdle (lateral view)

6. Modern lissamphibian orders

Frogs (Batrachia: Anura)

• General: Most highly derived hindlimb & girdle (saltatory locomotion); modifications involved elongation of hindlimb, strengthening of zeugopod; reduction of trunk vertebrae, and consolidation of anterior caudal vertebrae into rod-like urostyle

• Pectoral & pelvic girdles - scapula and coracoid distinct; cleithrum and clavicle present, but interclavicle lost; elongate iliac blade; pubis (often cartilaginous) and ischium positioned posterior, rather than ventral

• Fore- and hindlimbs - humerus and femur slender; both stylopod and zeugopod elongated; tibiale and fibulare elongated; both manual (2-2-3-3) and pedal (2-2-3-4-3) phalangeal counts highly conserved

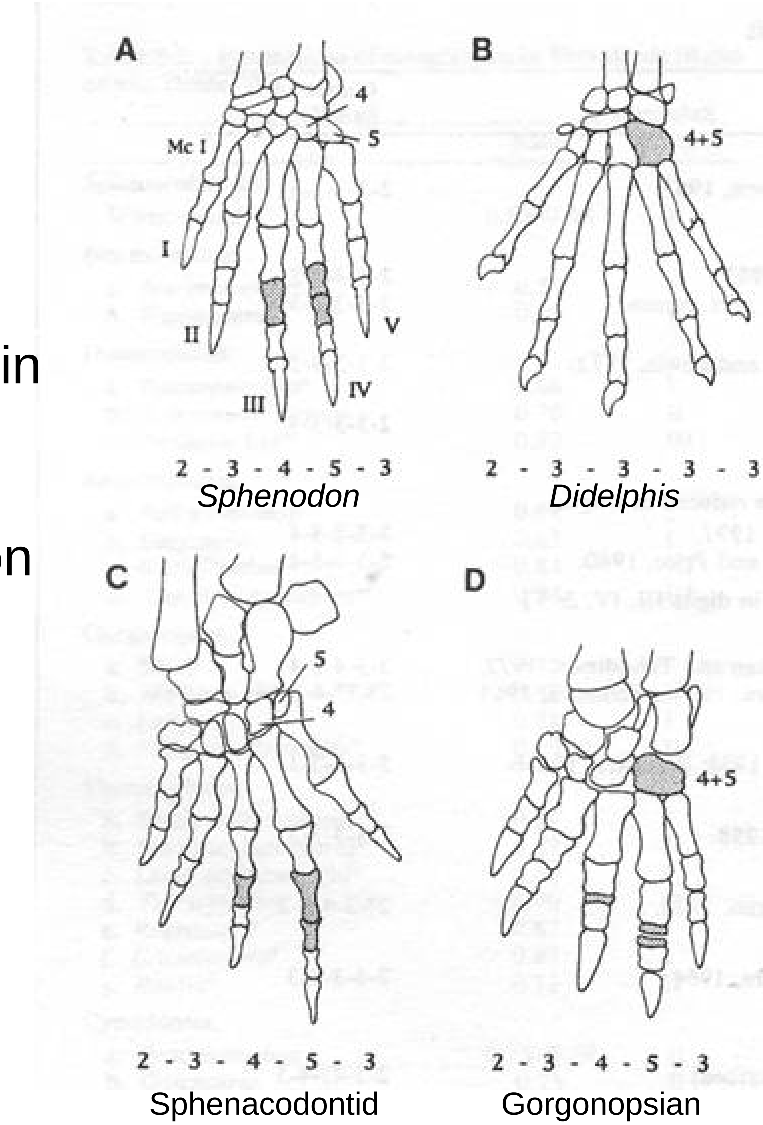
Chapter 14: Limb diversity and digit reduction in reptilian evolution

M. Shapiro, N. Shubin, & J. Downs

• Bones are often lost during adaptive evolution of new designs

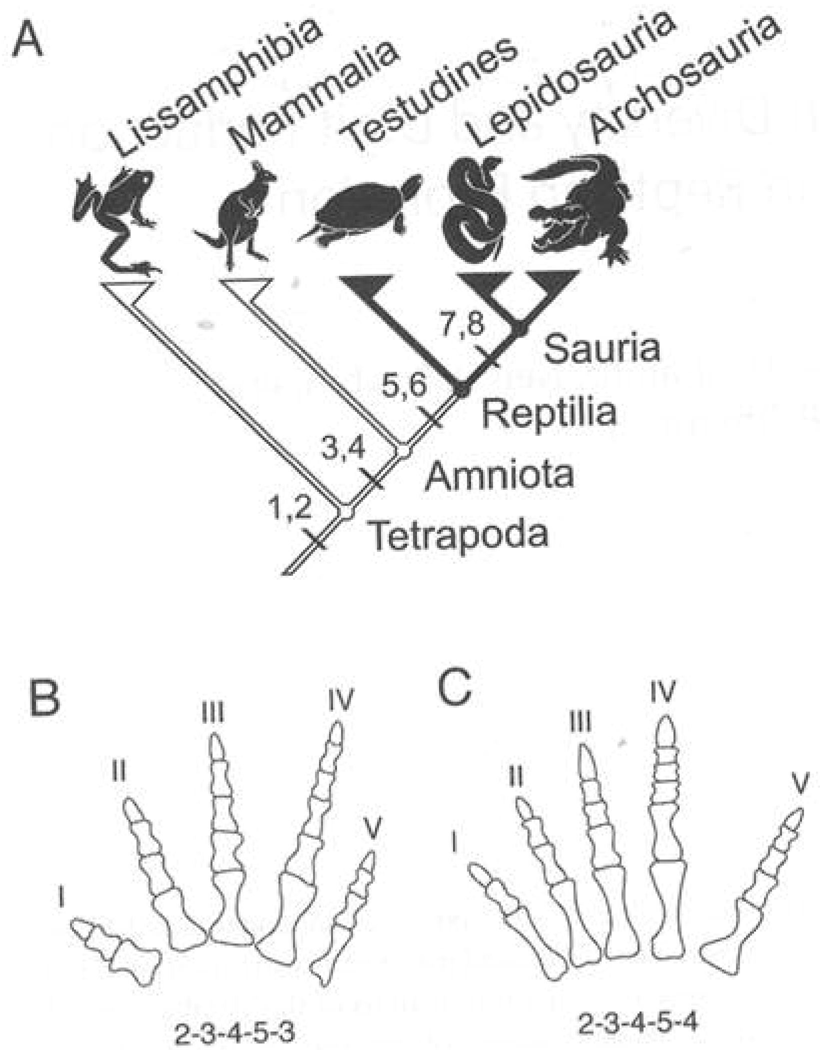
• Only *Sphenodon* and some lizards retain the ancestral phalangeal formula

• Reduction is widespread in the evolution of the terrestrial vertebrate skeleton, and has been studied in salamanders, frogs, and synapsids (incl. mammals)



(from Hopson 1995)

1. What is a 'reptile'?

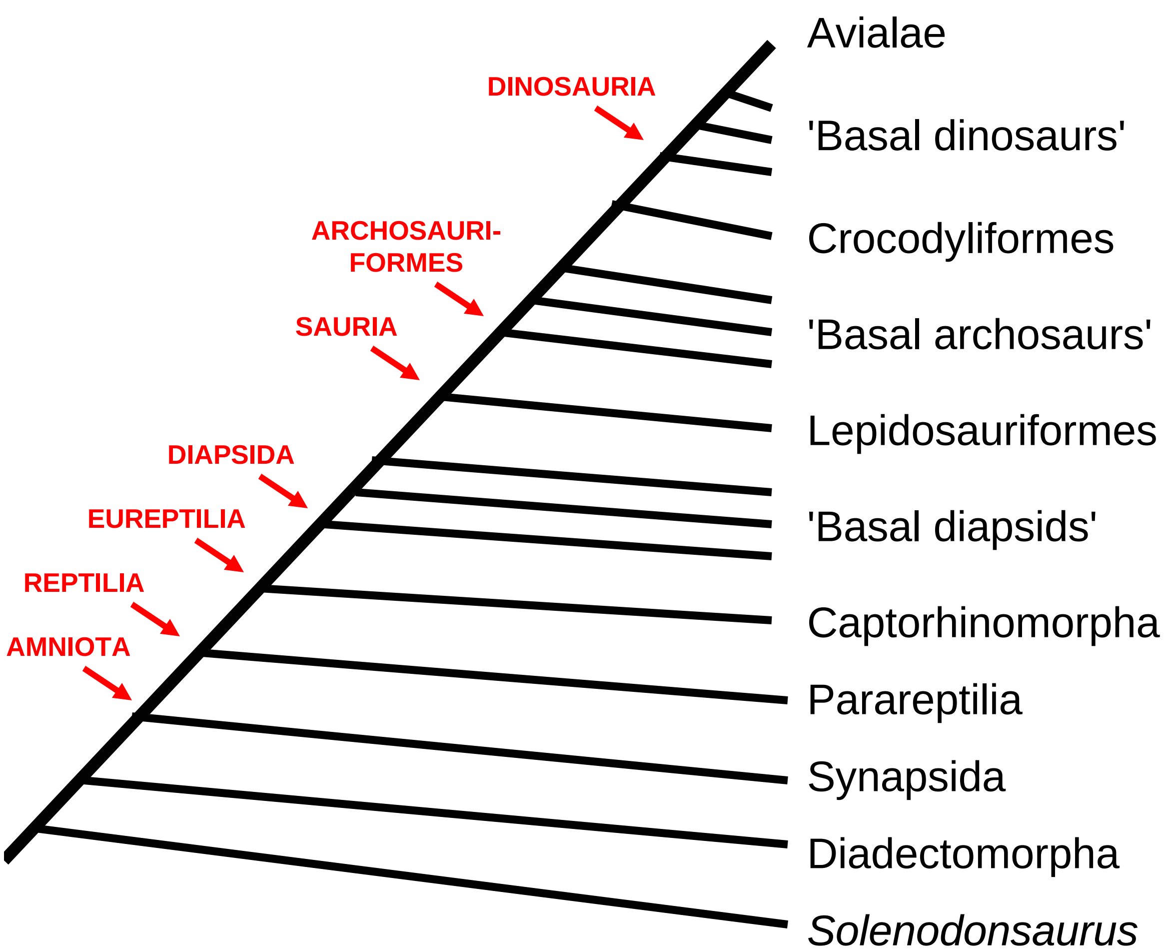


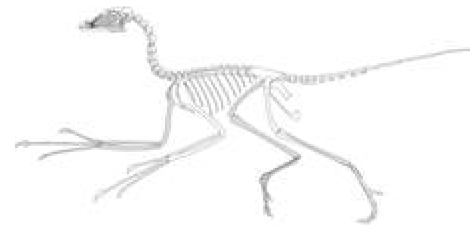
- Because "reptiles" are diagnosed by a suite of plesiomorphic characters, associated with a primitive (nonmammalian-nonavian) terrestrial lifestyle, they are Paraphyletic

- Attempts have been made to designate Reptilia as monophyletic

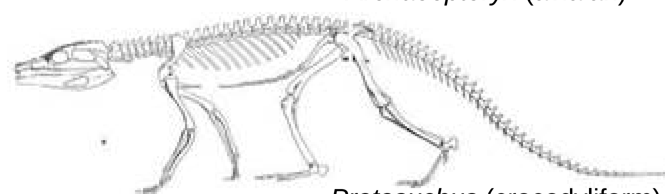
- Primitive phalangeal formula exemplified by captorhinomorphs

1. What is a 'reptile'?

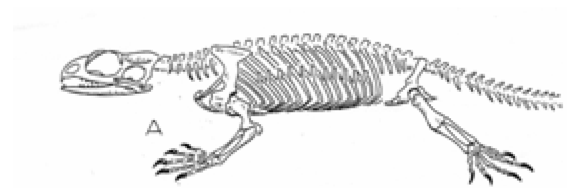




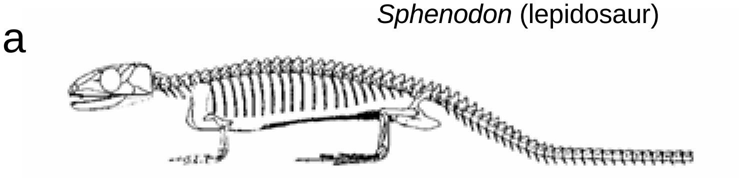
Archaeopteryx (avialan)



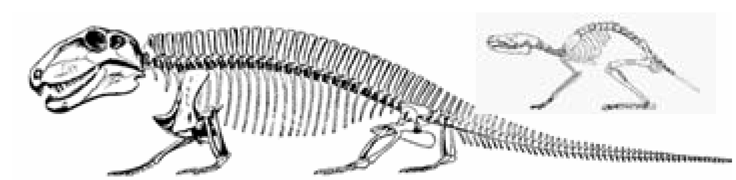
Protosuchus (crocodyliform)



Sphenodon (lepidosaur)



Hylonomus ('protorothyridid')



Sphenacodon (synapsid)

2. Construction of database and mosaic plots

(1) To study trends in digit reduction, authors compiled database of phalangeal formulae from neontological & paleontological literature and museum specimens

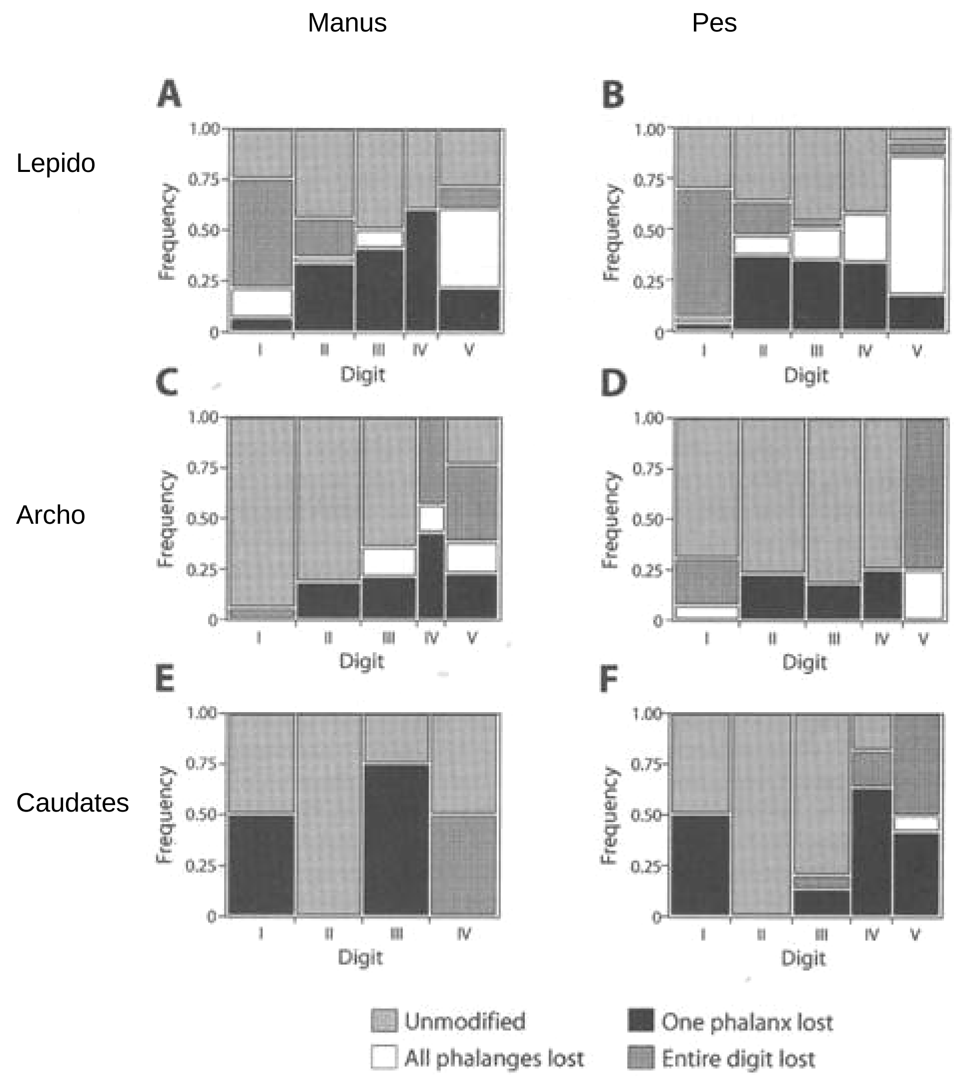
(2) Scoring digit / phalangeal counts:

- absence of digit coded "X"
- reduction to metapodial coded "0"
- example from *Equus* = X-0-3-0-X
- instances of hyperphalangy or complete limb loss excluded from analysis

2. Construction of database and mosaic plots

(3) Mosaic plots:

•represent "frequency of different patterns of reduction" ....



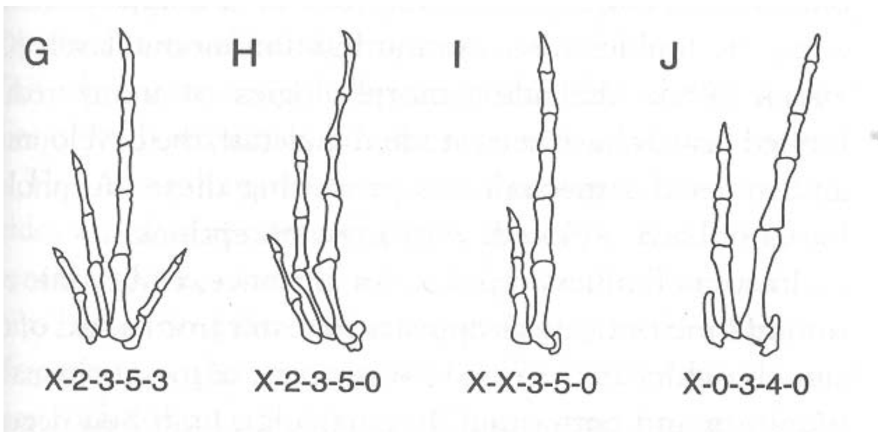
3. Results I: Testudines

- Manus - digit I variable and often lost; digits II-V tend to reduce to similar counts (e.g., 2-2-2-2-2)

- Pes - digit I always retains two phalanges; digit II only shows loss in 1/3 of configurations; digit III always altered from primitive condition; digits IV-V variable


4. Results II: Lepidosaurs

- Manus - digit I usually either complete or absent; digit II loses either one or all phalanges (bimodal); digits III-IV variable but rarely ever lost; digit V undergoes frequent reductions
- Pes - digit I frequently reduced; digit II bimodal; digits III-IV tend to lose the greatest number of phalanges (IV is usually last to be lost); digit V most frequently reduced



Lepidosaurs *Lerista* (G-I) and *Hemiergis* (J) pedal configurations

5. Results III: Archosaurs

- Manus - digits I-II highly conserved; digit III never lost but exhibits a whole range of phalangeal counts; tendency for reduction of digits IV-V, with extreme reduction in theropod dinosaurs
- Pes - digit I has either all or none of its phalanges; digit II is never lost and has two or three phalanges; digit III usually bears four phalanges; digit IV retains at least four phalanges in most configurations; frequent reductions of digit V, only rhamphorhynchoid pterosaurs have more than a single phalanx

6. Discussion

(1) Digit reduction versus loss:

- Digit *reduction* = loss of some or all phalanges in a digit
- Digit *loss* = loss of all phalanges plus the supporting metapodial

e.g., **Lepidosaurs** - often reduce both digits I & V, but patterns of complete loss vary considerably between those digits (i.e., digit V usually retains metapodial); digit V is highly resilient in terms of digit loss

Morse's Law (1872) -	I>V>II>III>IV
New (manus) -	I>II>V>(III,IV)
New (pes) -	I>II>V>III>IV

* New observations follow *reverse order* of developmental digit primordia appearance; patterns of chondrogenesis may be a predictor of loss, but not necessarily reduction

6. Discussion

(2) Integrated and correlated digit reduction: shaping the hand and foot:

- Reduction and loss of outer digits is principle mode of *pedal* evolution in lepidosaurs & archosaurs e.g., (0-3-4-5-X) and (X-3-4-5-X)
- In archosaurs, *manual* digits I & II are nearly always present, whereas digits IV & V are most frequently absent
- Many archosaurs and testudines reduce the digits in a manner that they are uniform or differ only by one phalanx
- Thus, similar patterns emerge in shaping the foot that are *independent of phylogeny*

6. Discussion

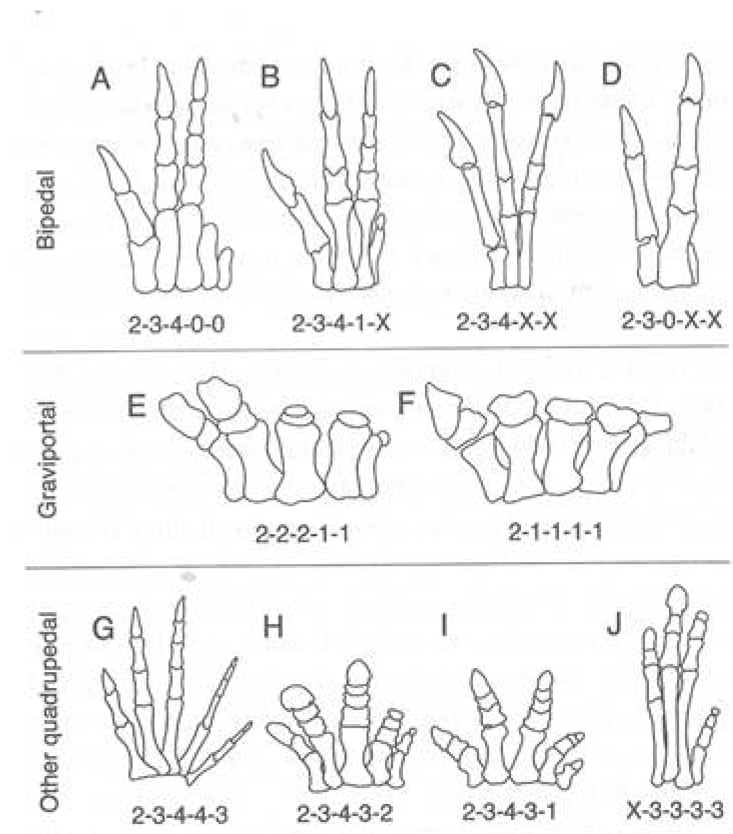
(3) Functional correlates of digit reduction

• Reduction patterns among archosaurs correlate with functional differences ....

1. Manus of theropods often retain digits I-III, but reduce/lose IV-V; retention of preaxial digits may preserve grasping specializations (Sereno 1997)

2. Sauropods & stegosaurs may reduce to one or two phalanges across *all digits*

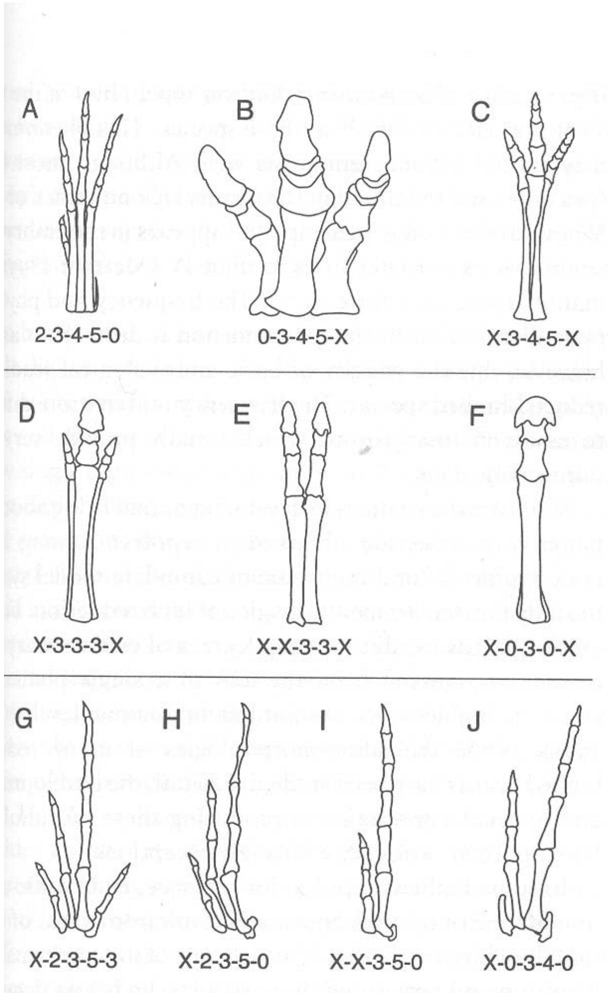
3. Modest reductions associated with sprawling, quadrupedal gait



6. Discussion

(3) Functional correlates of digit reduction

- Localized outer digit reductions in lepidosaurs ....
  - pedal configurations may lose outer digits *and* variably reduce central digits, unlike theropods who often conserve central digits
  - due to mechanical constraints of different locomotory means

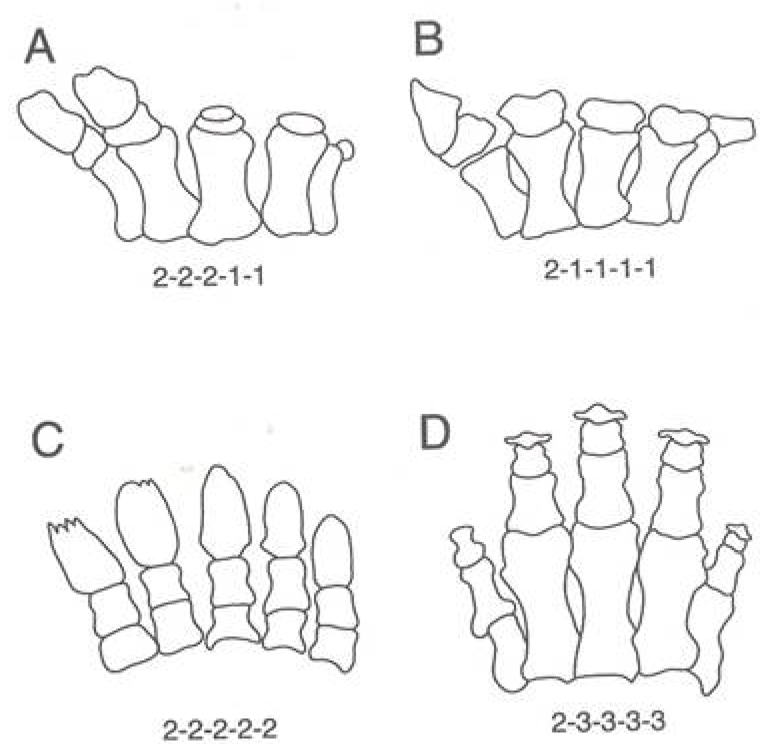


Archosaur (A-C), mammal (D-F) and lepidosaur (G-J) pedal phalangeal counts

6. Discussion

(3) Functional correlates of digit reduction

- Uniform reductions in turtles ....
  - manus & pes follow pattern of graviportal dinosaurs
  - most configurations bear one or two phalanges on manus & pes



Graviportal dinosaur (A,B), turtle (C), and *Elephas* (D) manual digit reductions

6. Discussion

(4) How to deconstruct a limb: developmental origins of limb reductions

- Digit I is lost more frequently than any other digit
  - *developmental implications*: digit I can either (1) condense w/ two phalanges; (2) condense then regress; (3) not condense at all
- Digit V may condense but *not segment*
- Digits II-IV often exhibit modest reduction

What changes in development might bring about these changes?

6. Discussion

(4) How to deconstruct a limb: developmental origins of limb reductions

Changes in development ....

- Reptiles offer a number of model systems to study these phenomena (e.g., digit reductions, complete limb loss, etc.)
- Limb bud degeneration breaks down AER w/ loss of distal signals & arrest of mesenchymal proliferation & patterning
- experimental treatments w/ mitotic inhibitor cytosine-arabinofuranoside results in loss of peripheral digits *first*, then central digits
- So, limb losses/reductions in evolution may be linked w/ shortage of tissues during development ....

Lizard & salamander experiments do not necessarily show widespread truncation of remaining digits; these represent novel configurations (e.g., Hemiergis)

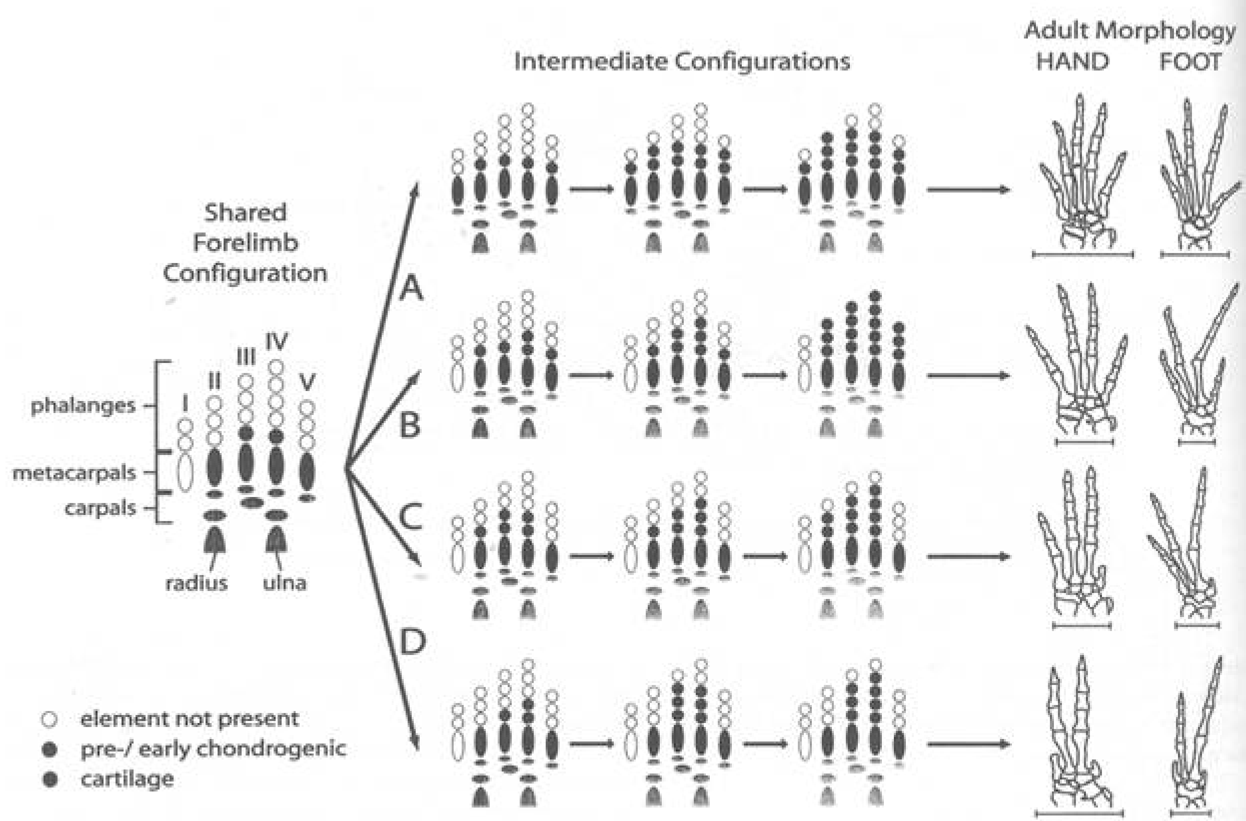


Figure 14-6 Limb skeletal development in *Hemiergis*. In all diagrams, distal is at the top and anterior is to the left. Following shared, early skeletal configuratio (left), the developmental trajectories of (A) *H. initialis* (5/5), (B) *H. peronii* (4/4), (C) *H. peronii* (3/3), and (D) *H. quadrilineata* (2/2) autopodia diverge, culminating different adult morphologies (right). The shared and intermediate stages depict forelimb configurations only, but hindlimb data are virtually identical. Intermedia configurations are based on data from whole mounts and serial sections, and do not necessarily represent identical embryonic stages among all four morphs. Sc bars = 1 mm for adults. (After Shapiro et al. 2003.)

7. Conclusion

- Tetrapod limb reduction operates at different levels of organization (e.g., digit primordia initiation & subsequent segmentation)

- At another level, limb reduction trends likely have functional (adaptive) correlates

- The last digits to form are typically the first to be lost, but losses don't follow a universal model of heterochronic truncation; truncations at *intermediate stages* may produce a series of incomplete digits

- Future studies should address whether reptile limb *convergence* is a product of common developmental-genetic pathways