Biology 680 - 2007
Evolution of the Vertebrate Limb
Weeks 1-2
Dr. Stuart Sumida

Introduction

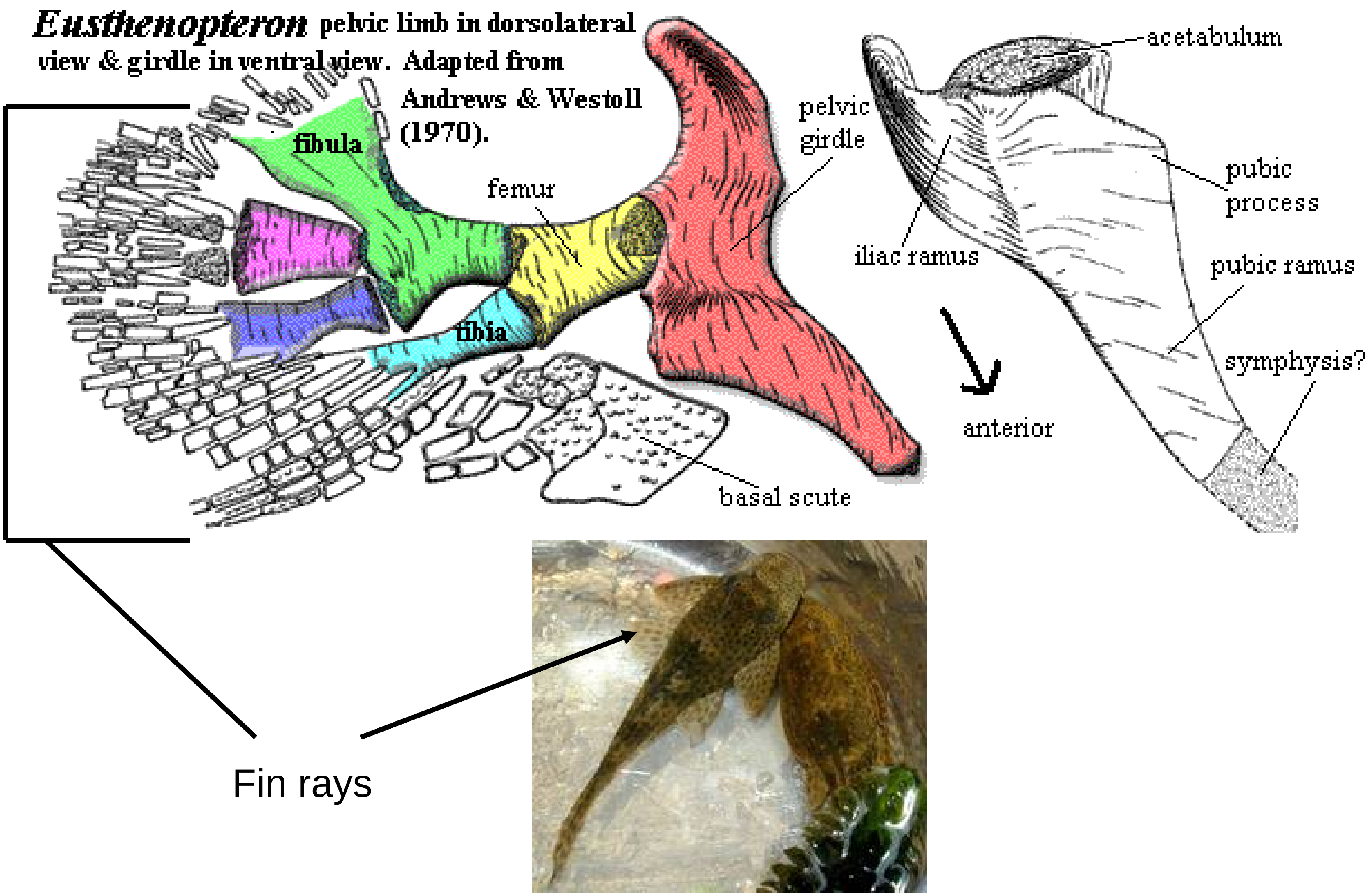
Skeletal Changes in the Transition from Fins to Limbs

Evolution of Paired Appendages in Vertebrates

Focus on the skeletal component of the appendages
- Morphology
- Development
- Developmental Genetics

Appendages are:
- Fins (“Fish”)
- Limbs (“Tetrapods”)

“Fins minus fins rays plus digits equal limbs.”



Book and (therefore) Course Focus:

Appendages/Limbs:

- Development, growth, structure, maintainence, function, regeneration, and evolution.
- Transformation of fins to limbs at the origin of tetrapods.
- Transformation of limbs to “fins” in secondarily aquatic vertebrates and wings of flying vertebrates.
- Adaptations associated with specialized modes of life.
- Digit reduction and complete limb reduction in some taxa.

All the skeletal elements of the tetrapod limb are derived from embryonic mesoderm, as are the cartilagenous elements of fish limbs.

Fin rays are derived from neural crest.

Transformation of fins to limbs involves supression of the neural crest (fin ray) component and elaboration of a distal mesodermal component from which digits arose.

Historical and “Adaptationist” Perspective on Origin of Limbs

1. More than one origin of amphibians? Don’t confuse [probable] multiple origin of extant Lissamphibia with single origin of Tetrapoda.

2. Why move from water to land? “Why would a fish take a risk venturing out into a new and hostile environment?”
   - Escape predators
   - Food on land – insects.
   - Romer: early fish may have moved acoss land to get back into the water (one pond to another).

SKELETAL CHANGES IN THE TRANSITION FROM FINS TO LIMBS

Phylogenetic Context for Origin of Tetrapods

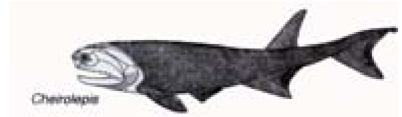
Skeletal Structure in Representative Groups in the Phylogenetic Context

Structural Transformational Trends Seen in Those Groups

Older Taxonomy:

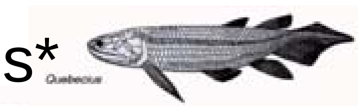
- Osteichthyes (bony fishes)
  - Actinopterygii (ray-finned fishes)
  - Sarcopterygii (lobe finned fishes)
    - Dipnoi (lungfishes)
    - Crossopterygii
      - Actinistia (coelacanths)
      - Porolepiformes
      - Osteolepiformes
        - Panderichthyidae
        - Tetrapoda

- Osteichthyes (bony fishes)
    - Actinopterygii (ray-finned fishes)



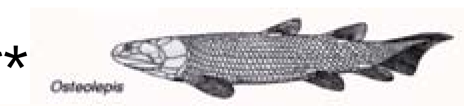
    - "Stem-group Sarcopterygians"
    - Crown-group Sarcopterygii
        - Coelocanths (Actinistia)

        - Dipnomopha
            - Stem Dipnoans*

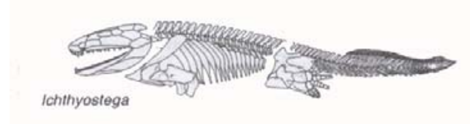


            - Dipnoans

            - Tetrapodomorpha
                - Sister taxa to Tetrapods**



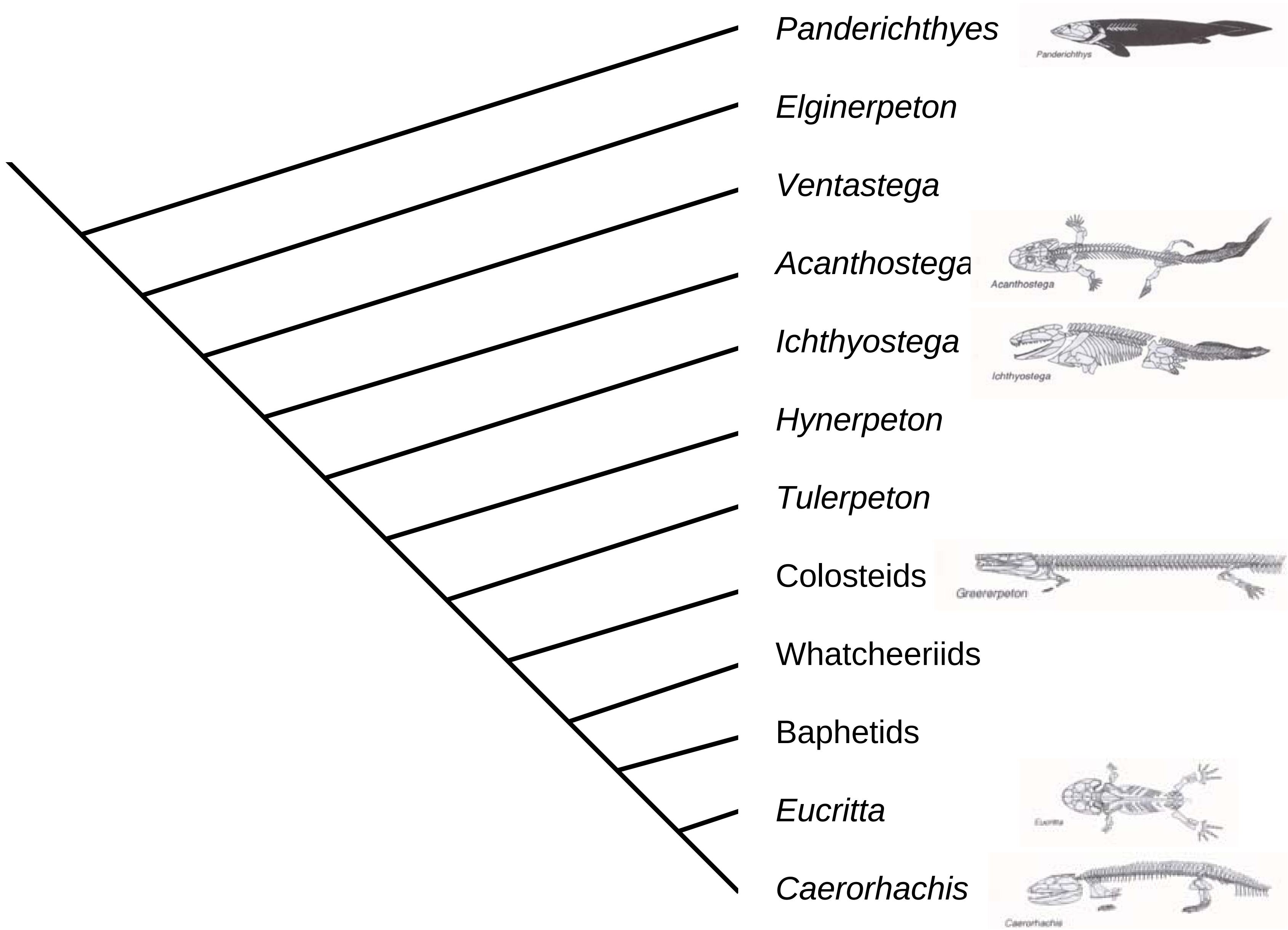
                - Tetrapoda



*Includes taxa formerly called Porolepiform Crossopterygians

**Includes taxa formerly called Osteolepiform Crossoptrygians

Basal Tetrapod Phylogeny, Coates and Ruta (2003, 2007)



Survey of Major Taxonomic Groups Spanning the Skeletal Transition from Fins to Limbs

COELACANTHS
(Also “Actinistia”)

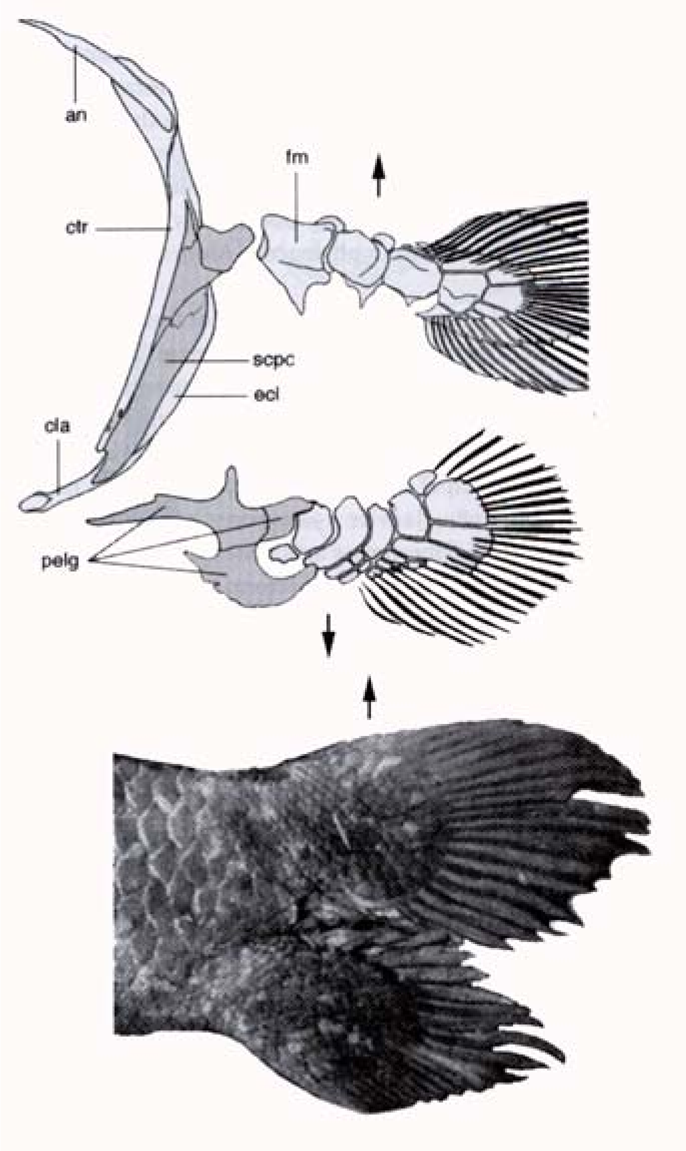
Known from lowest Upper Devonian (Frasnian) to present.

Formerly considered central examples of crossopterygians fishes.

Lobe-finned, muscular fins.

Noteably, glenoid and acetabulum are convex unlike concave condition in tetrapods.

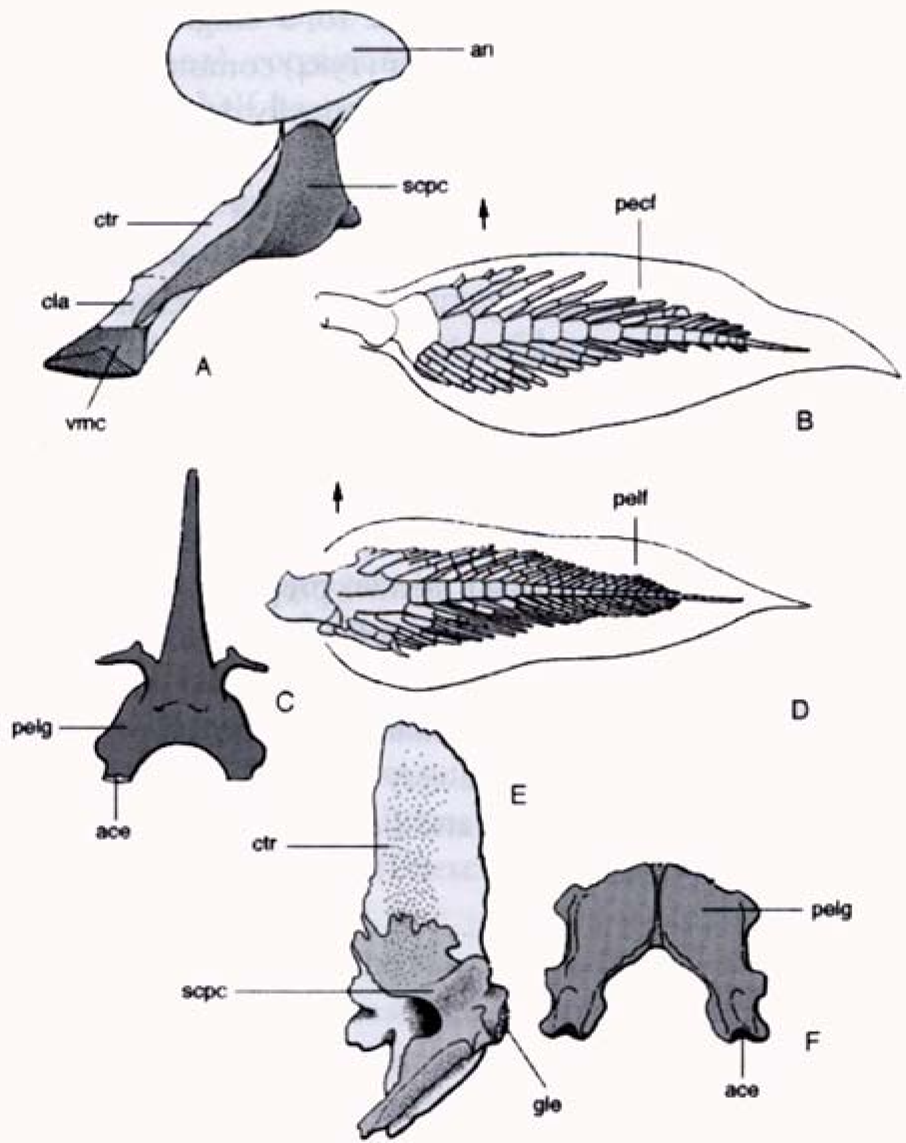
Pelvic girdle is abdominally deep and endochondral – a condition that persists all the way to Tetrapoda.

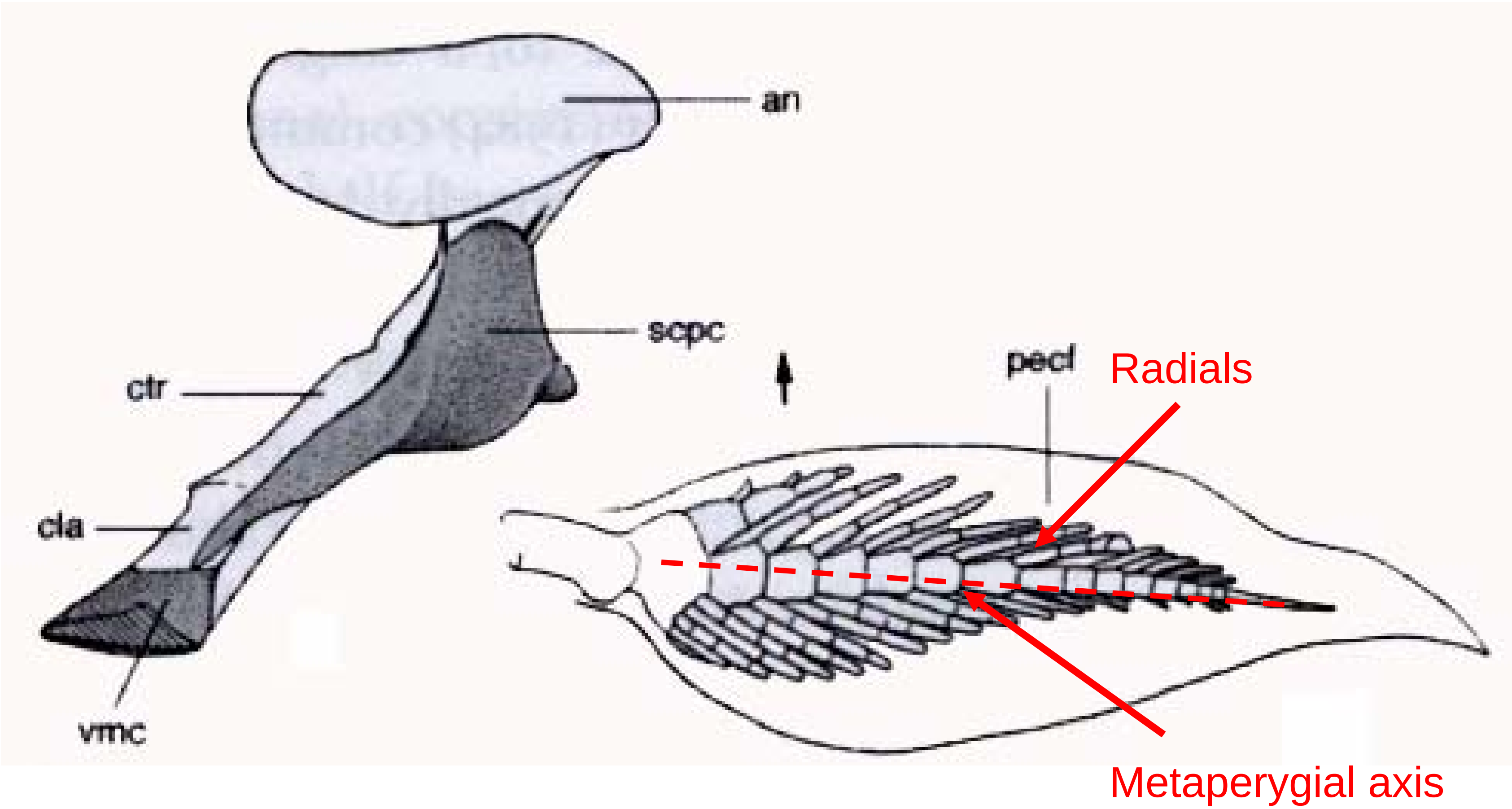


DIPNOI (lungfishes)

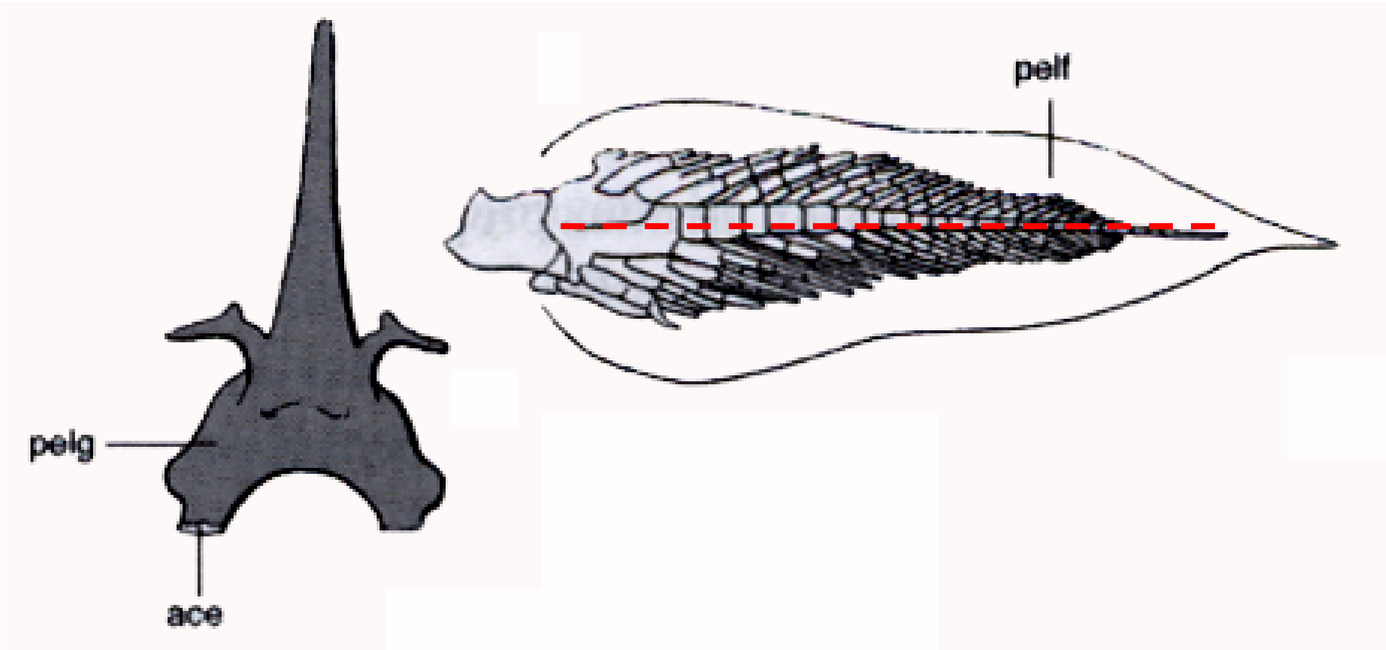
Known from later part of Early Devonian to present.

Long ago, considered potential close relatives to tetrapods given the ability of extant taxa to breathe air. No longer considered the case, though in 1981 Rosen et al. resurrected the concept of them being tetrapod sister group. (Lots of problems and errors in this interpretation.)





•Lungfish pectoral girdle has complete compliment of paired dermal elements: anocleithrum, cleithrum, and clavicle.
•Fin is clasically described as “leaf-shaped”; a complete or full “archypterygium”.
•Median “metaperygial axis” is flanked by both pre- and postaxial radials to create the leaf-shaped structure.



Pelvic fin in dipnoans is also a complete archypterium, leaf-shaped fin.

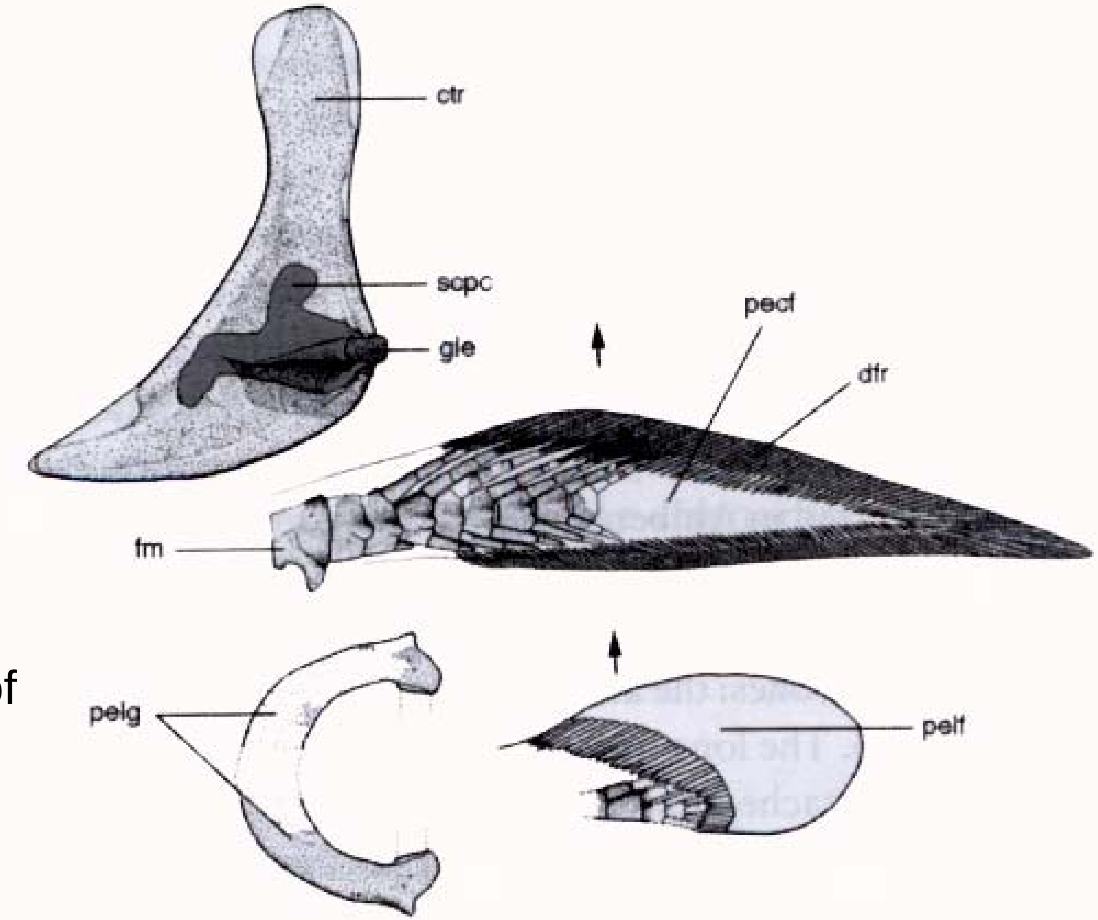
POROLEPIFORMES
Early Devonian to Early Carbonferous.

Members of this group of fishes used to be considered with Osteolepiformes to be the main components of the Crossopterygii.

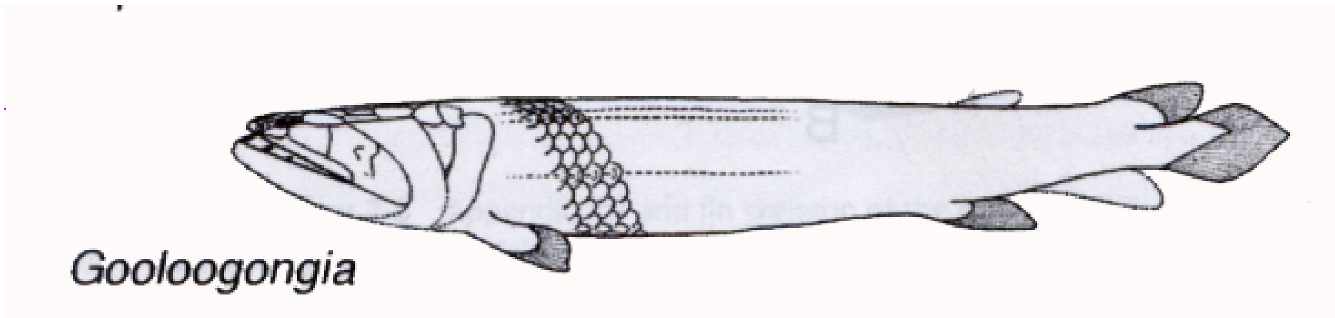
In the phylogeny presented in the book, they belong in the "Dipnomorpha" as more basal members of that group – a group of organisms that (here) I call "stem-dipnoans".

Pectoral girdle is similar to that in coelacanths, whereas pectoral fin is reminiscent of that in lungfish.

However, pelvic fin is similar to that of primitive actinopterygians (ray-finned fishes.



RHIZODONTS



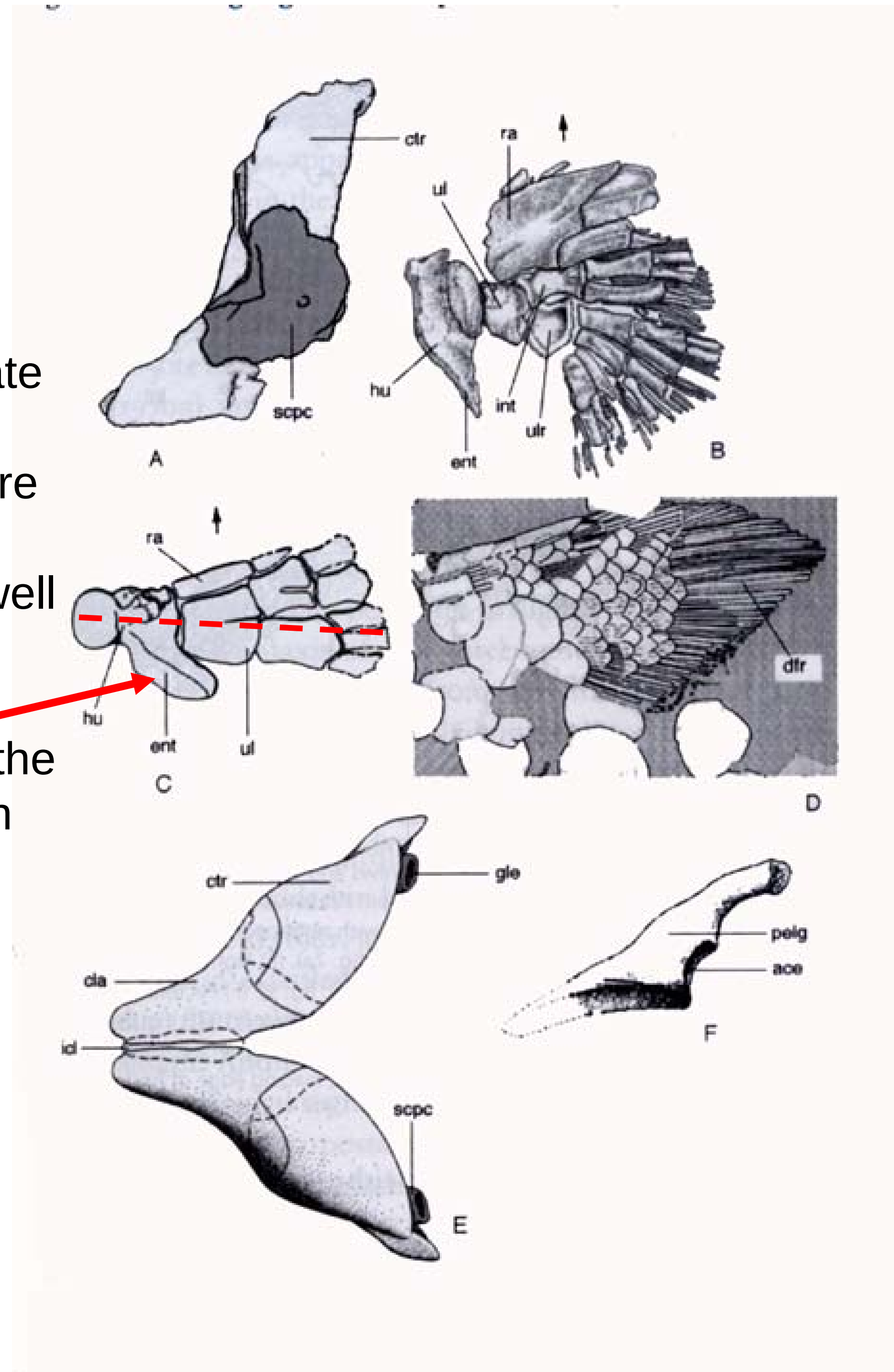
Upper Devonian to Upper Carboniferous.

Even though authors don’t plot the phylogenetic position of rhizodonts on their cladogram, they descrie them as the most basal of the stem group leading to tetrapods.

In rhizodonts, the demal skeleton is still dominant in the pectoral girdle, but endochondral scapulocoracoid is becoming better developed.

The pectoral limb is most basal to demontrate the chunkier example of what is commonly called an "abbreviate archypterygium" – more chunky and (with muscular) more lobe-shaped. However, dermal fin rays remain well expressed.

The postaxial process – entepicondyle – is the largest seen in the phylogenetic progression thus far.

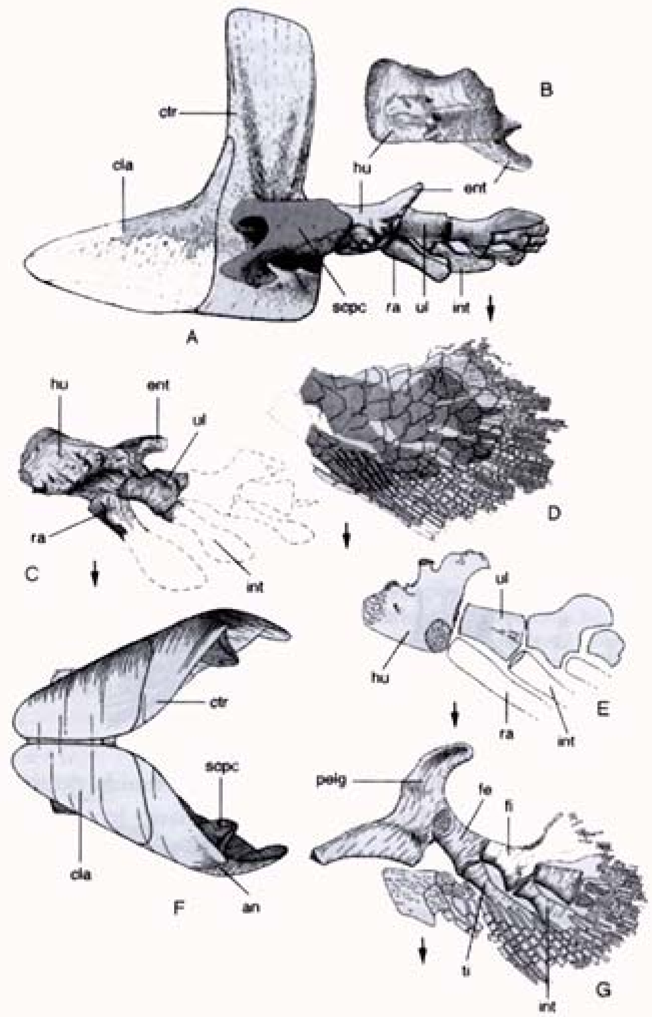


OSTEOLEPIFORMES

Middle Devonian to Lower Permian. (Youngest of this paraphyletic “group” was most recently described by Kim Scott, grad student at CSUSB.)

Members of this group of fishes used to be considered with Porolepiformes to be the main components of the Crossopterygii. Now known to be a paraphyletic “grade”. However, members of this grade have historically been critically important to our understanding of the origin of tetrapods.

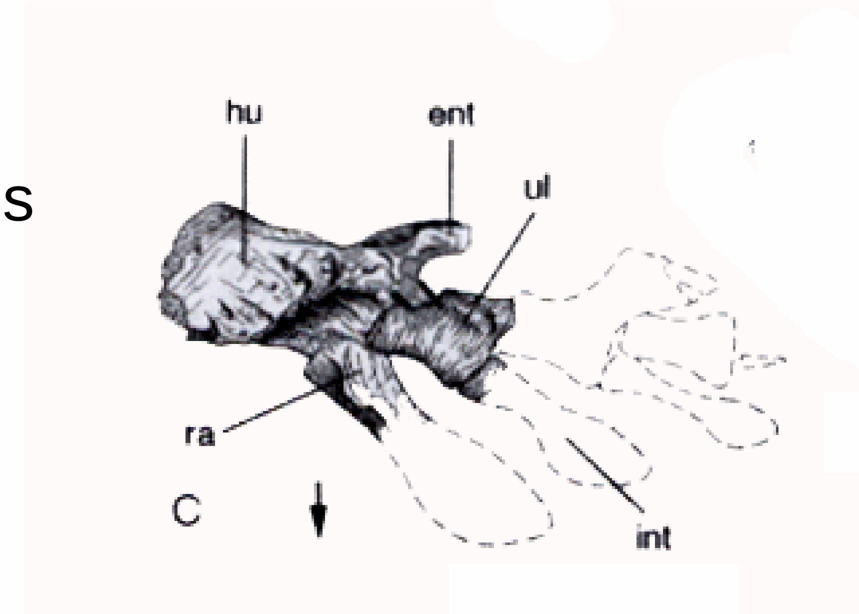
Eusthenopteron remains one of the most carefully characterized of all Paleozoic fishes. *Osteolepis* and *Sterropterygion* have also been very important members of the group.

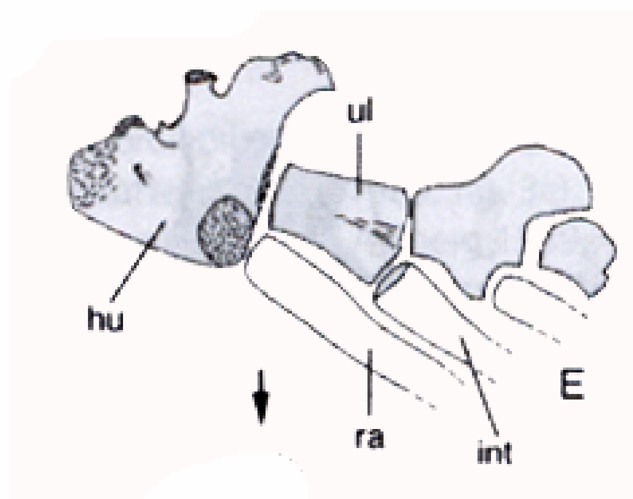


The pectoral fin in “osteolepid crossopterygians” shows what is considered by many to be the classic abbreviate archypterygium.

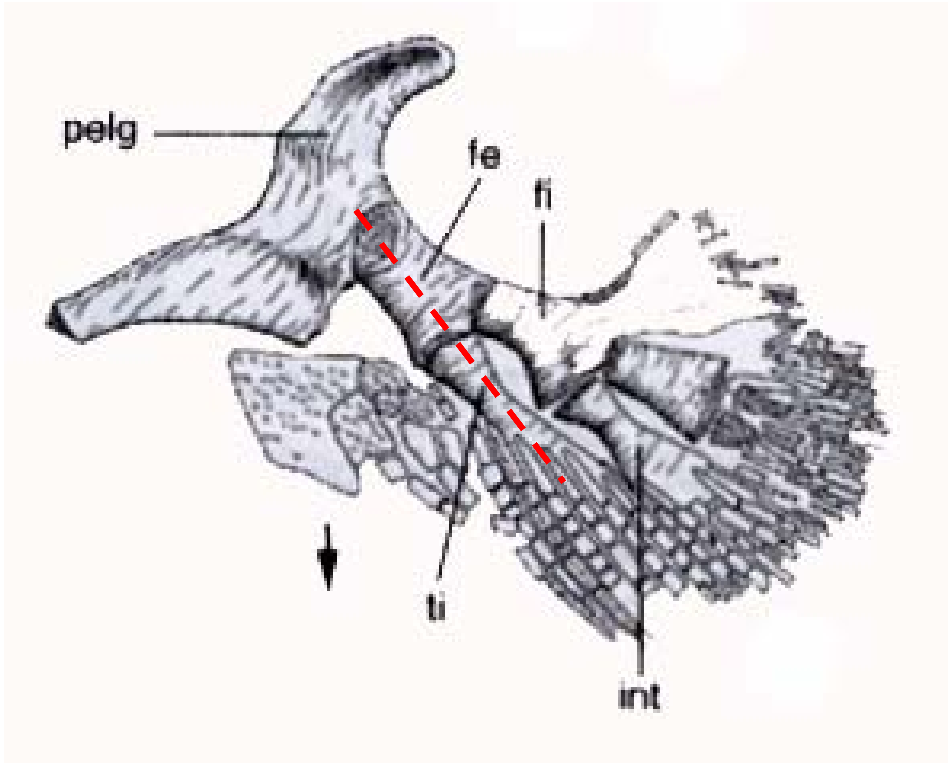
Radials are present only on the preaxial (cranial) side, the largest and most proximal the RADIUS itself.

Rachoff’s (1980) work on *Sterropterygion* demonstrated the probably position that the pectoral fin was actually carried in the living fish.





Pelvic fin in osteolepids – the pelvic girdle is small and bar-like. It was obviously burried in musculature, not attached to vertebral column.



Note that the acetabulum is now concave, accepting a convex femoral articulation.

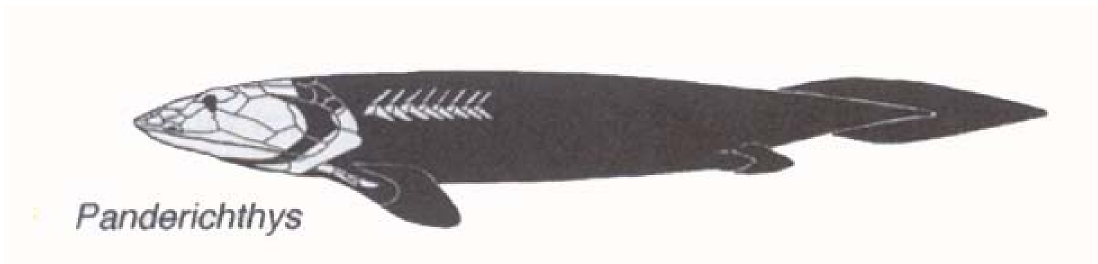
Tibia is the pre-axial side element distal to the femur. Thus, the tibia is serially homologous to the radius. Fibula is serially homologous to ulna.

Fin rays still present as typical lepidotrichia.

Eusthenopteron


OUT OF THE OOZE
AND BORN TO CRUISE

PANDERICHTHYIDA (*Panderichthyes, Elpistostega, Obruchevichthyes*)



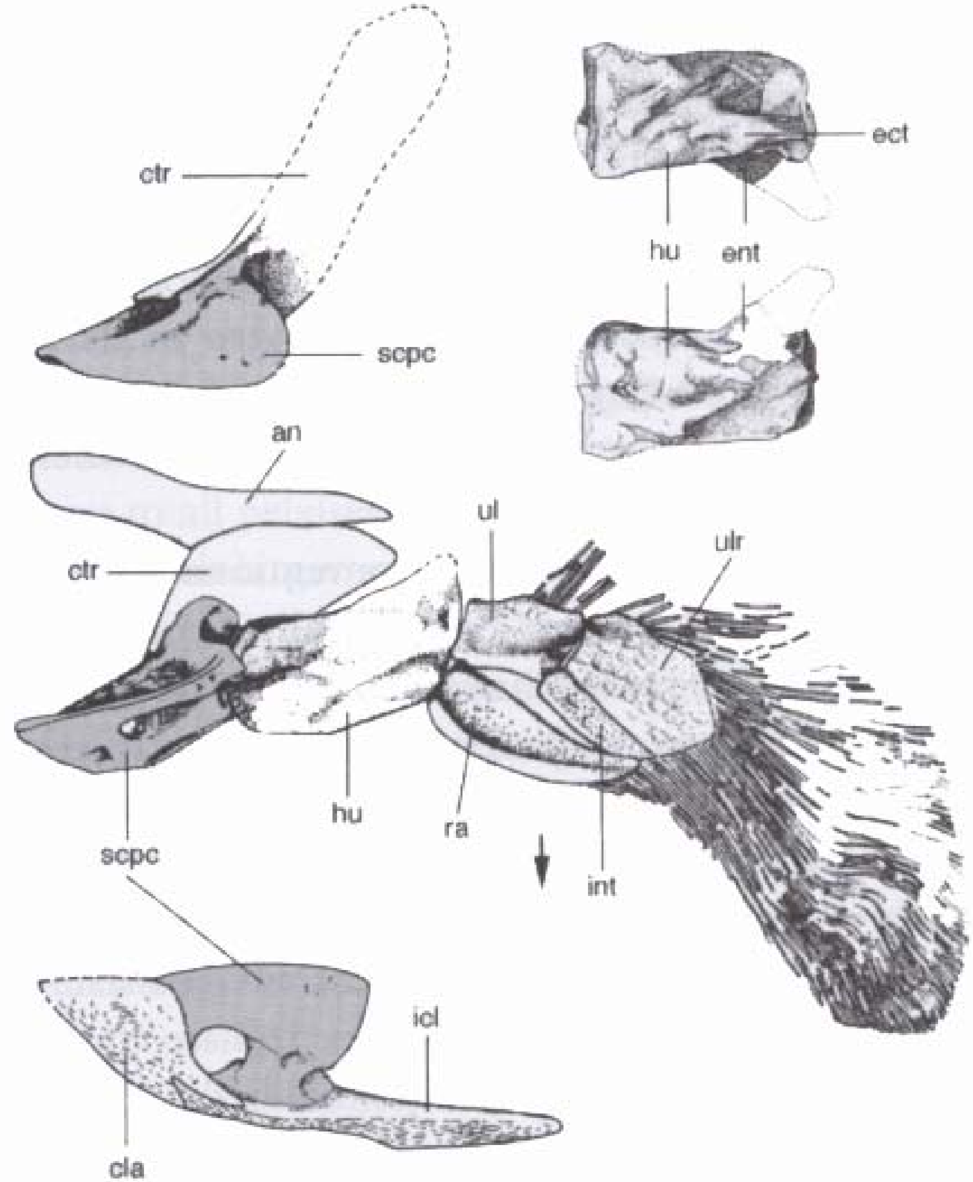
Late Devonian (Frasnian).

Formerly considered most advanced of osteolepiform crossopterygians, this group is still clearly the closest sister-group to tetrapods, and thus critical to understanding the transition from fish fins to tetrapod limbs. (Cranial anatomy of [particularly] *Panderichthyes* and *Elpistostega* is closest of any fish group to tetrapod skull.)

Pectoral girdle in panderichthyids includes all dermal elements.

Although dermal elements aren't drastically different from that of osteolepids, the endochondral scapulocoracoid element is significantly larger.

Both pectoral and pelvic fins placed relatively more ventrally than in more primitive taxa.

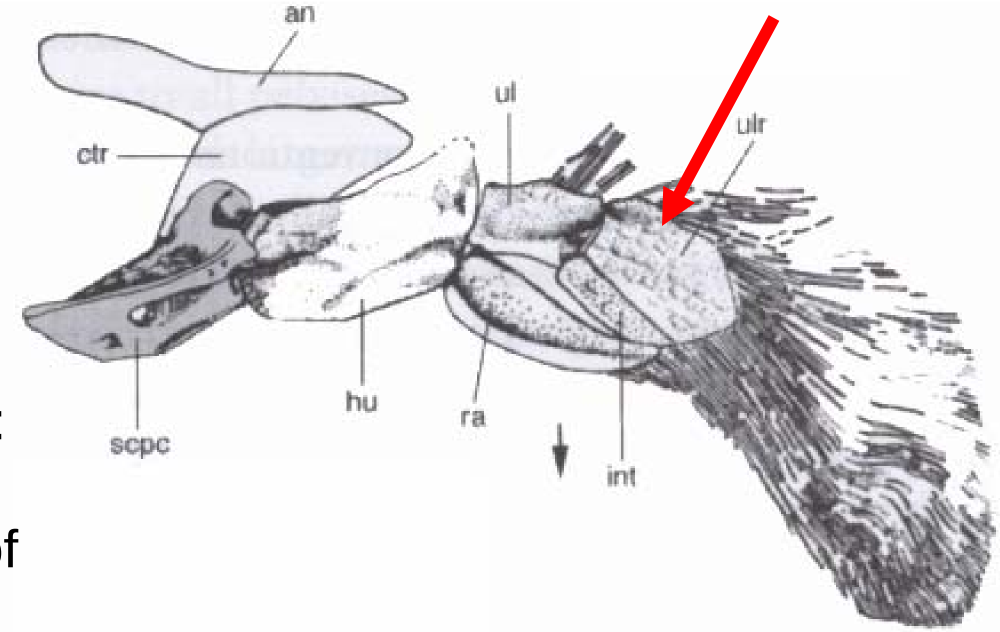


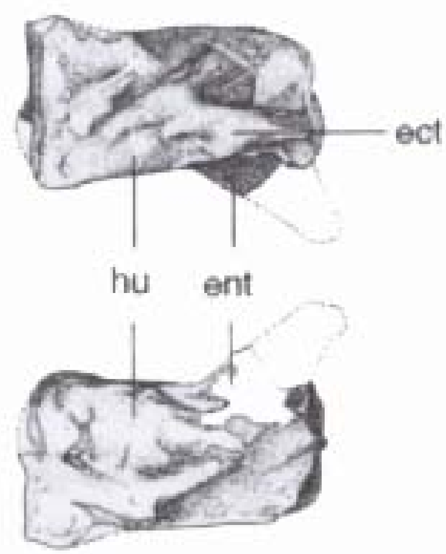
In panderichthyids, there is no clear proximo-distal iterative pattern along the limb as in more primitive fish.

Elements along the pectoral limb are limited to just three elements: humerus, ulna, and ulnare (element also found in the wrist of tetrapods).

Fin skeleton contains fewest elements of any described thus far.

Humerus is dorsoventrally compressed. Again, more like tetrapods than fish.

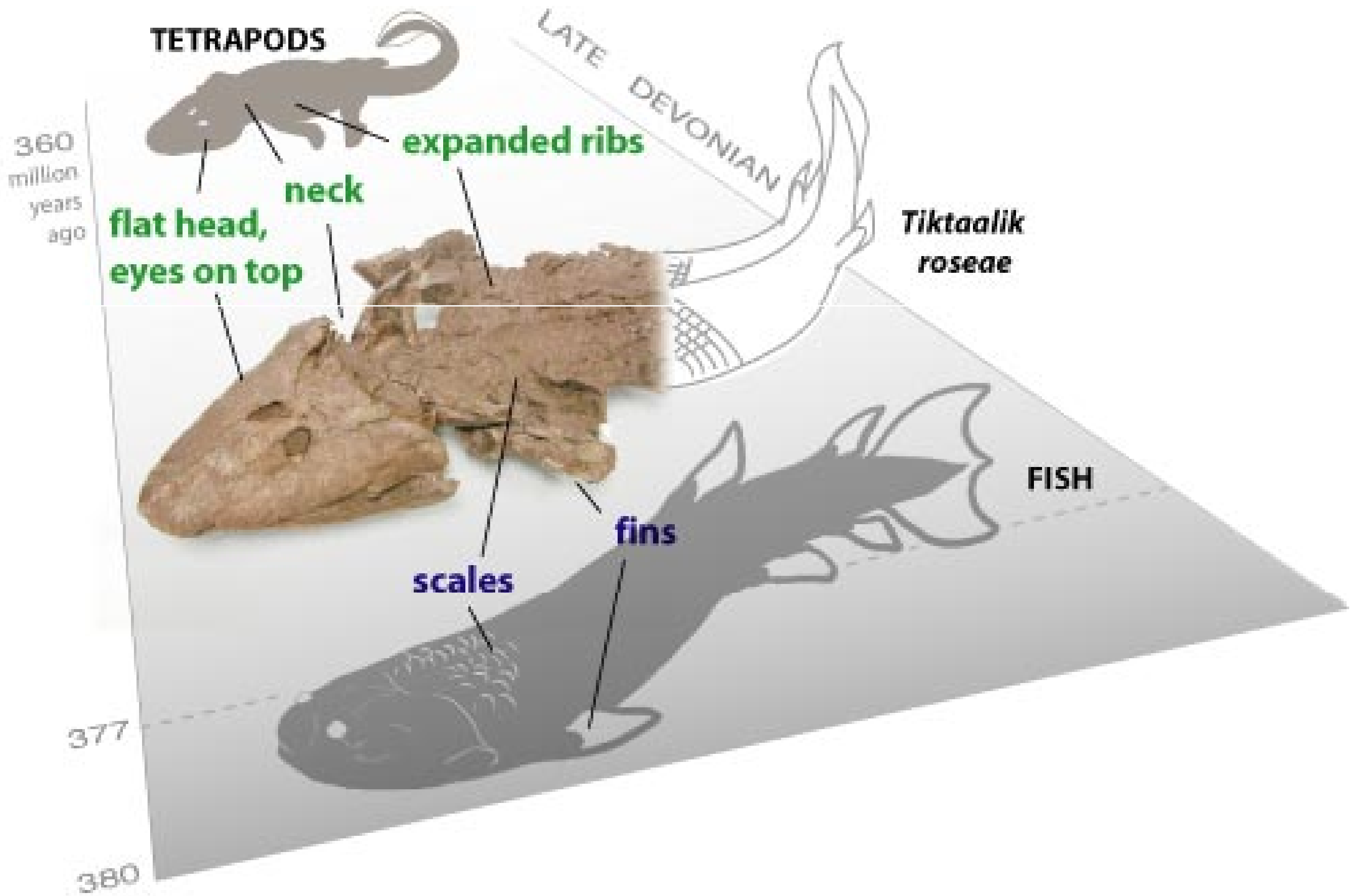




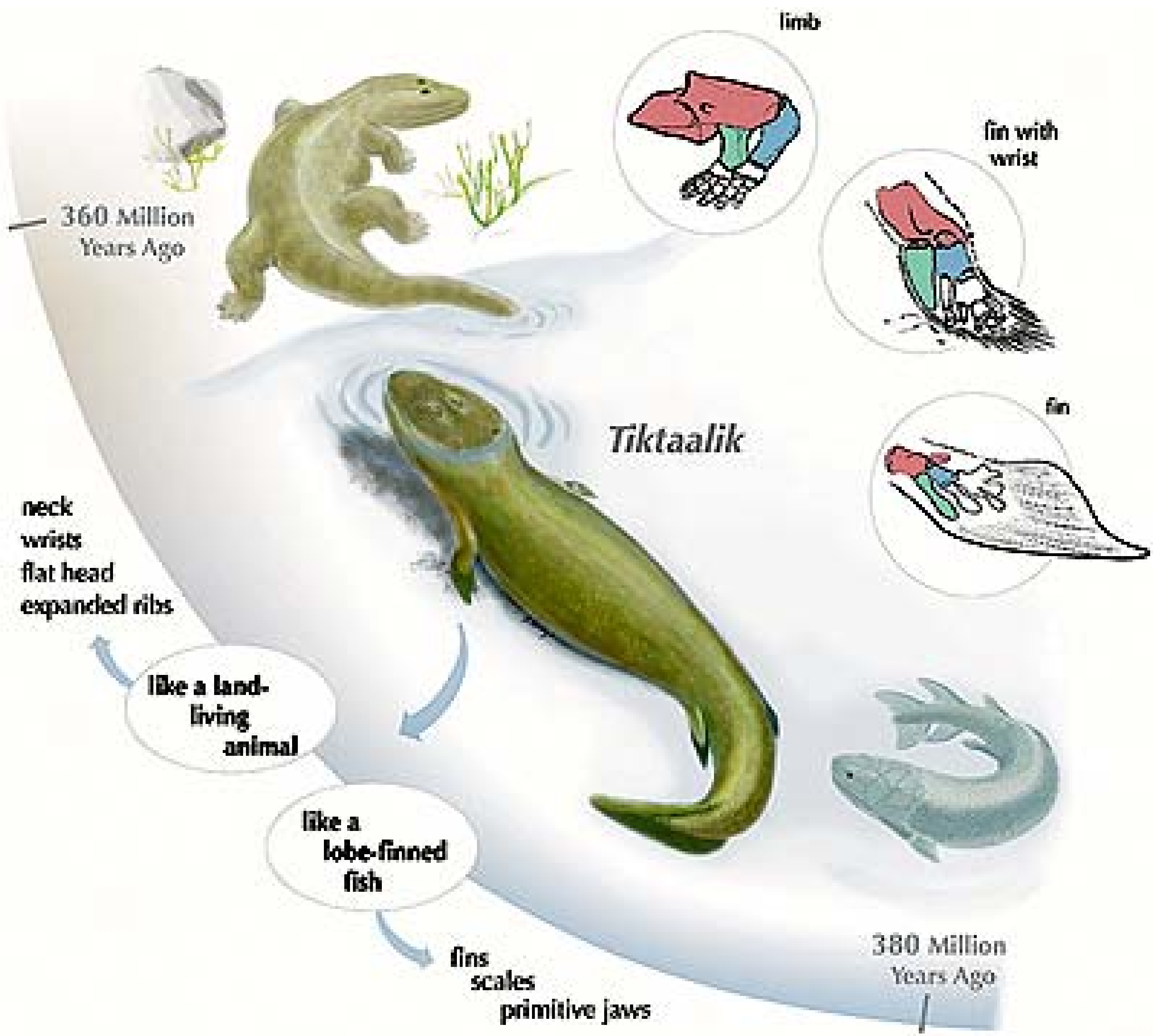
TITAALIK

Since this book went to press, a new fossil, *Tiktaalik* was discovered. *Tiktaalik roseae* – a lobe-finned fish intermediate between typical sarcopterygians and basal tetrapods.

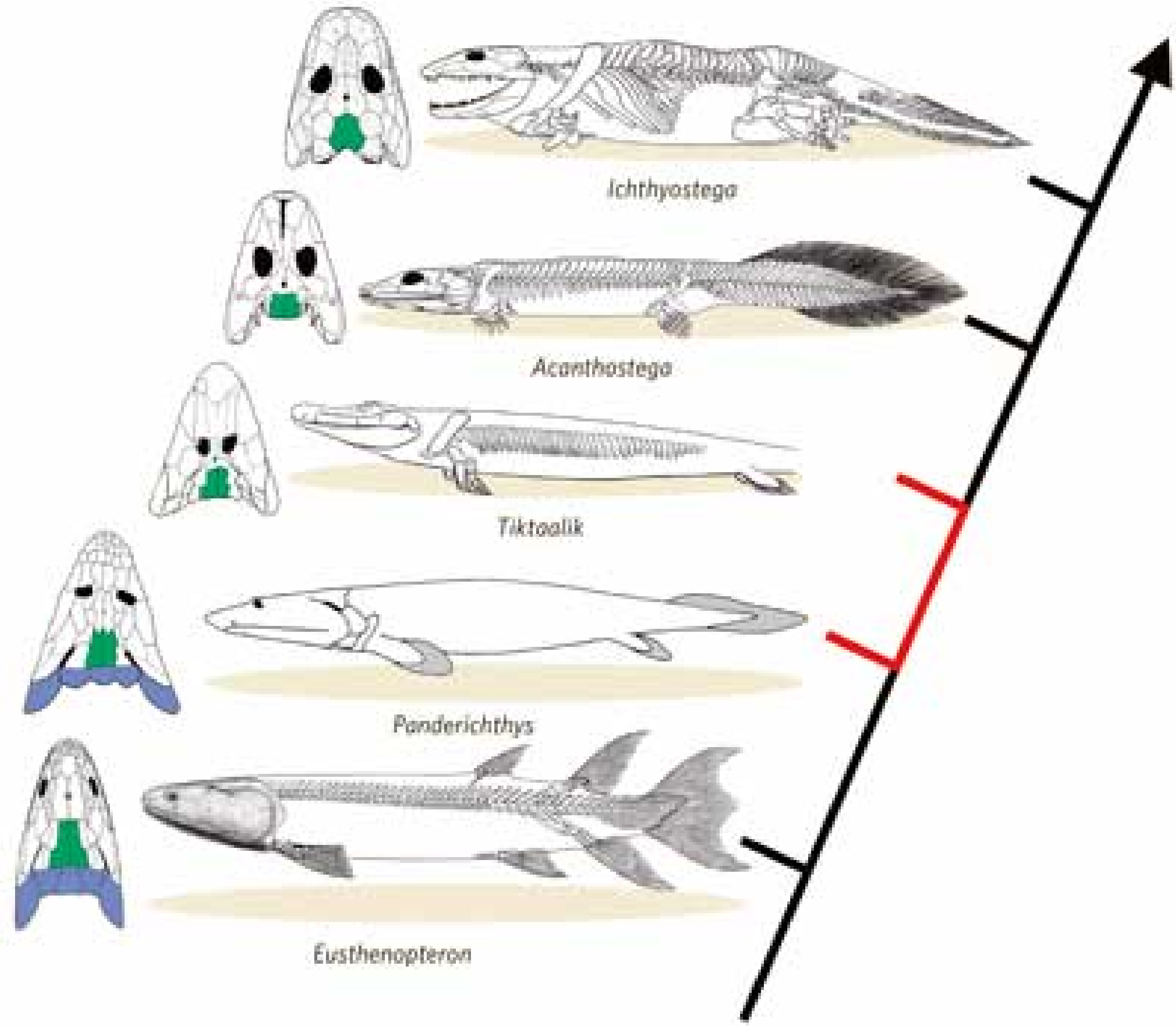
Mid to Late Devonian; 375 million years old.



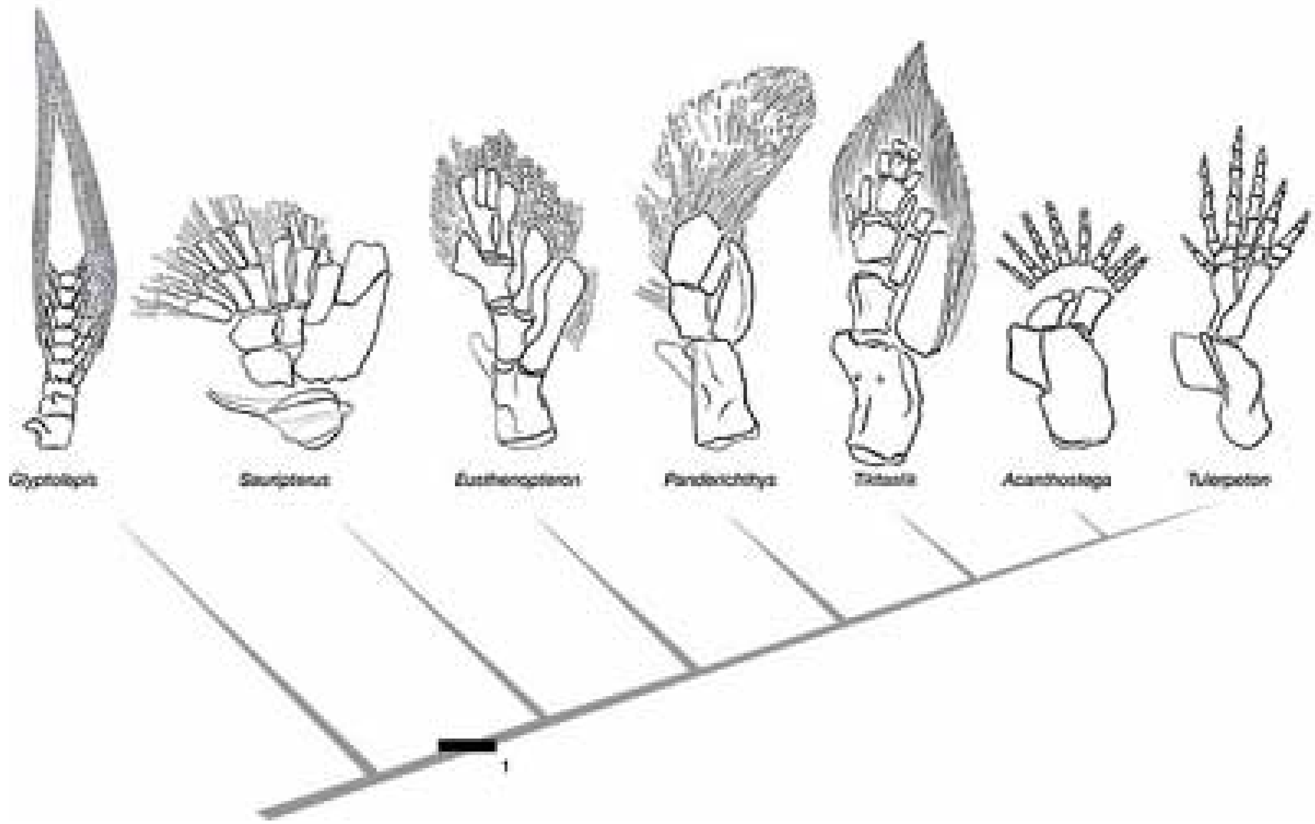
Tiktaalik is probably a panderichthyid fish or close relative of them.



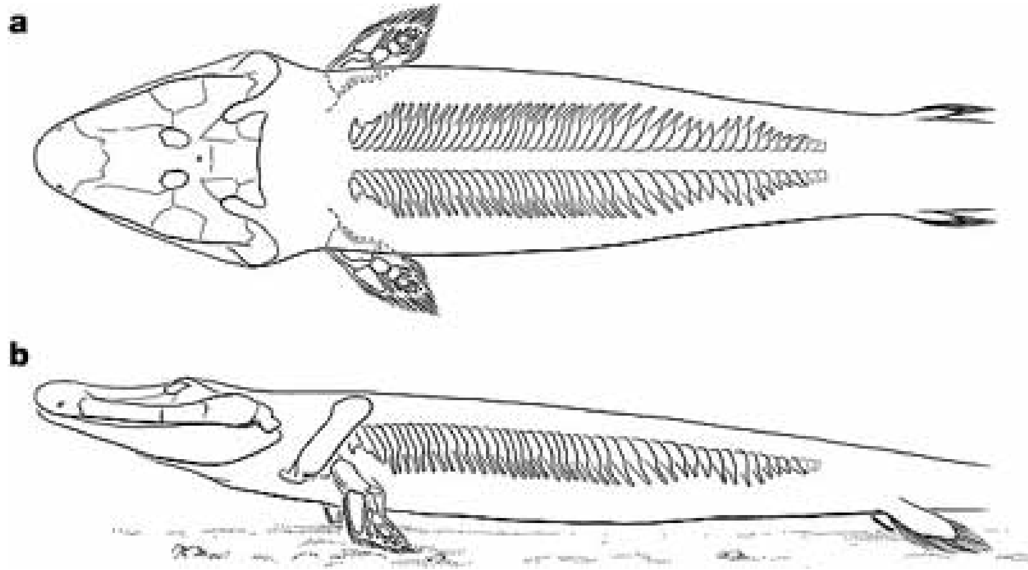
limb
fin with wrist
fin
360 Million Years Ago
Tiktaalik
neck
wrists
flat head
expanded ribs
like a land-living animal
like a lobe-finned fish
fins
scales
primitive jaws
380 Million Years Ago

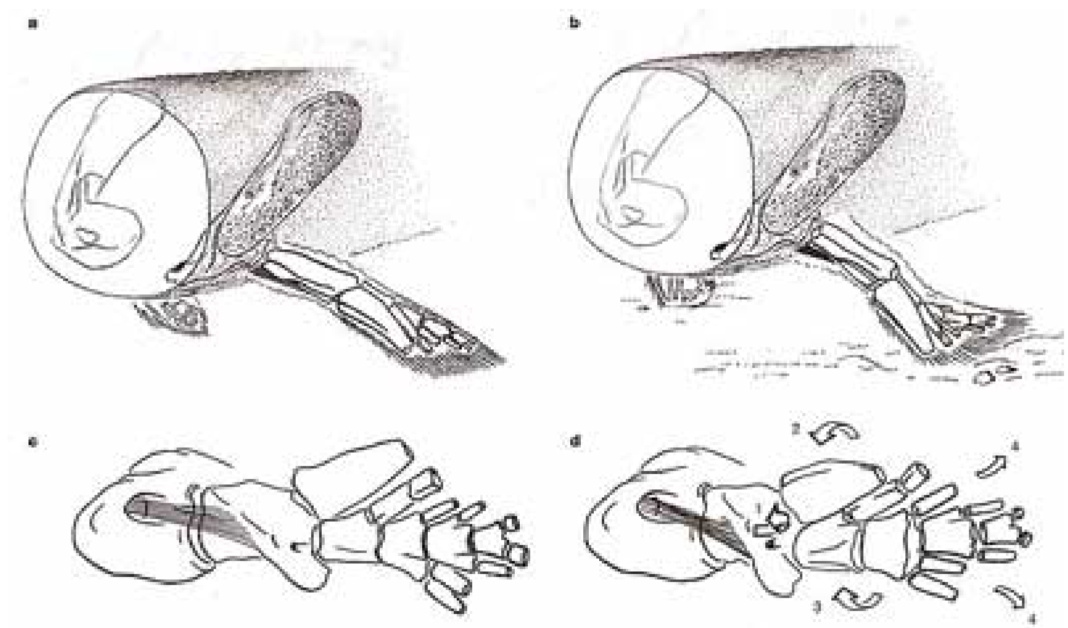


Ichthyostega
Acanthostega
Tiktaalik
Panderichthys
Eusthenopteron



Tiktaalik is a fish with rist bones, yet still retaining lepidotritichia (fin rays)


a
b

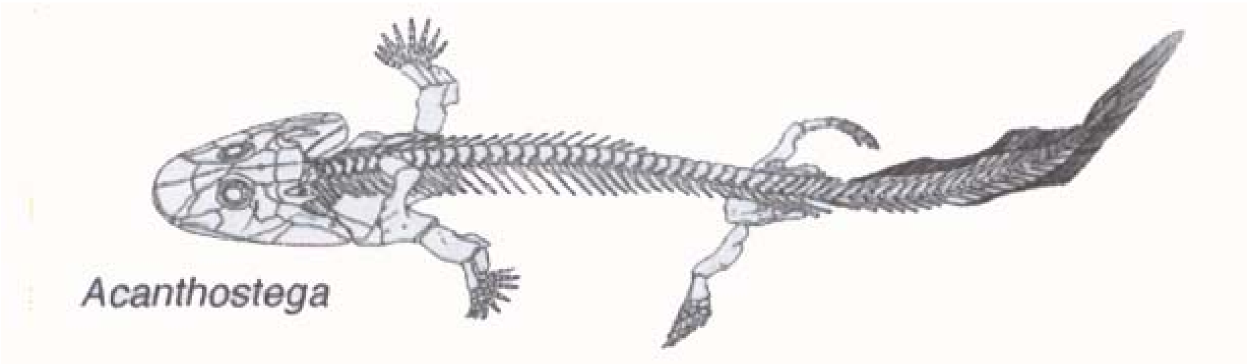

a
b
c
d
2
4
3
4

ACANTHOSTEGA

Upper Devonian (Frasnian)

The most basal tetrapod considered here. Acanthostega, Ichthyostega, and Ventastega have been grouped as Ichthyostegalia, but they are considered seperately here and in the book.

Despite that it retains many fish-like characteristics, its limb girdles and limbs differ considerably from those of panderichthyids and osteolepids.



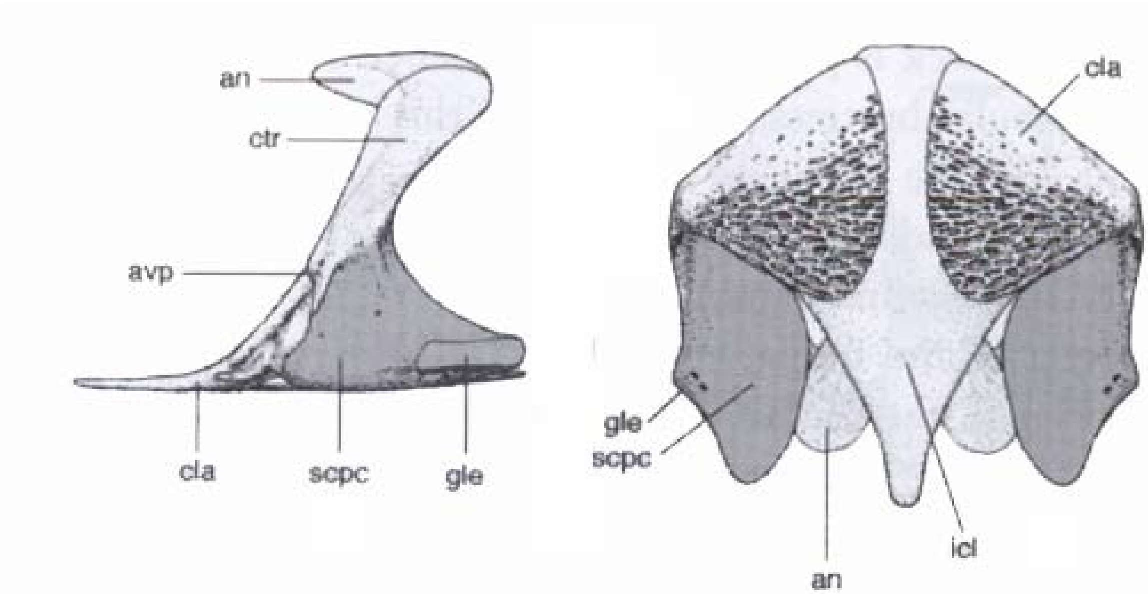
Acanthostega gunneri

(Image courtesy of Jenny Clack)

Acanthostega gunneri (Image courtesy of Jenny Clack)

Acanthostega gunneri (Image courtesy of Jenny Clack)

Acanthostega gunneri (Image courtesy of Jenny Clack)



Pectoral girdle in *Acanthostega* has significantly enlarged scapuocoracoid component, almost as large as dermal component. Note retention of anocleithrum, but no supracleithrum.

The glenoid shows the first example of a non circular morphology, in this case “strap-shaped” – on the way to the twisted or “screw-shaped” glenoid of tetrapods.

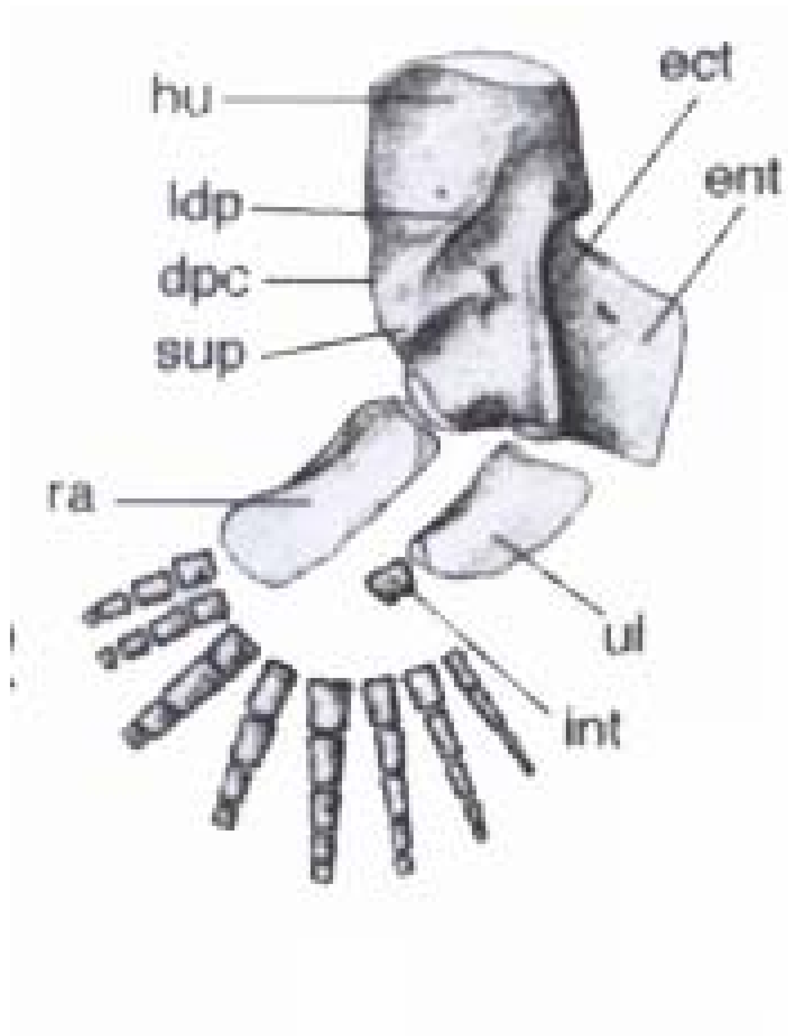
Humerus in *Acanthostega* “L-shaped” as in most primitive tetrapods.

Radius and ulna approximately subequal in length.

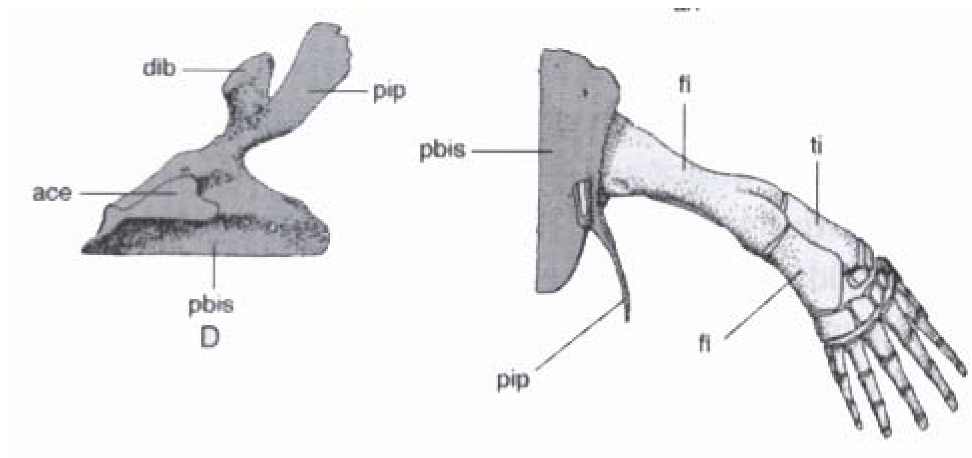
Although an ulnare is known in *Panderichthyes* only an intermedium is known for the wrist in *Acanthostega*.

Polydactylous – eight digits present. A very “fin-like” hand.

No dermal fin rays.

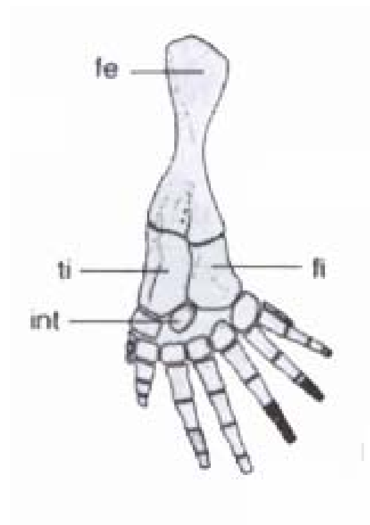


Pectoral girdle in *Acanthostega* much more robust, showing approximately triangular shape characteristic of tetrapods.



Thre separate ossifications of ilium, ischium, and pubis not distinct, but all three regions clearly present.

Femur has a distinct shaft.



Tibia + fibula distinctly shorter than femur.

Elements of the ankle clearly developed: tibiale, intermedium, fibulare.

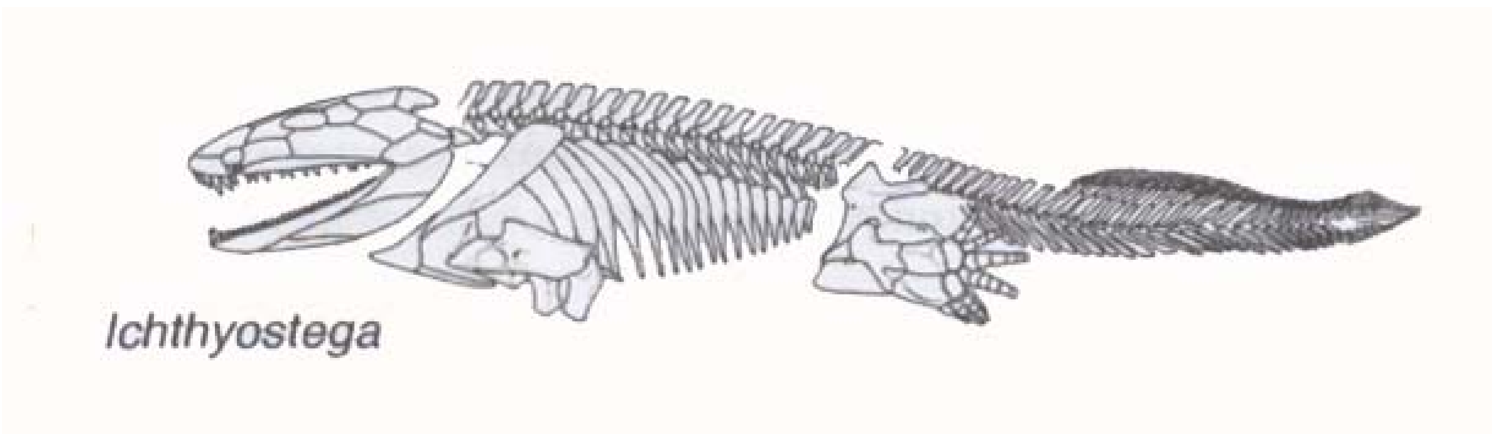
Eight digits.

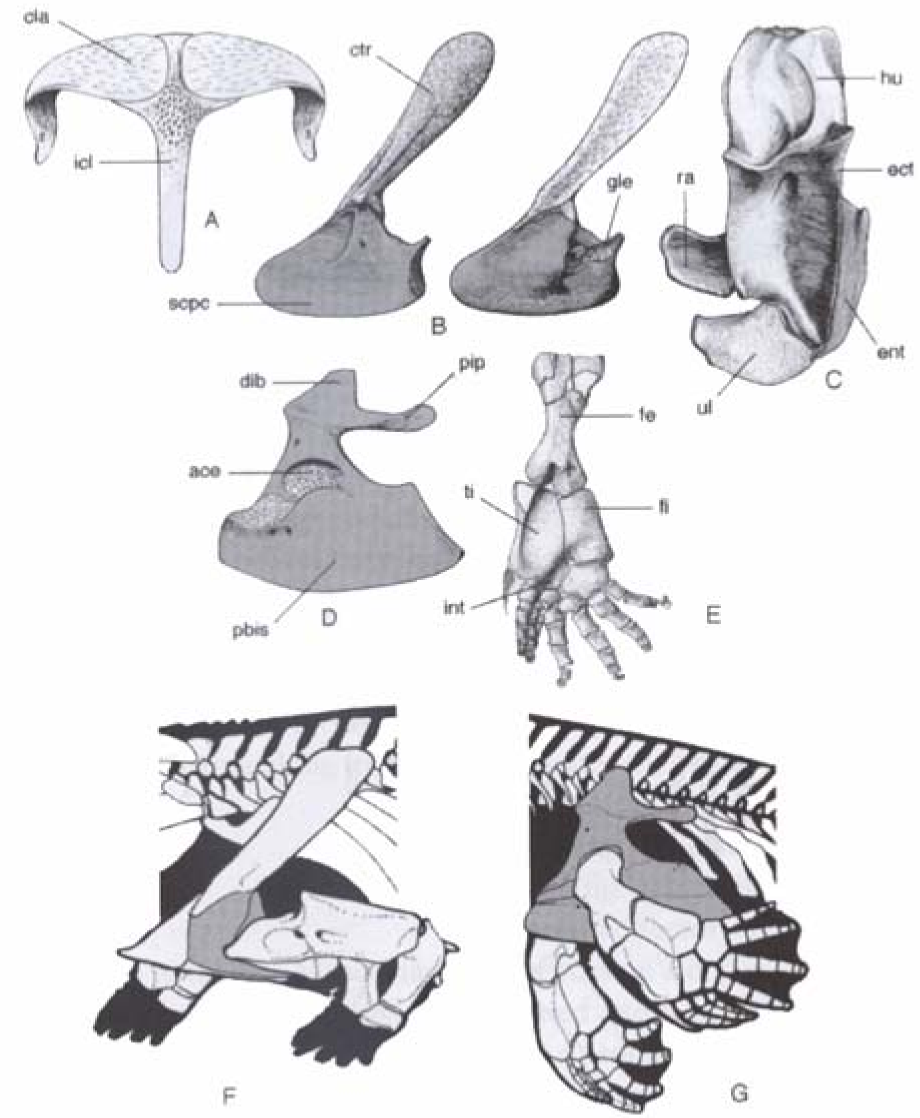
ICHTHYOSTEGA

Upper Devonian (Frasnian)

THE classic earliest tetrapod, due primarily to work of Erik Jarvik and later Michael Coates and Jenny Clack.

However, now no longer considered the most primitive known tetrapod, but somewhat more derived than *Acanthostega*.



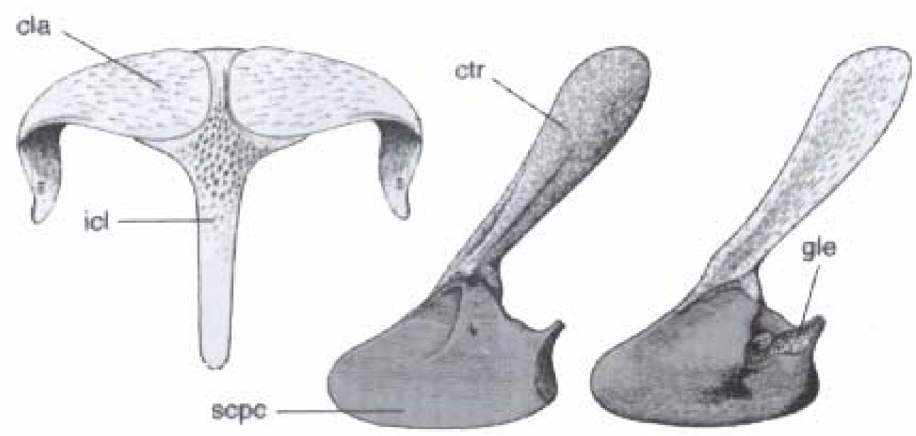


ICHTHYOSTEGA

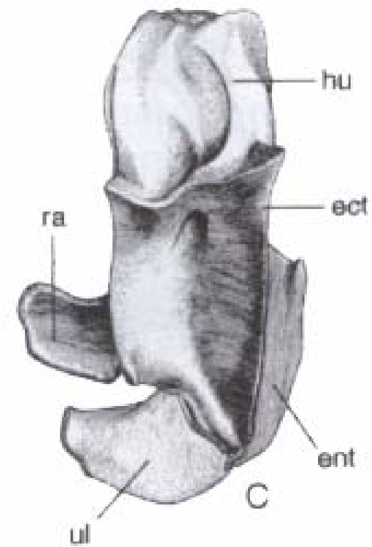
Dermal elements of pectoral girdle in *Ichthyostega*: cleithrum, clavicle, interclavicle.

Scapulocoracoid large and well ossified.

Glenoid with characteristic strap-shape of early tetrapods.



Humerus in *Ichthyostega* is a more robust element than in *Acanthostega*.



Radius and ulna subequal in length.

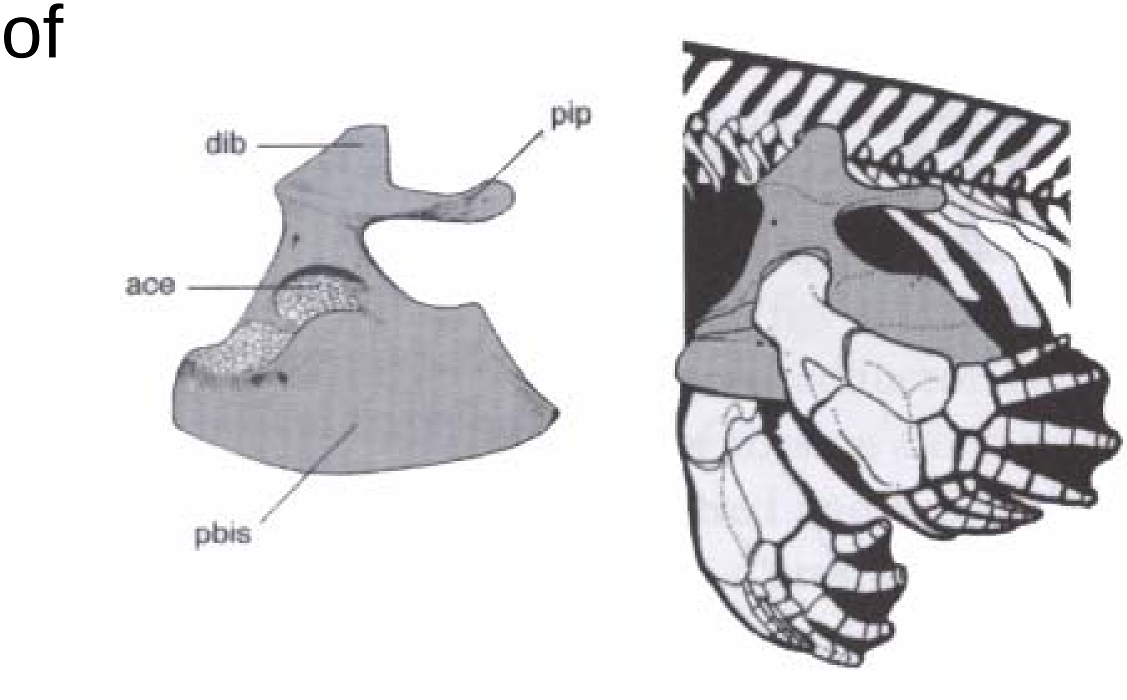
First evidence of a distinct olecranon process on ulna.

Manus not known, but if pes is any indication, then it was almost certainly polydactylous.

Pelvic girdle in *Ichthyostega* is pair of well ossified plates.

Still no evidence of separate ilium, ischium, and pubis.

Clear evidence for articulation with a sacral rib at iliac apex.

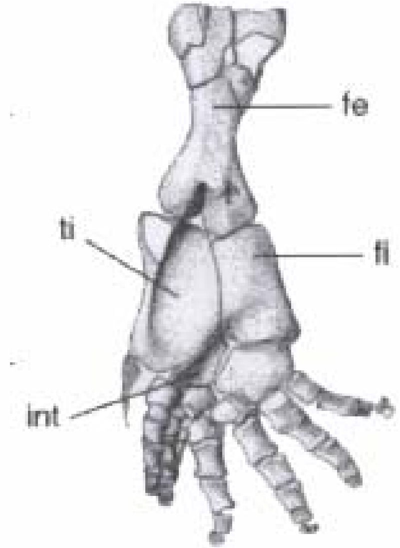


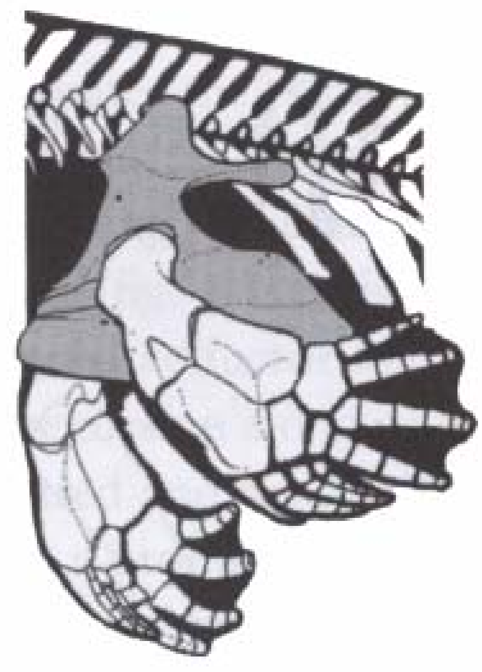
Hindlimb in *Ichthyostega* very similar to that in *Acanthostega*.

Elements flat, contributing to a paddle-like shape to the limb. (Still fish-like.)

Ankle is well ossified.

Seven digits (reduced from eight in *Acanthostega*).

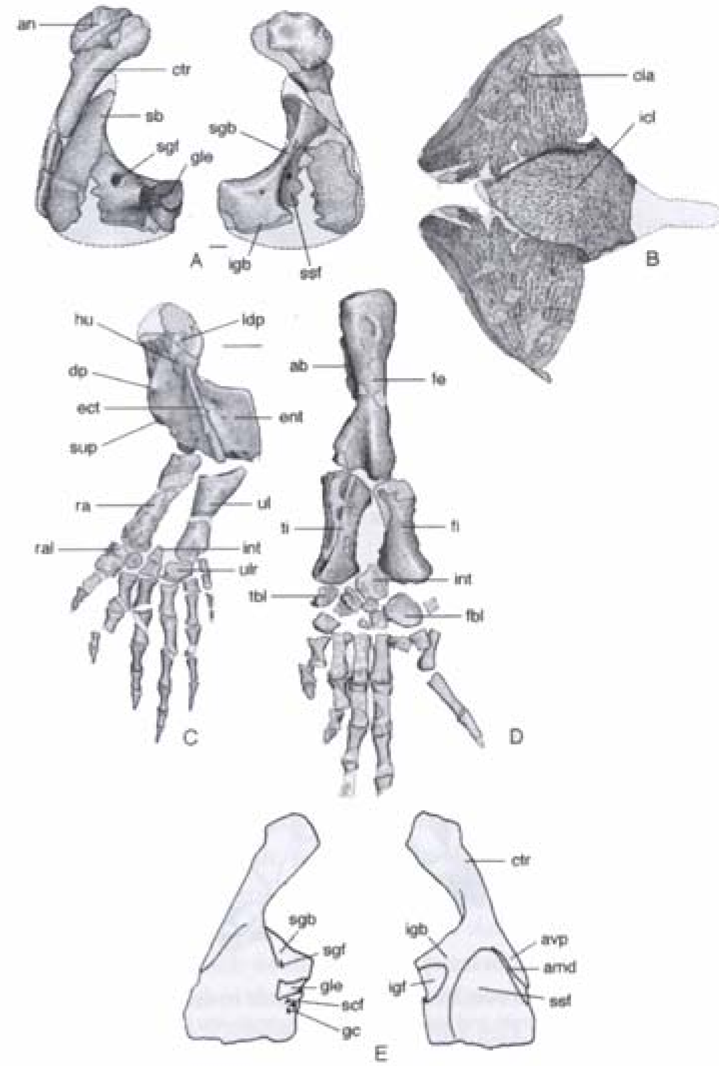




TULERPETON

Upper Devonian of central Russia.

First polydactylous tetrapod ever discovered and recognized as such.



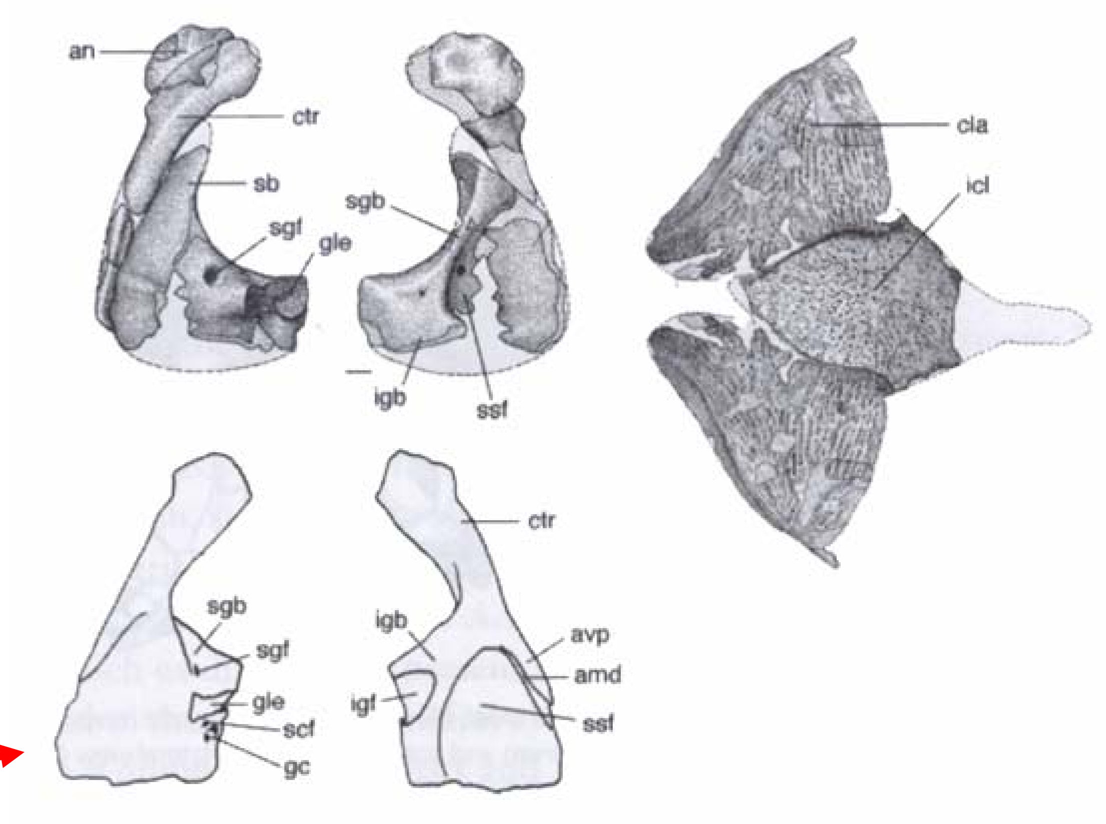
Expanded dermal clavicles in *Tulerpeton* meet in midline. Much more like slightly more derived tetrapods like colosteids.

Interclavicle has clearly developed, robust stem.

Anocleithrum still present.

Earliest example of an expanded scapular region.

Condition in *Hynerpeton* is very similar.



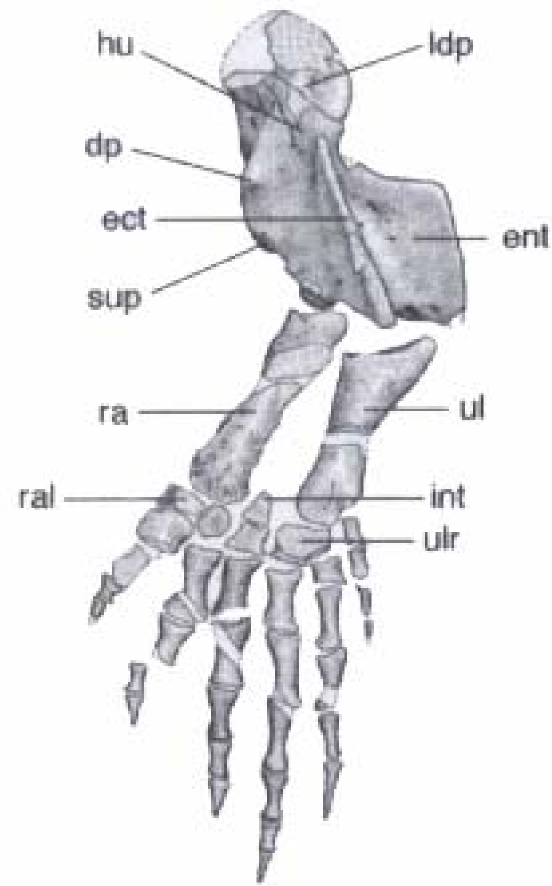
Pectoral limb in *Tulerpeton*, humerus is less flat and paddle-like.

Moderate torsion between proximal and distal ends of the humerus. This is the earliest tendency toward standard tetrapod condition of humeral heads at 90 degree angles to one another.

Supinator process and radial condyles now distinctly seperated (by notch).

Six phalanges.

Phalanges distinctly elongate.

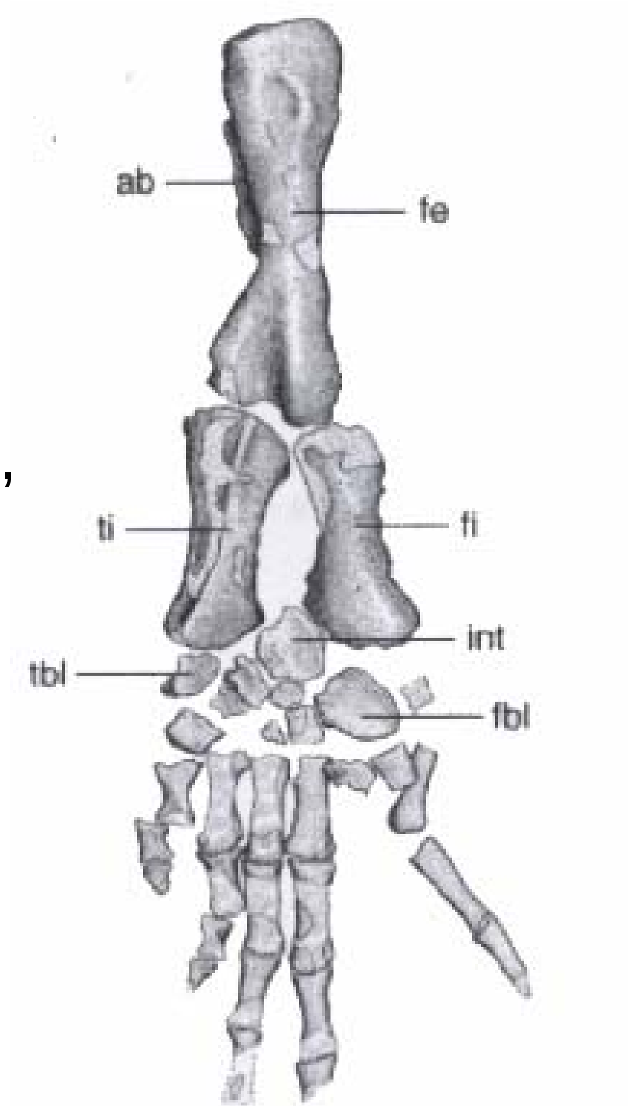


Hindlimb in *Tulerpeton* has a femur with well developed neck, distinct intertrochanteric fossa, and robust adductor blade.

Tibia and fibula are no longer flattened, and are approximately cylindrical in shape. They show a distinct interepipodial space for interosseous membrane.

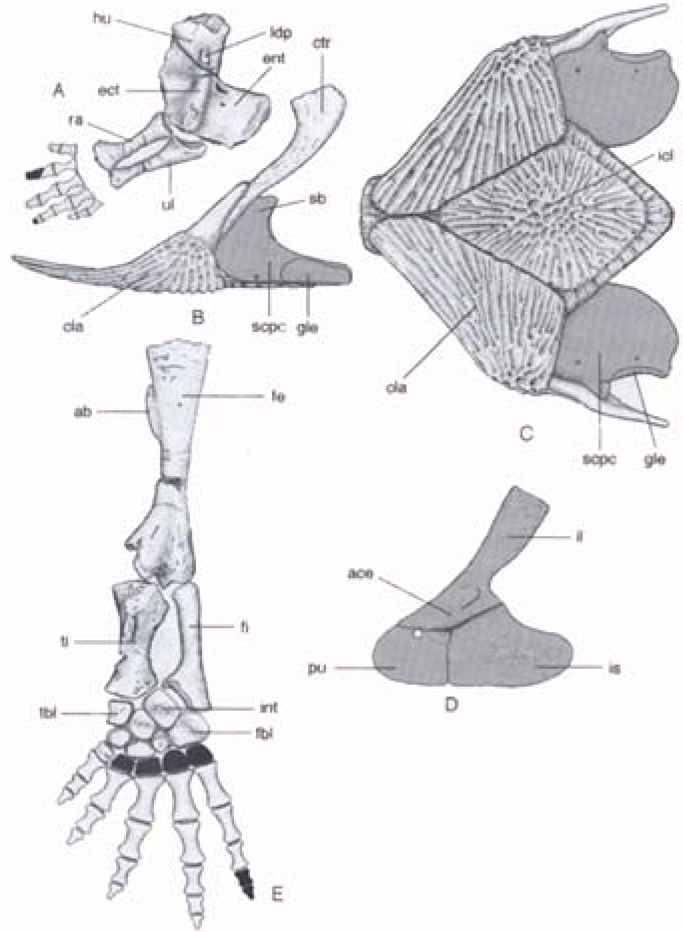
Distinct distal tarsal series.

Six pedal digits.



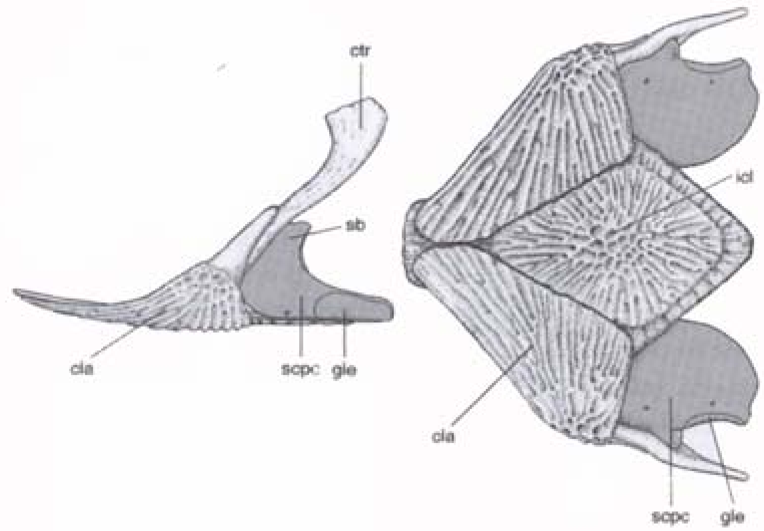
COLOSTEIDAE

Carboniferous – late Visean to late Moscovian (330-300 mybp).



Pectoral girdle in colosteids (here illustrated by *Greererpeton*) lacks anocleithrum. Large rhomboidal interclavicle.

Scapulocoracoid enlarged and coracoid plate expanded posteriorly.

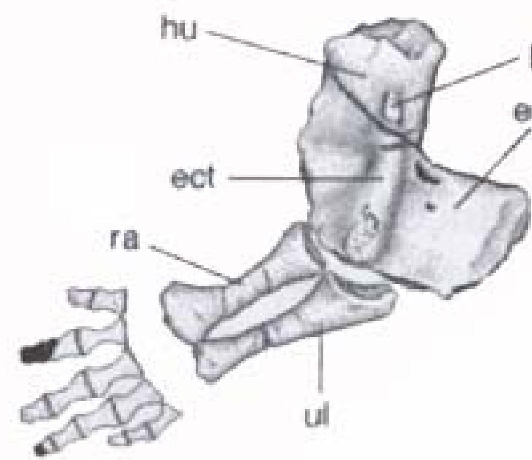


Humerus distinctly "L-shaped". Humeral head narrower than in ichthyostegalians.

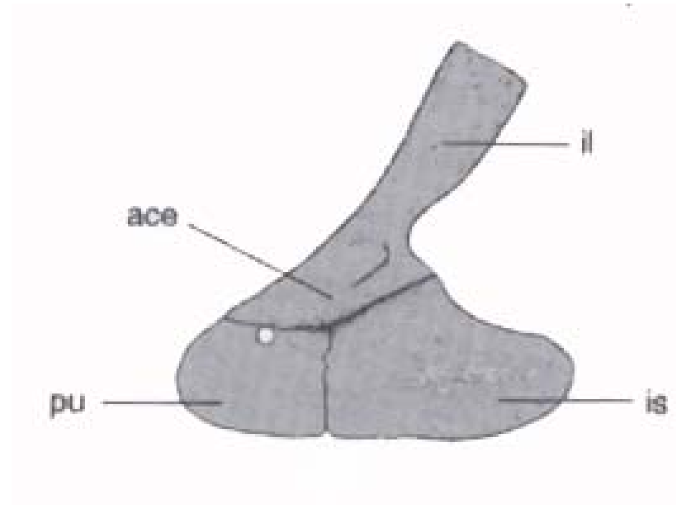
Well developed interepipodial space between radius and ulna.

Pentadactyl.

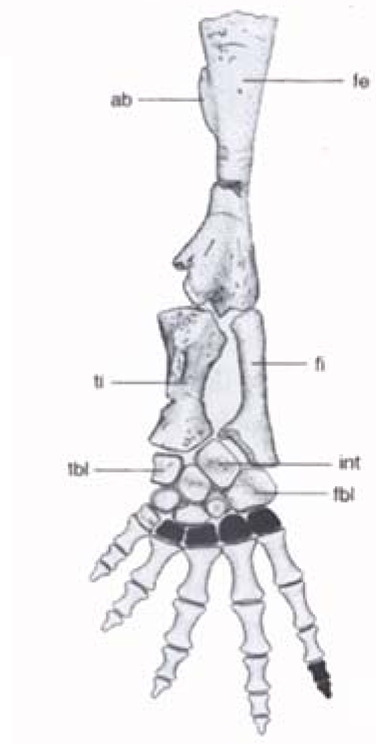
Manual formula 2-3-3-4-3.



Pubis, ischium, and ilium are seen as suture separated entities for first time in colosteids.



Tibia has prominent cnemial crest.



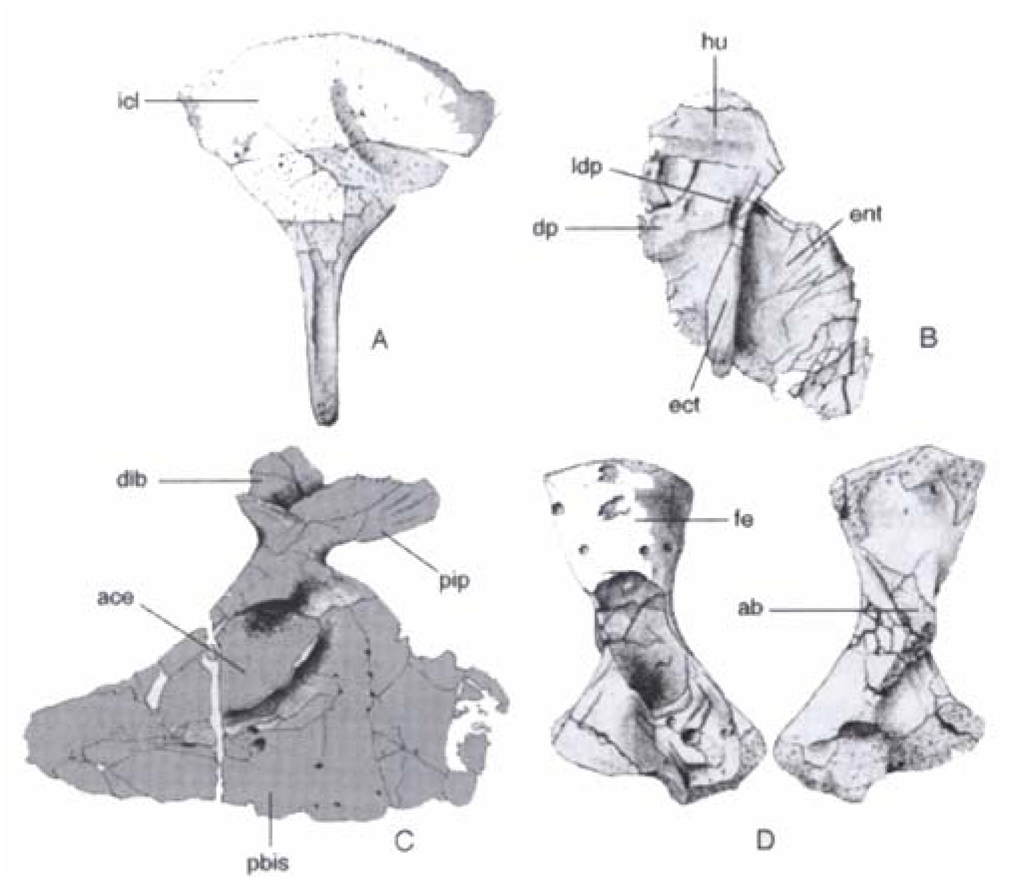
Pentadactyl.

Pedal formula is 2-2-3-4-2(+)

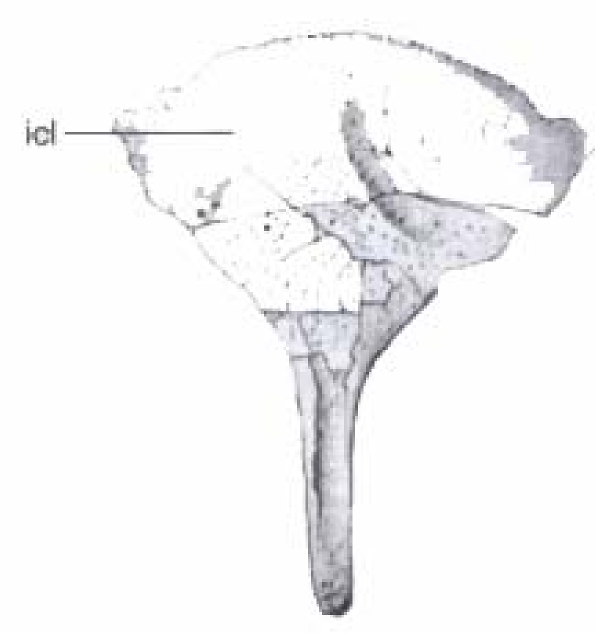
WHATCHEERIDAE

Known from *Whatcheeria deltae* (from near the town of Whatcheer, Iowa).

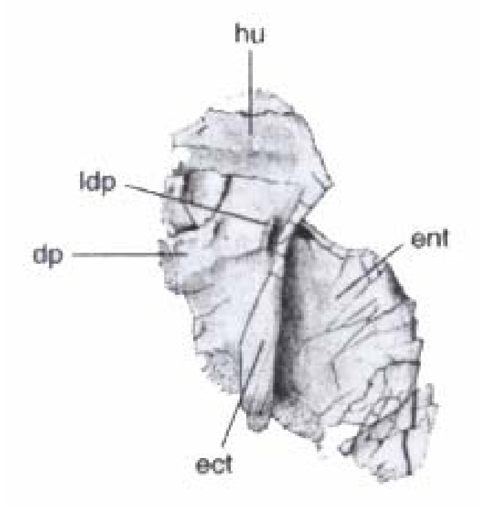
Carboniferious (Pennsylvanian) – Chesterian/Visean.



Pectoral limb in *Whatcheeria* – interclavicle shows unusual primitive retention of a very long stem.



Humerus is massive, with considerably more torsion than in colosteids or ichthyostegalians.

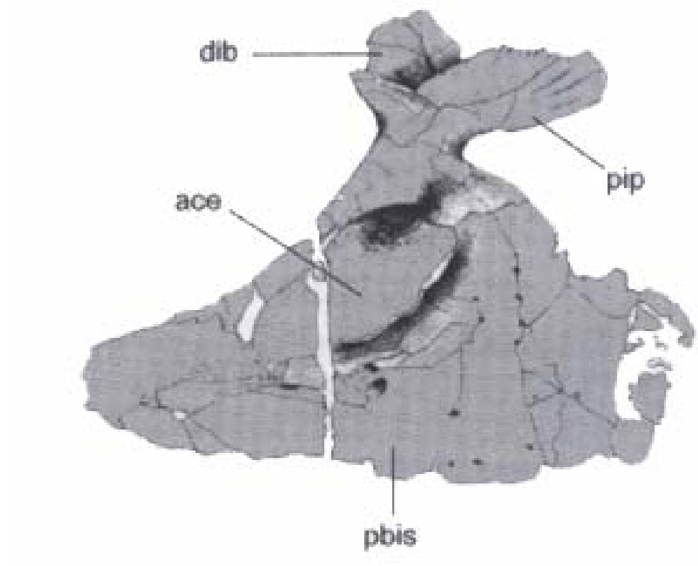


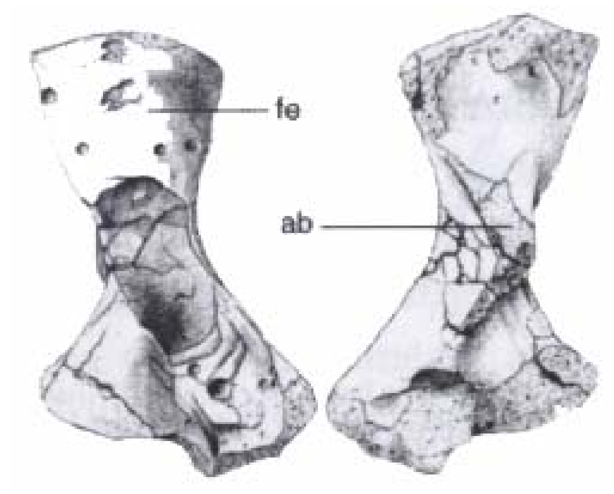
Distinct ilium, ischium, pubis in *Whatcheeria*.

Robust femur.

Tibia and fibula also robust.

Many phalangeal elements known, but articulated condtition not known.



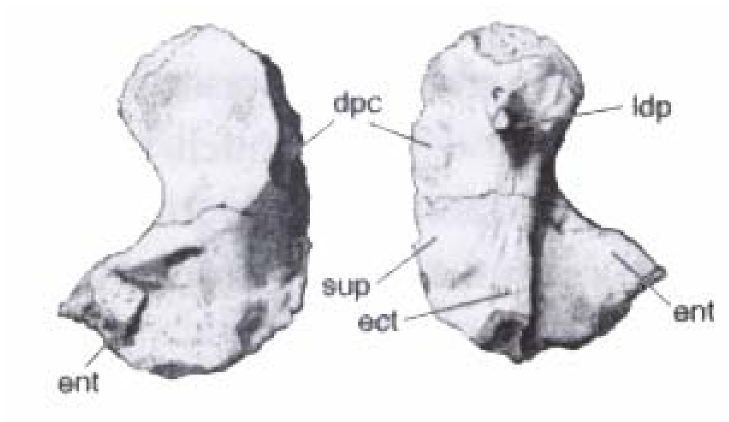


BAPHETIDAE

Formerly Loxommatidae.

Carboniferous, Visean to Westphalian.

Appendicular features show features that are a mix of features found in *Tulerepeton* and *Whatcheeria*.



MAJOR “EVENTS” IN TANSITION FROM FINS TO LIMBS – I

RHIZODONTIDS
•Abbreviate archipterygium.

OSTEOLEPIFORMS
•Both pectoral and pelvic fins as abbreviate archipterygium.

PANDERICHTHYIDA
•Relatively larger scapulocoracoid.
•Fins more ventrally placed.
•Humerus dorso-ventrally flattened.
•Ulnare

TIKTAALIK
•Elaboration of wrist bones beyond ulnare while still retaining fin rays.

ACANTHOSTEGA
•Dermal and endochondral components of pectoral girdle approximately equal.
•Strap-shaped glenoid.
•Pectoral limb subdivisible into stylopodium (brachium, upper arm), zeugopodium (antebrachium, forearm), and autopodium (hand).
•Humerus “L-shaped”
•Femur has a distinct shaft.

MAJOR “EVENTS” IN TANSITION FROM FINS TO LIMBS – II

ACANTHOSTEGA (continued)

- Elements of the ankle clearly developed: tibiale, intermedium, fibulare.
- Eight digits.
- No dermal fin rays.

ICHTHYOSTEGA

- First evidence of an olecranon process.
- Pedal digits reduced to seven.

TULERPETON

- Expanded dermal clavicles meet in midline.
- Interclavicle has clearly developed, robust stem.
- Earliest example of an expanded scapular region.
- Moderate torsion between proximal and distal ends of the humerus. Supinator process and radial condyles now distinctly seperated (by notch).
- Six phalanges.
- Phalanges distinctly elongate.
- Tibia and fibula are no longer flattened, and are approximately cylindrical in shape.
- Tibia and fibula show a distinct interepipodial space for interosseous membrane.
- Distinct distal tarsal series.

MAJOR “EVENTS” IN TANSITION FROM FINS TO LIMBS – III

COLOSTEIDS

Well developed interepipodial space between radius and ulna.

Pubis, ischium, and ilium are seen as suture separated entities for first time in colosteids.

Tibia has prominent cnemial crest.

Pentadactyl.

WHATCHEERIDAE

- Humerus is massive, with considerably more torsion than in colosteids or ichthyostegalians.

MAJOR SKELETAL TRENDS IN THE TRANSITION FROM FINS TO LIMBS

•Reduction in the paired (more dorsal) dermal elements of the pectoral girdle (anocleithrum, supracleithrum, cleithrum, clavicle).

•Increase in size of more ventral interclavicle.

•Relative increase in size of endochondral components of pectoral girdle (scapula and coracoid).

•Humerus becomes more dorsoventrally flattened with distince entepicondyle, then ectepicondyle.

•Elaboration of wrist bones and ankle bones was incremental, starting earlier in hindlimb.

•Reduction from hyperdactylous (greater than five digits) to pentadactylous condition.

•Reduction and loss of dermal fin rays of fishes.

HOMOPLASY IN MAJOR SKELETAL TRENDS IN THE TRANSITION FROM FINS TO LIMBS

Certain events probably occurred more than once:

- Separation of pectoral girdle from skull.
- Enlargement of scapulocoracoid
- Dermal fin ray loss.
- Pelvic girdle enlargement, especially in fish taxa.

FUNCTIONAL CONSIDERATIONS IN MAJOR SKELETAL TRENDS IN THE TRANSITION FROM FINS TO LIMBS

Vast majority of the changes described to this point probably took place in aquatic realm.

To date, there is insufficient evidence for (the desired) “lockstep” of directed adaptive change (Sumida, 2003).

Cleithrum reduction may be associated with loss of functioning internal gill chamber.

Increase of clavicle-interclavicle complex may have added pectoral stability.

Aquatic features persisted well into “amphibians”.

FINS AND LIMBS AND THE STUDY OF EVOLUTIONARY NOVELTIES

The phylogenetic context section of this chapter is nowhere near as detailed as Coates and Ruta in Chapter 2, so it will not be resummarized here.

Other major themes of the chapter:

- Develoopmet of the autopodium (manus)
- Development of digits
- Origin of the tetrapod limb
    - Metaperygial Axis
    - Digital Arch Model
    - The Autopodium as a Neomorph
        - Evolution of the Autopodial Field
        - Evolution of Digits

Wagner and Larsson distinguish between the origin of new body parts – novelties, and new functions – innovations. The authors asset that tetrapod limbs are an evolutionary novelty. SPECIFICALLY, THEY ASSERT THAT THE AUTOPOD (HAND & FOOT) ARE NOVELTIES.

ADAPTATIONS – traits/features that arise due to natural selection (features that enhance survival and reproductive success of individuals).

NOVELTIES – characters that open up new functional and morphological possibilities to the lineage possessing them. In other words, new functions, not necessarily the same as original function (if there was one). Classic examples are feathers (whose function in flight has nothing to do with their original function in dinosaurs - probably insulation) or stapes articulation with otic capsule (whose function in hearing has nothing to do with its original function in fishes – hyomandibula for jaw suspension).

- Function of a developmental ene could be phylogenetically older than the novel character.

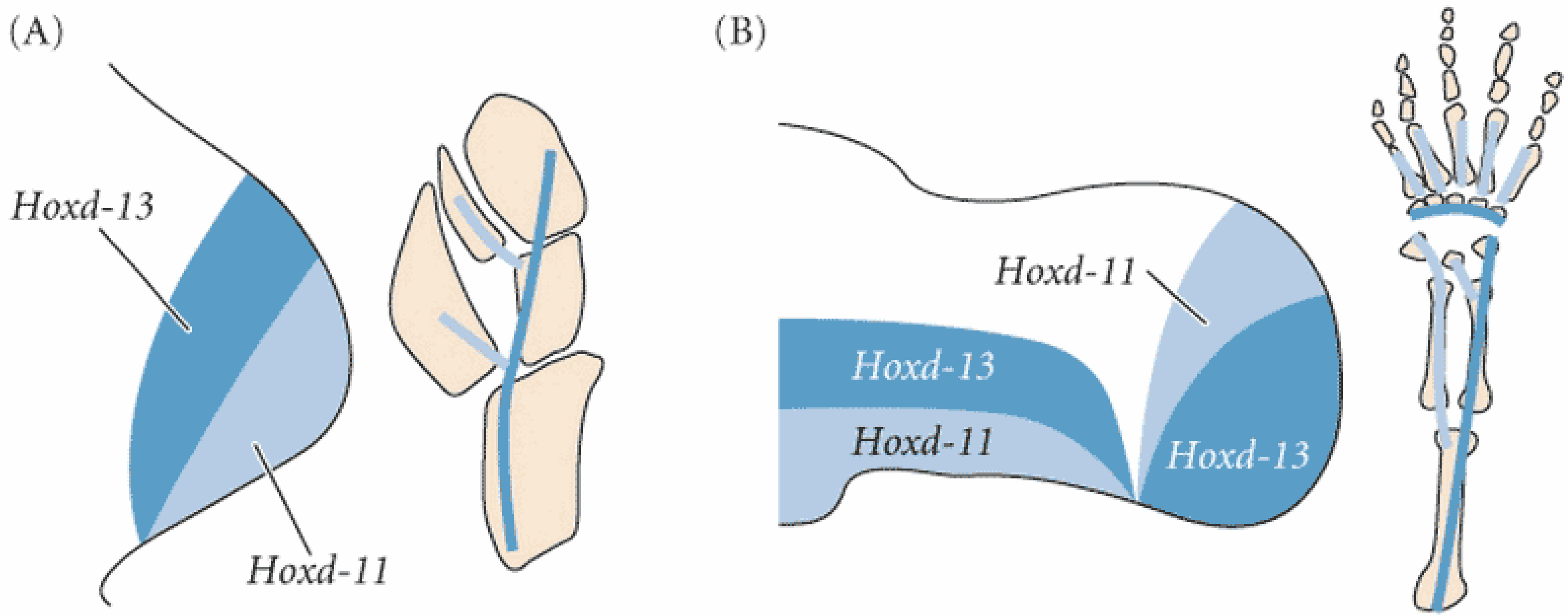
- Gene essential in derived species could have acquired a new function after character evolved.

Wagner and Larsson suggest earliest sarcopterygians with a discrete autopodium – probably *Tiktaalik, Acanthostega, Ichthyostega,* and *Tulerpeton* have a novel autopodium of a transverse series (carpals or tarsals) and elongate digits.

Development of autopodium involves distinct developmental events from those of mor proximal elements. Hox genes *Hoxa11* (more proximal) and *Hoxa13* (more distal) are involved.

Hoxa13 and *Hoxd13* are necessary for digit development. *Hoxa13* knockouts affect mesenchymal condensations of digits. *Hoxd13* knockouts affect the growth of a normal complement of digits.

Sonic hedgehog – *Shh* – modulates number and morphology of digits.



Differences in *Hoxd-11* and *Hoxd-13* expression in fish and tetrapod embryonic appendages. (A) Fin of a fish, wherein *Hoxd-11* expression is distal to *Hoxd-13* expression. The fin axis extends distally. (B) In tetrapods, *Hoxd-13* expression becomes distal to *Hoxd-11* expression, and the limb axis shifts anteriorly from its original proximal-distal orientation. The digits originate from the posterior side of the axis.

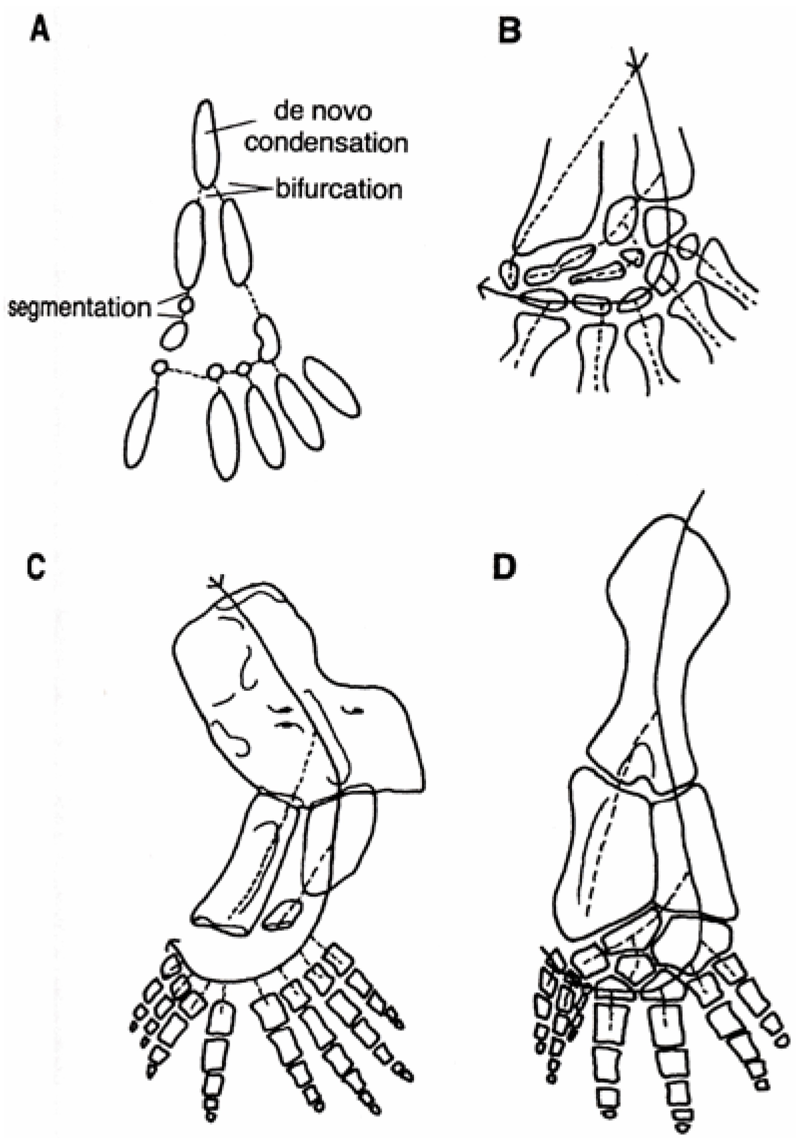
Scenarios for the Origin of the Tetrapod Limb

- Metaperygial Axis
- Digital Arch Model
- The Autopodium as a Neomorph

METAPTERYGIAL AXIS

Preaxial Radial	Element
1	Radius
2	Intermedium
3	Centrale 1
4	Digit 4
Other preaxial radials	Digit 3
Other preaxial radials	Digit 2
Other preaxial radials	Digit 1
Postaxial pocesses of 3rd & 4th mesomeres	Pisiform & Digit 5

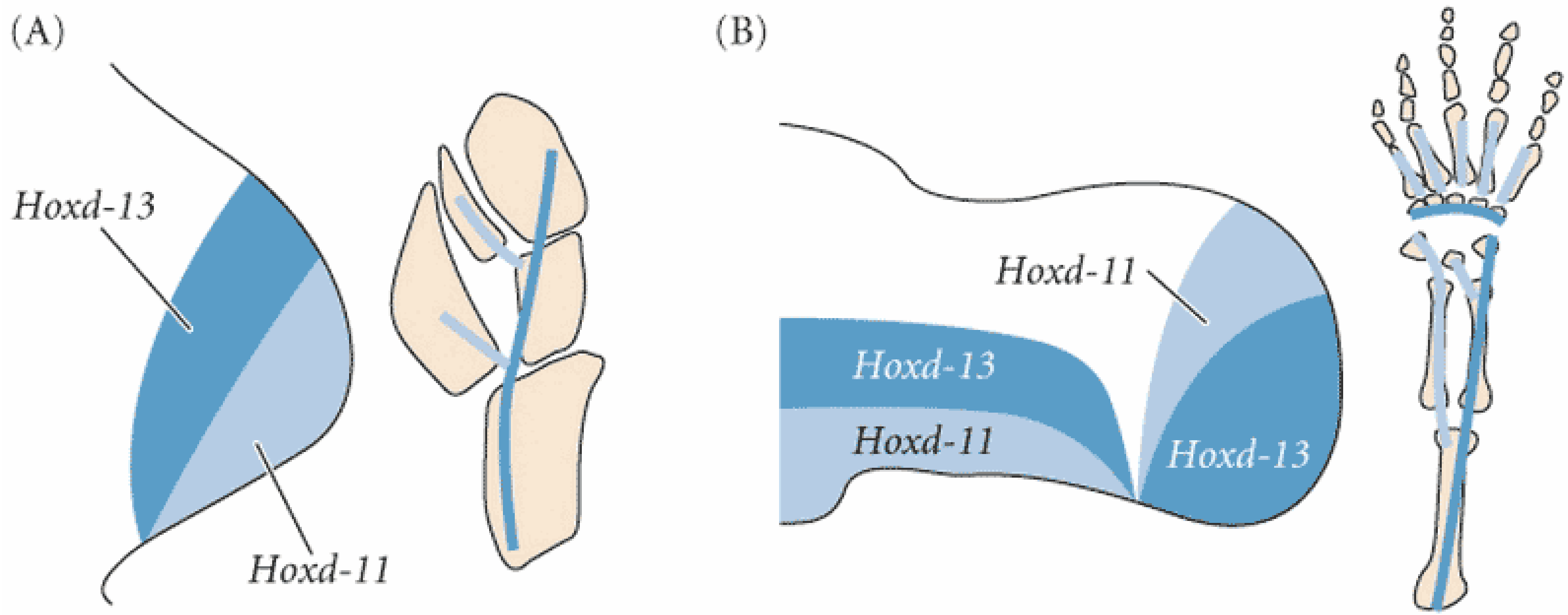
DIGITAL ARCH MODEL



A modified metapterygial axis passes through:
Humerus
ulna
Ulnare
(Bends preaxially through) 4th distal carpal
Distal carpal 3
Distal carpal 2
Distal carpal 1

In all cases, each element of autopodium is either an elongation of arch (segmented element) , or a single preaxial bifurcation which then elongates on its own.

Wagner and Larsson don’t support this idea.

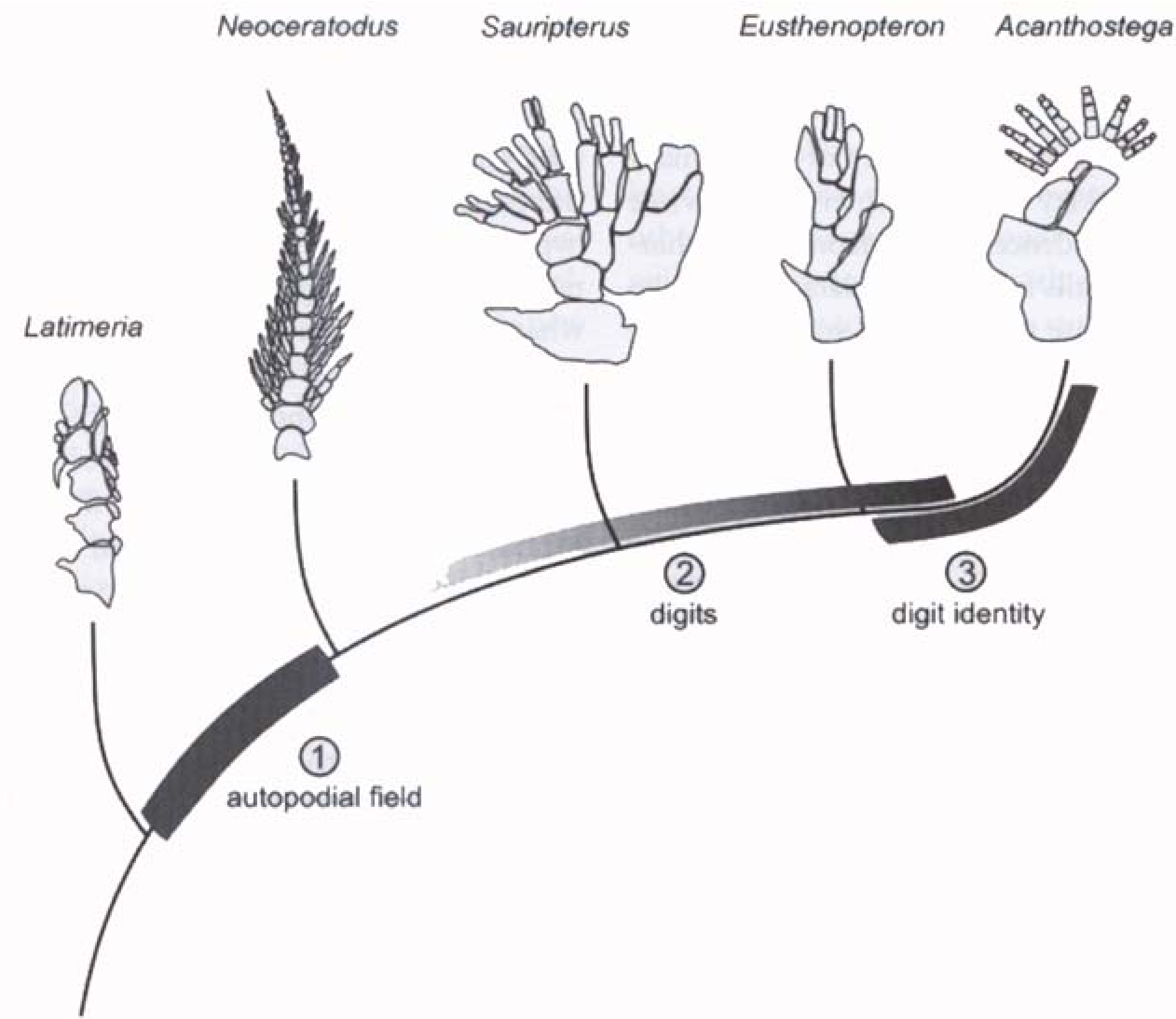


HOWEVER: Note that expression of *Hoxd-13* essentially mirrors pattern of the digital arch model!

NEOMORPHIC AUTOPODIUM MODEL

Wagner and Larsson suggest that fact that autopodial elements found in tetrapods, but not in sarcopterygian fishes *Eusthenopteron* and *Panderichthyes* means that wrist + digits = neomorph. The suggest this with the following model of genetic events:

1. Evolution of an Autopodial Field. Autopodial field is a morphogenetic field undewr control of *Hoxa13*, but to exclusion of *Hoxa11*.
2. Evolution of Digits. Probably under control of HoxD genes and Shh.
3. Reduction to Five Digits.


Neoceratodus
Sauripterus
Eusthenopteron
Acanthostega
Latimeria
② digits
③ digit identity
① autopodial field

NEOMORPHIC AUTOPODIUM MODEL

Wagner and Larsson suggest that fact that autopodial elements found in tetrapods, but not in sarcopterygian fishes *Eusthenopteron* and *Panderichthyes* means that wrist + digits = neomorph. However, this was suggested BEFORE the published discovery of the intermediate form *Tiktaalik*.