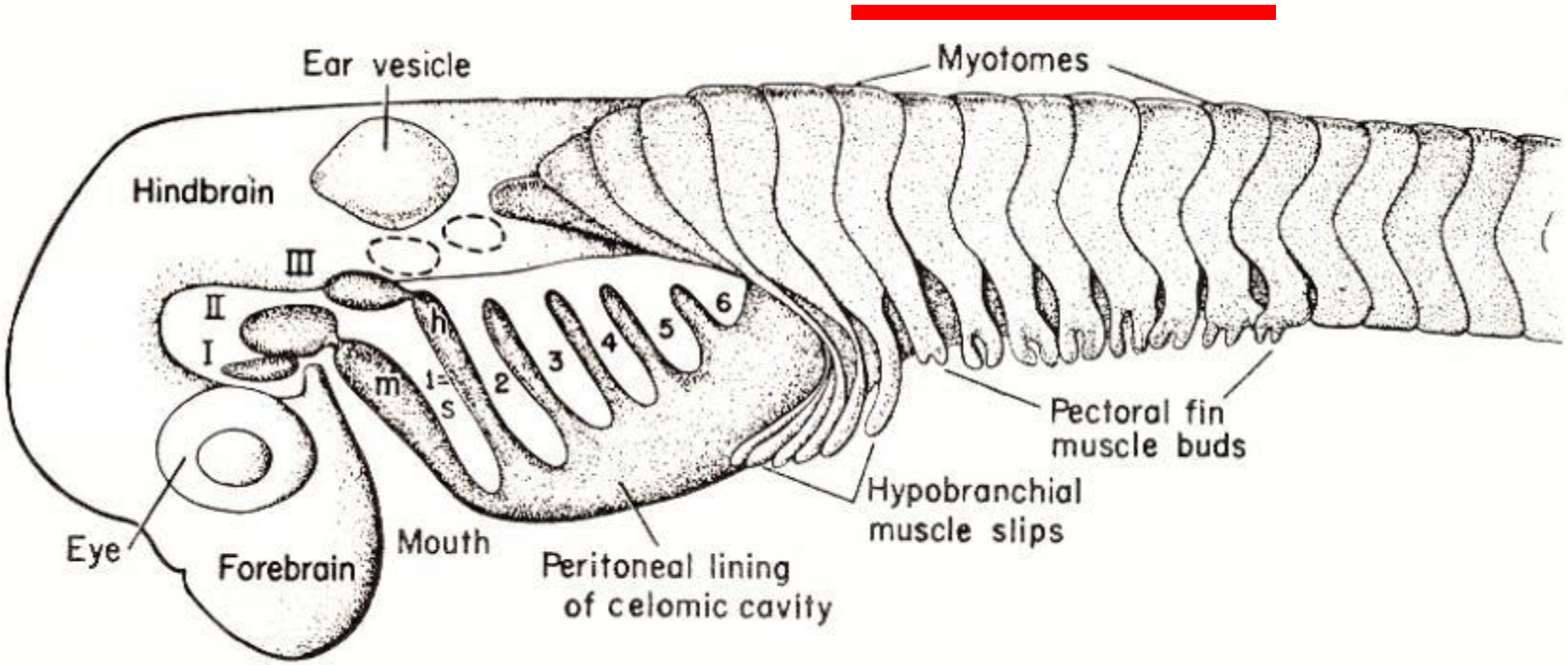
Biology 340
Comparative Embryology
Lecture 12
Dr. Stuart Sumida

Evo-Devo Revisited

Development of the Tetrapod Limb

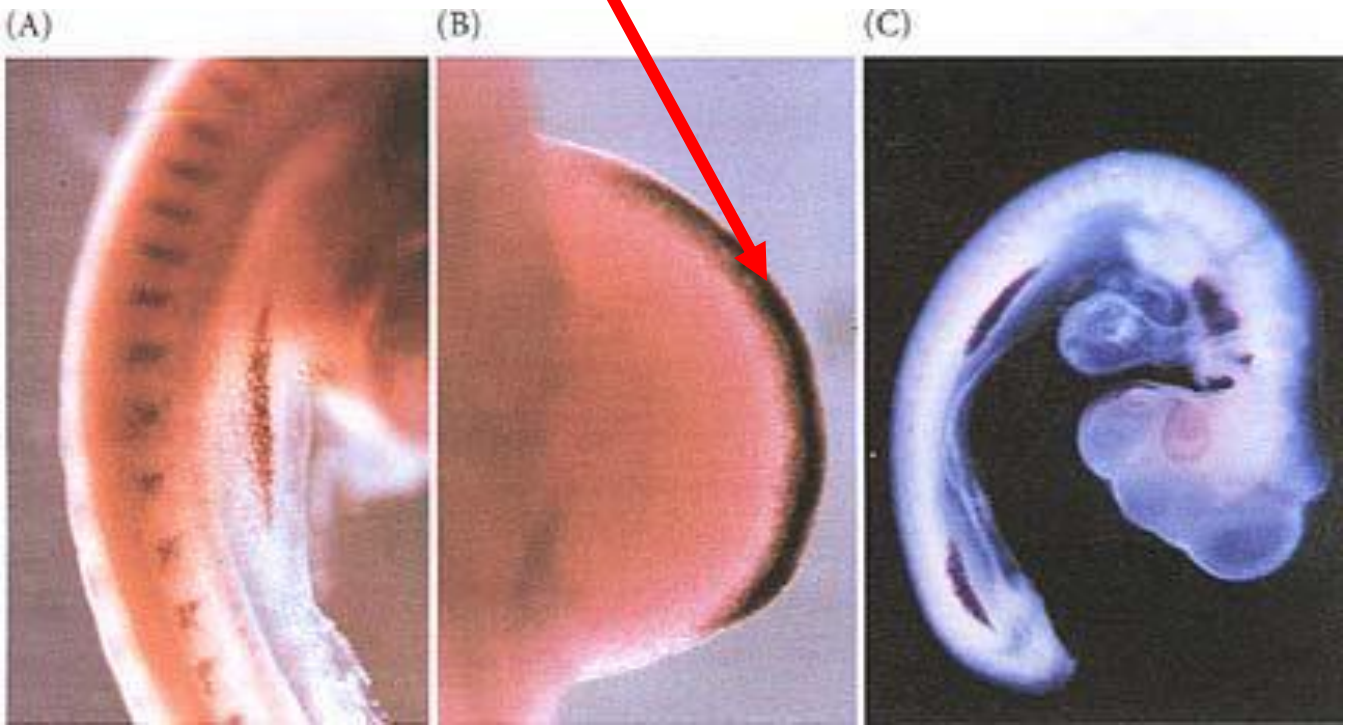
Limbs – whether fins or arms/legs for only in particular regions or LIMB FIELDS.



Primitively (fish) : mesoderm of somite (myotome) gives rise to limb skeleton and musculature.

Limbs – whether fins or arms/legs for only in particular regions or LIMB FIELDS.

Mesoderm interacts with an overlying ridge of ectodermal tissue called the APICAL ECTODERMALRIDGE – or AER.



Fibroblast growth factors (FGFs) are critical for the maintenance of the AER.

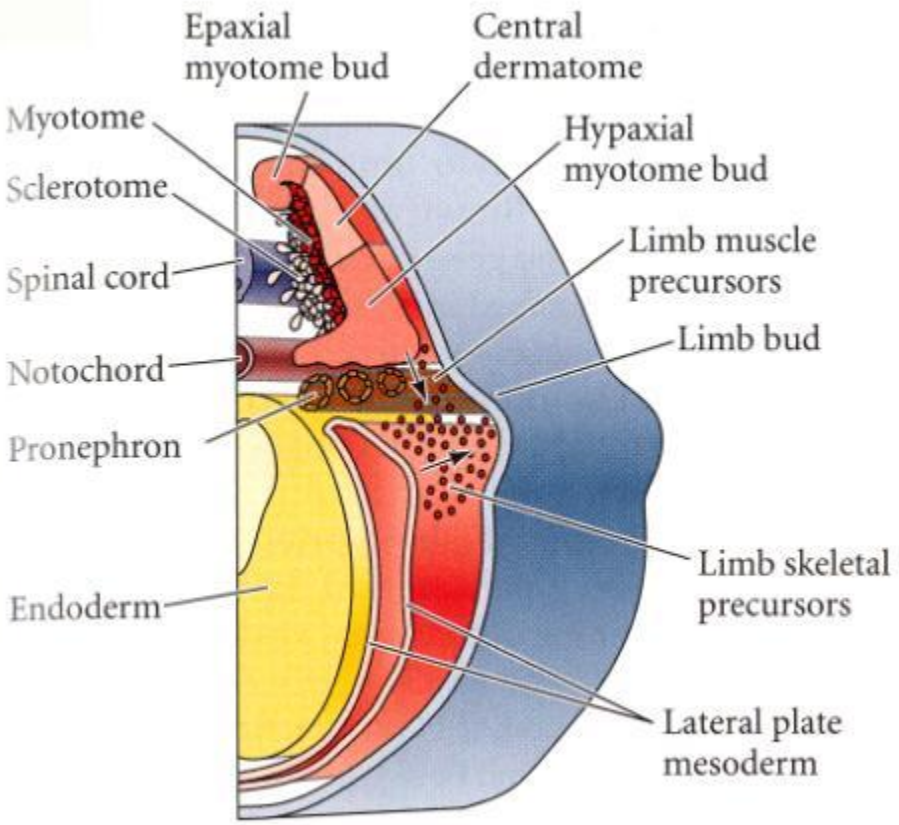
In turn, the AER maintains the proximal-to-distal organization of the limb.

Mesodermal Origin of Limb Mesenchyme:

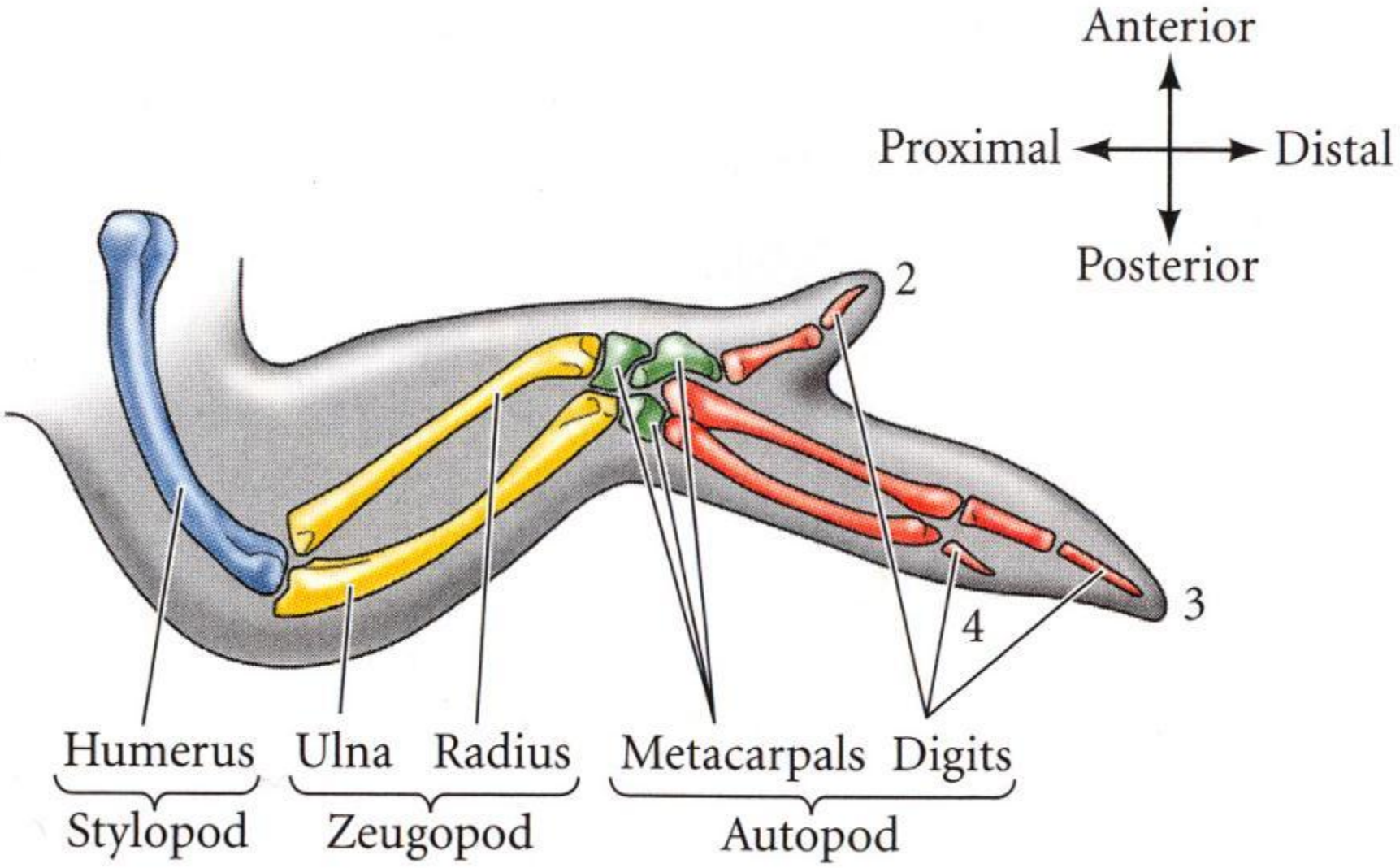
Fishes: Myotome of Somite

Amphibians: muscle from myotome of somite; skeleton from lateral plate mesoderm

Amniotes: Limb mesenchyme forms *IN SITU* (in place)



TETRAPODS: Stylopod, Zeugopod, and Autopod.

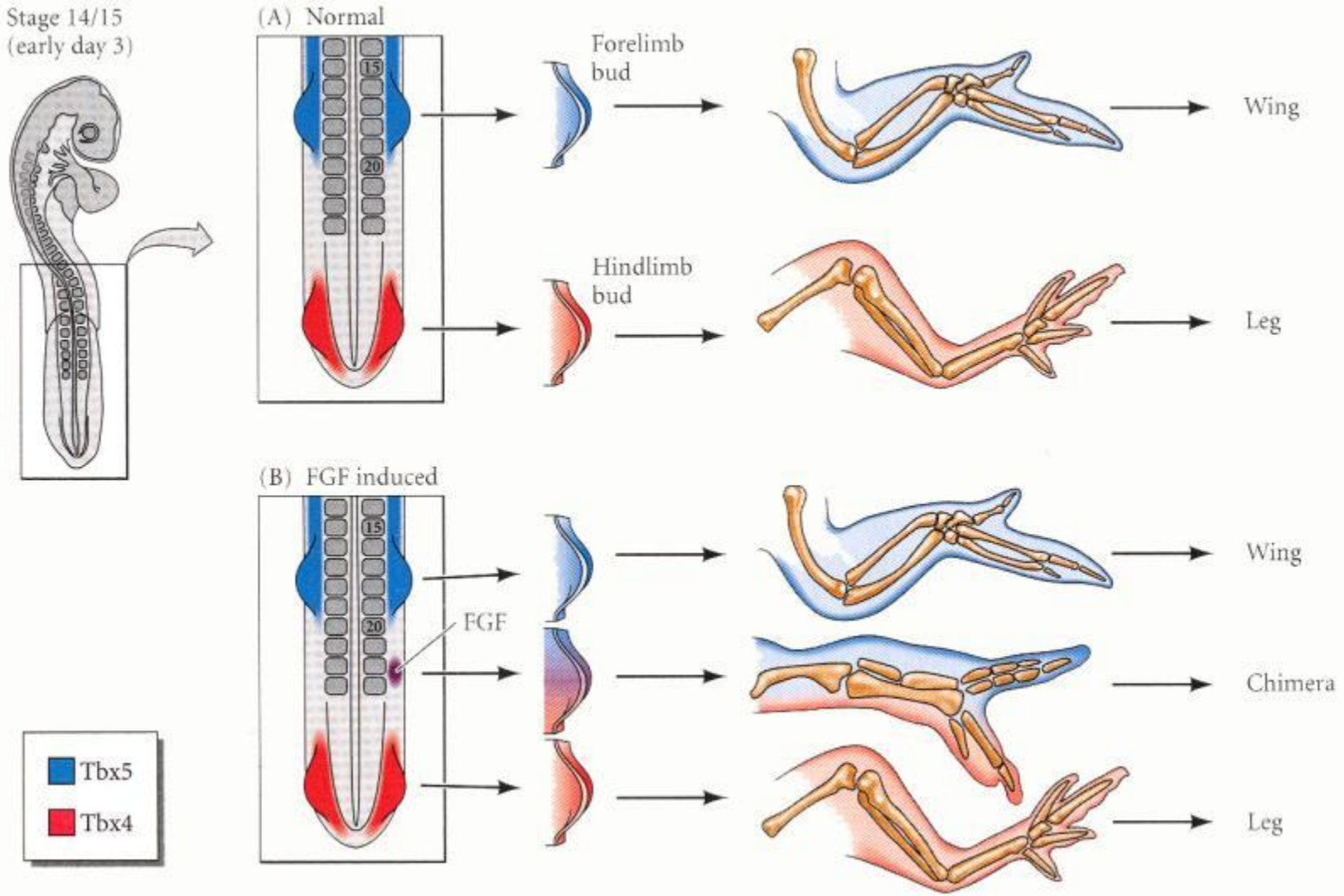


Where along the developing longitudinal axis of the embryo a limb develops is dependant on where along that axis certain HOX genes are expressed.

Once a limb bud is specified, whether it becomes a forelimb or a hindlimb is determined by the expression of one of two genes: Tbx4 or Tbx5.

Expression of Tbx4 gives a hindlimb.

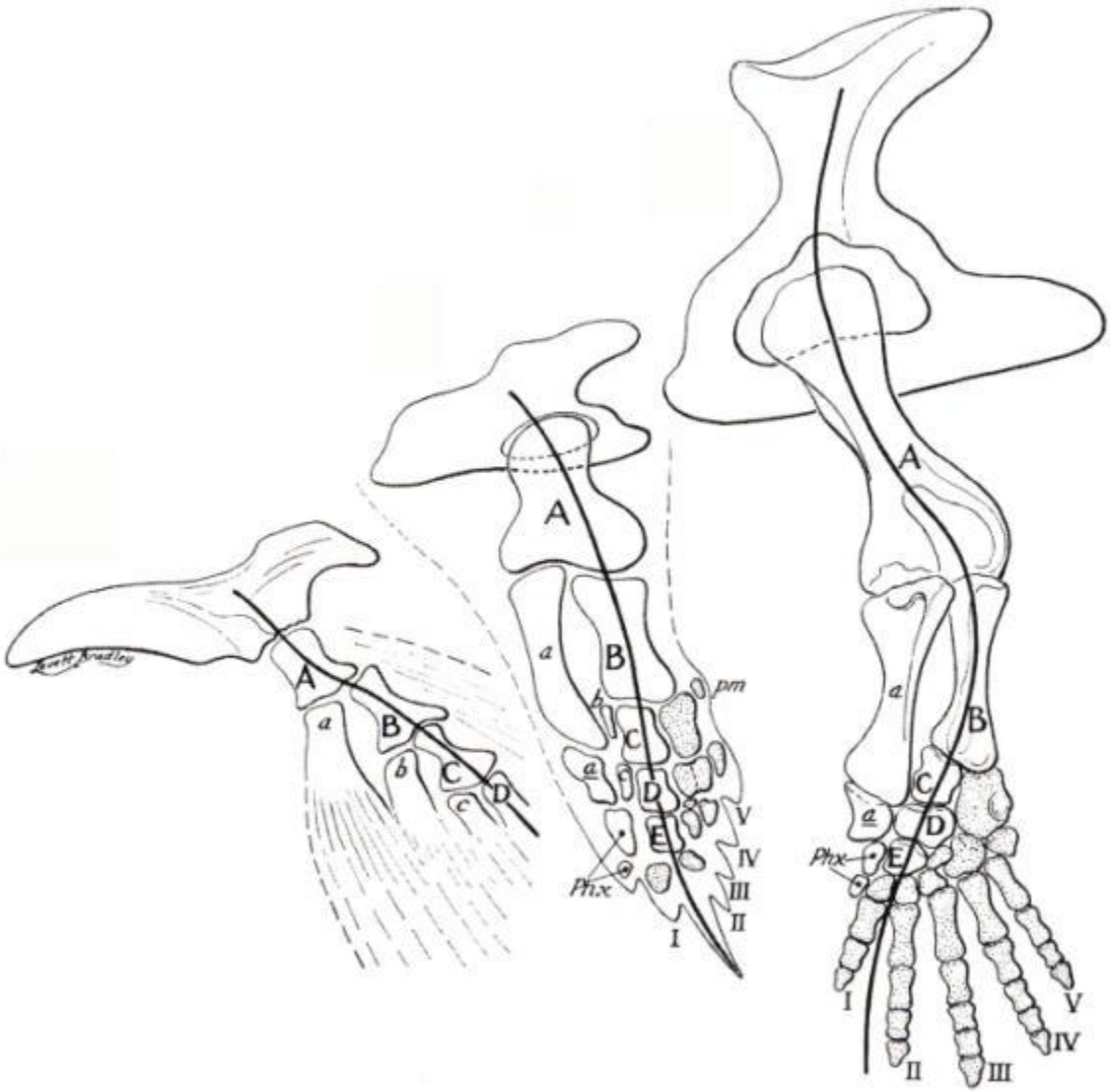
Expression of Tbx5 gives a forelimb.


Stage 14/15
(early day 3)
(A) Normal
15
20
Forelimb
bud
Wing
Hindlimb
bud
Leg
(B) FGF induced
15
20
FGF
Wing
Chimera
Leg
Tbx5
Tbx4

THE METAPTERYGIAL AXIS:

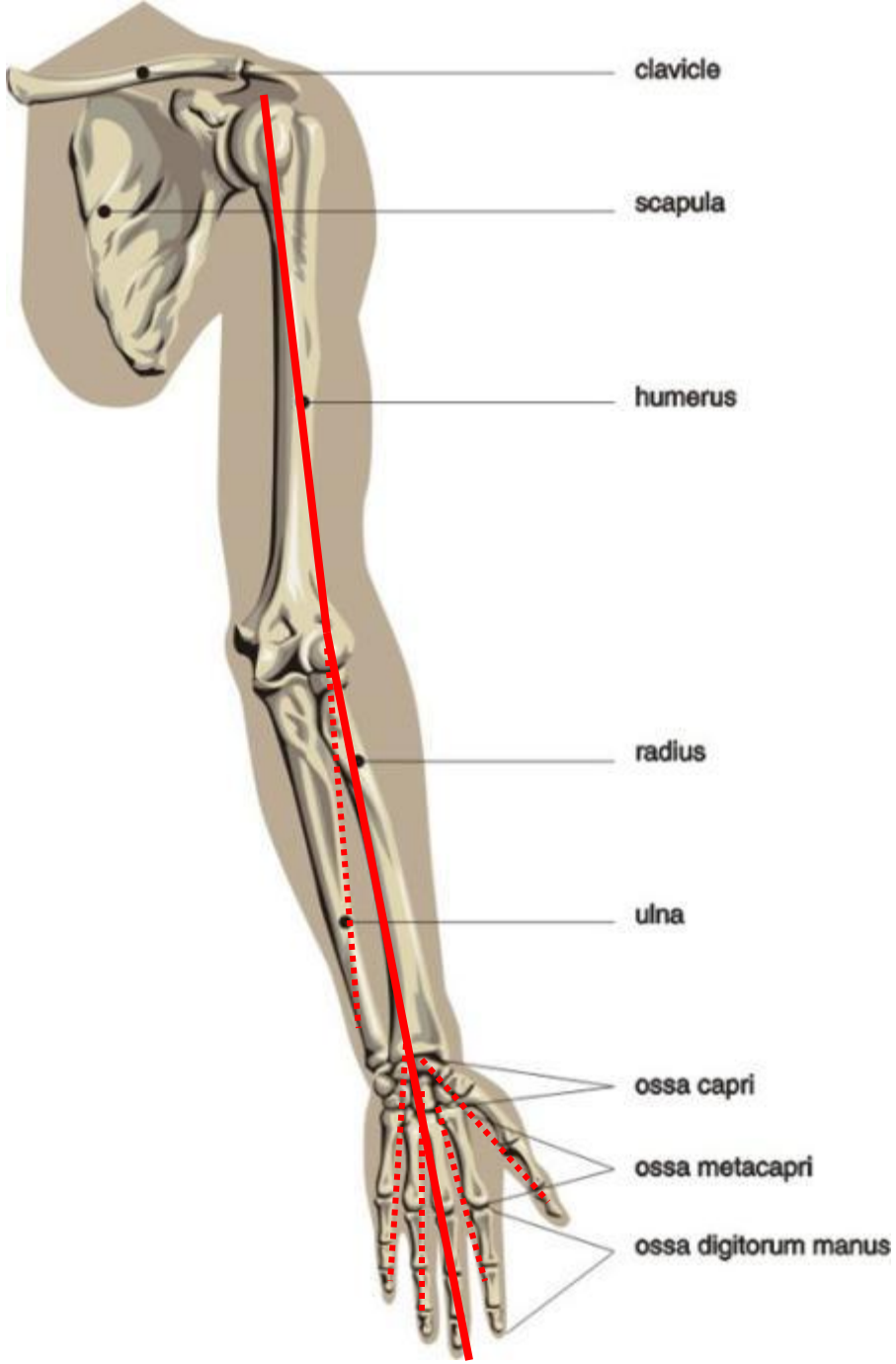
Ove the years, both developmental biologists and paleontologists have sought to define a central developmental axis of the limb in vertebrates – the METAPTERYGIAL AXIS.

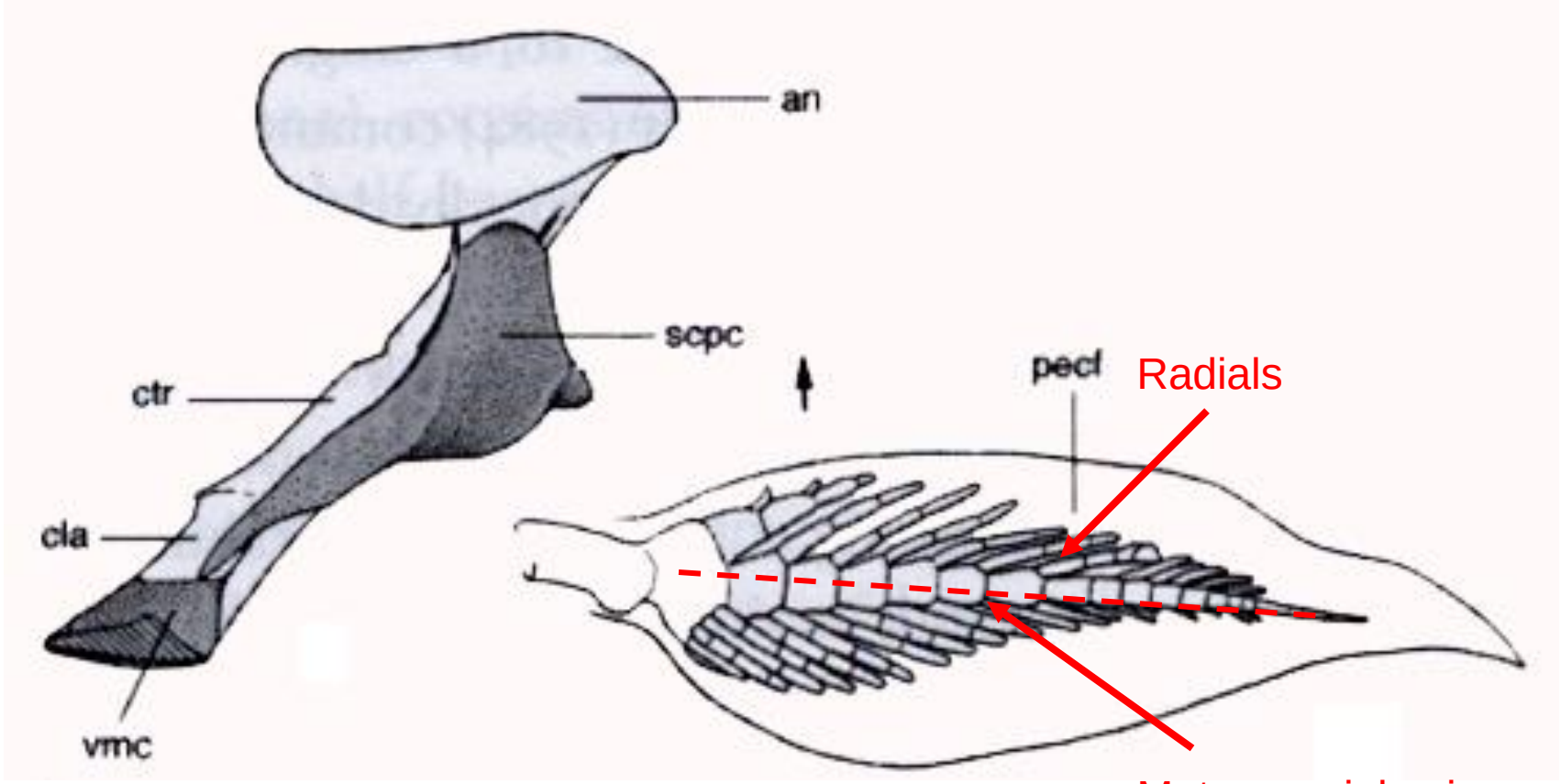
It was thought to extend through the stylopod, an element of the zeugopod, then usually a middle digit of the autopod.



It was long thought that the metapterygial axis ran through defined elements, and that all skeletal elements formed either by extension of the axis, of by single branches with subsequent extension of branches.

Further it was assumed that the axis always ran through homologous elements in related organisms.


clavicle
scapula
humerus
radius
ulna
ossa capri
ossa metacapri
ossa digitorum manus



•An example of a fish: a Lungfish pectoral girdle that has complete compliment of paired dermal elements: anocleithrum, cleithrum, and clavicle.

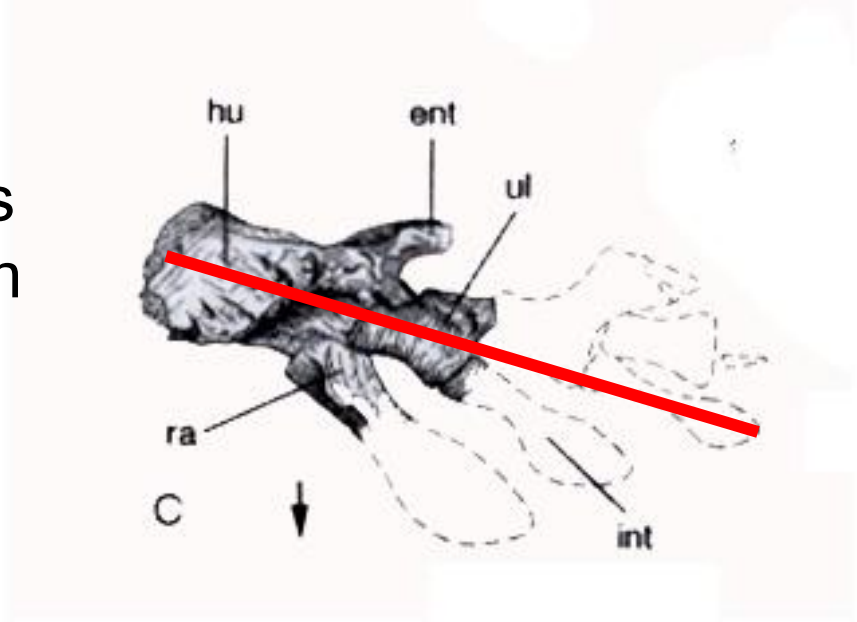
•Fin is clasically described as “leaf-shaped”; a complete or full “archypterygium”.

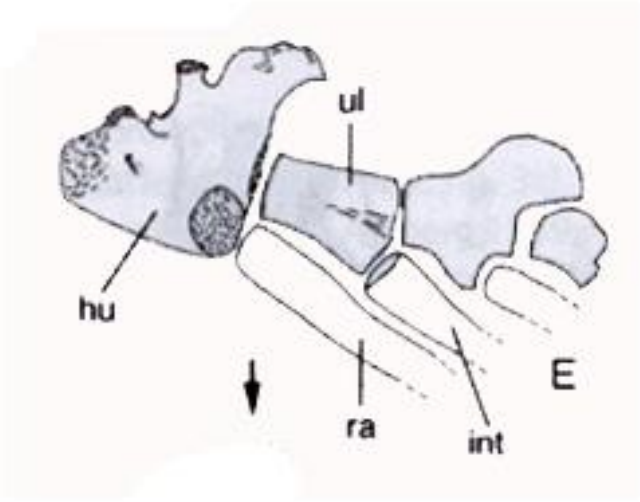
•Median “metaperygial axis” is flanked by both pre (cranial) - and postaxial (caudaly directed) radials to create the leaf-shaped structure.

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

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

You can still find an “axis” in it.

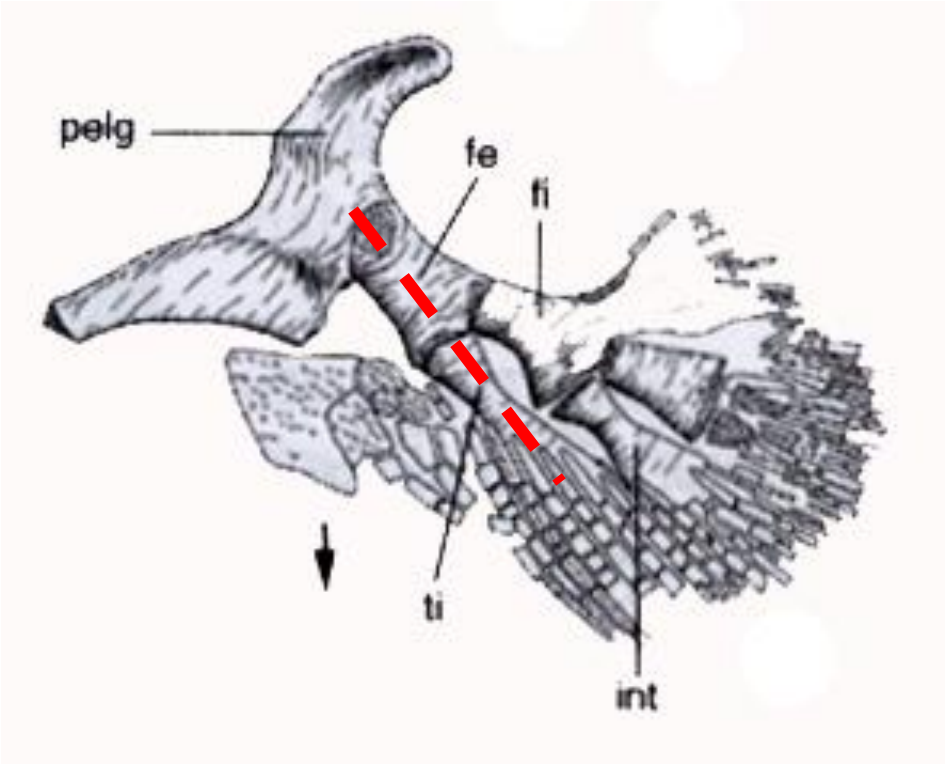


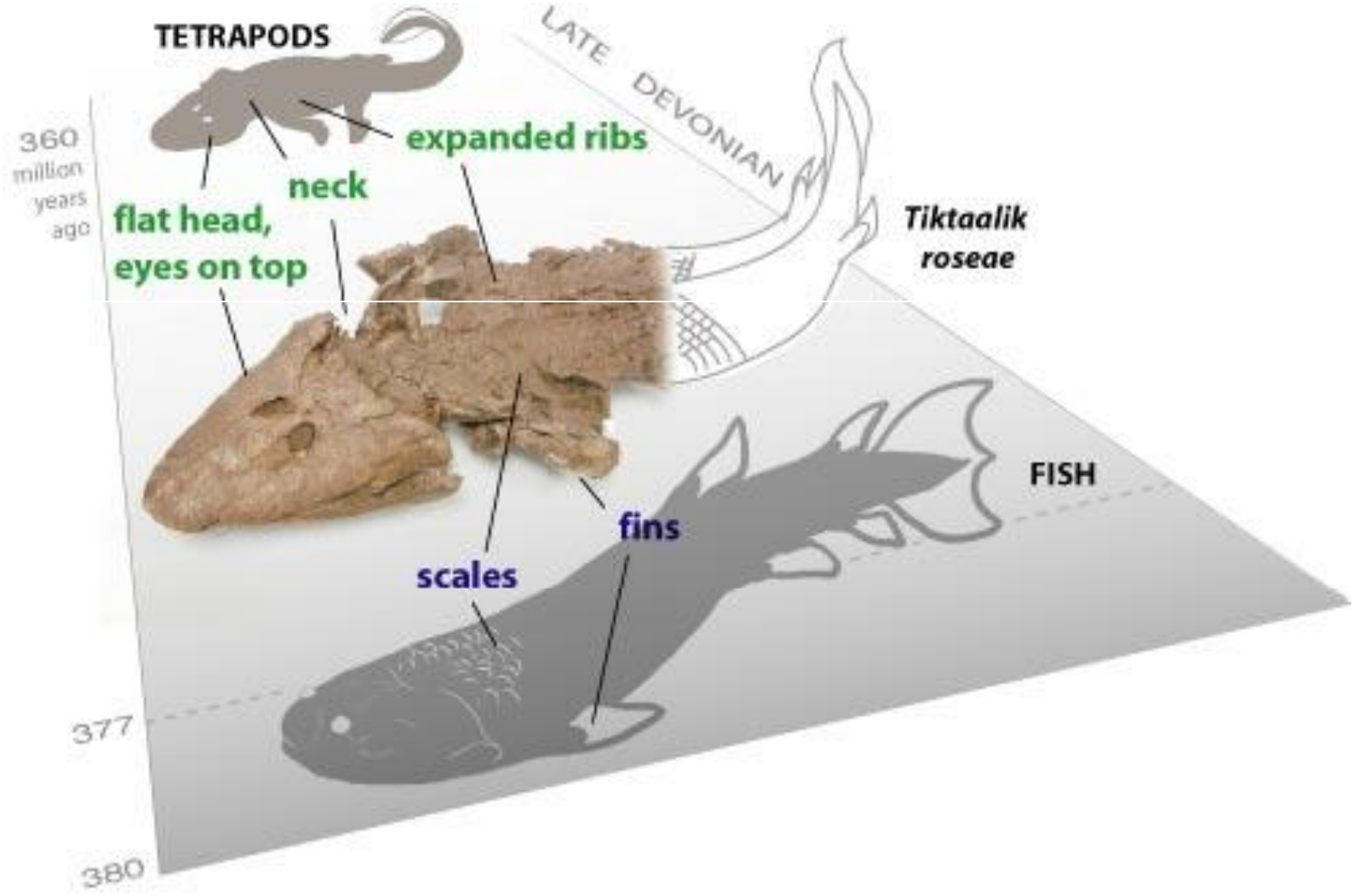


Pelvic fin in osteolepid crossopterygians – the pelvic girdle is small and bar-like. It was obviously buried in musculature, not attached to vertebral column.

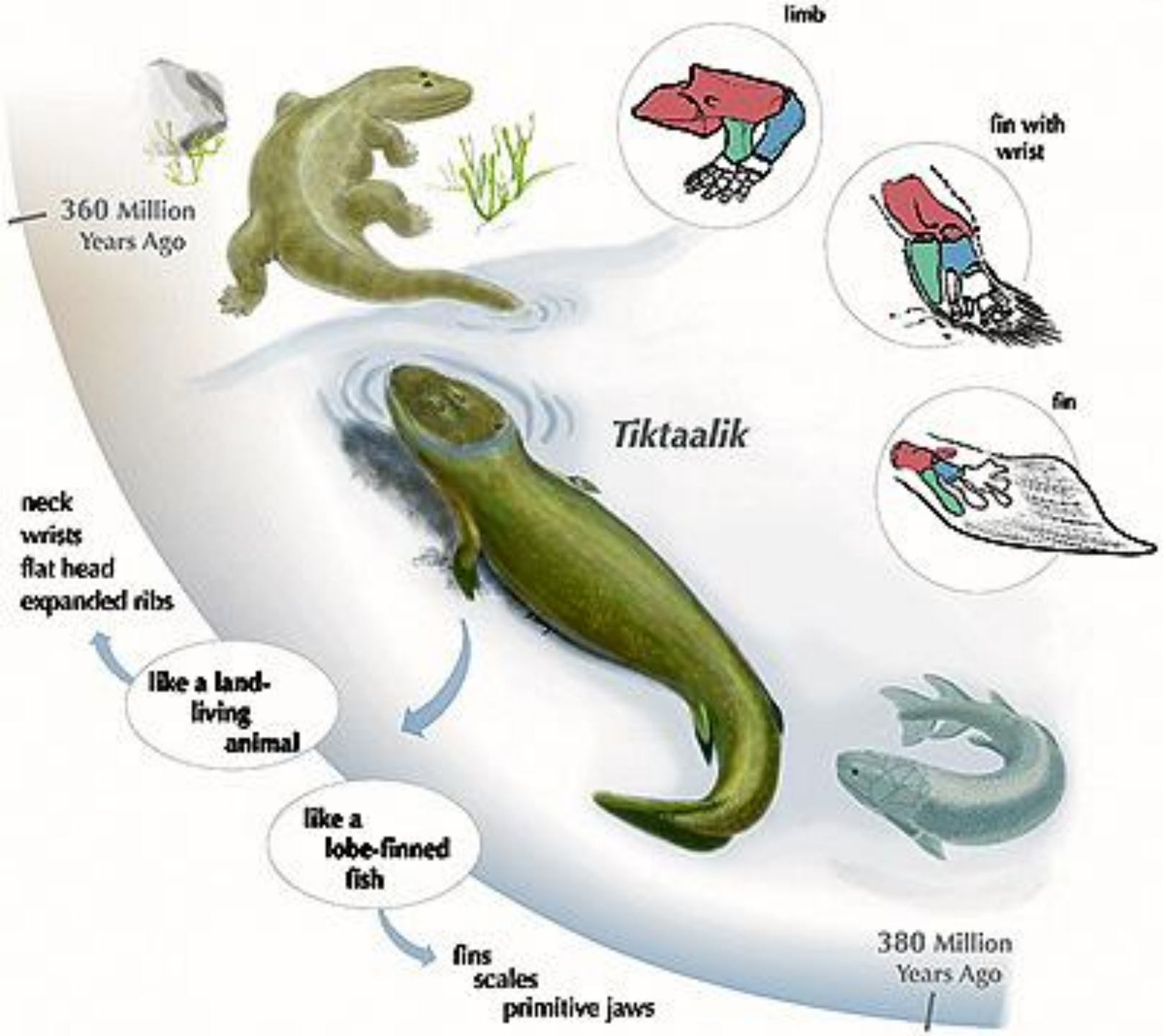
Tibia is the pre-axial side element distal to the femur. Thus, the tibia is serially homologous to the radius. Fibula is serially homologous to ulna.

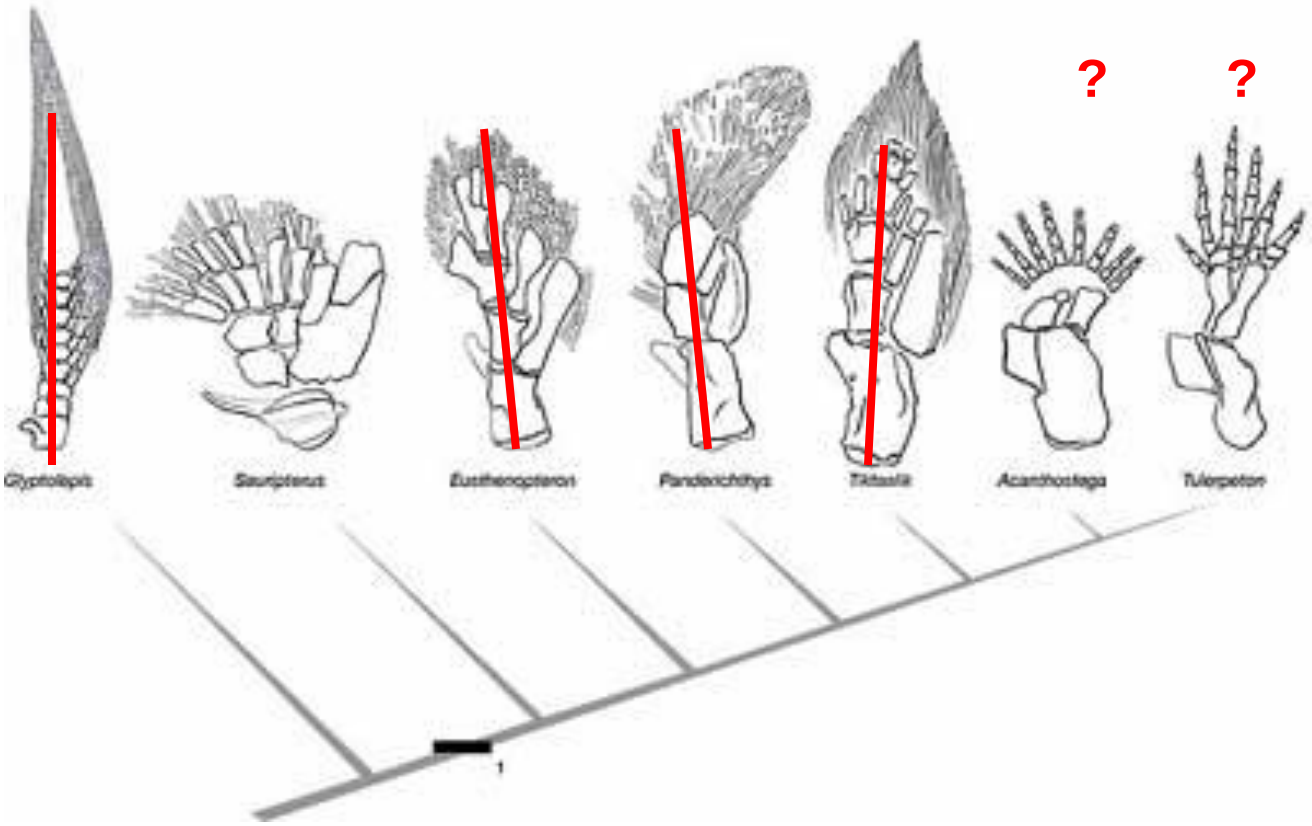
Fin rays still present as typical lepidotrichia.





Tiktaalik is probably a panderichthyid fish or close relative of them – closest relative to tetrapods.


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

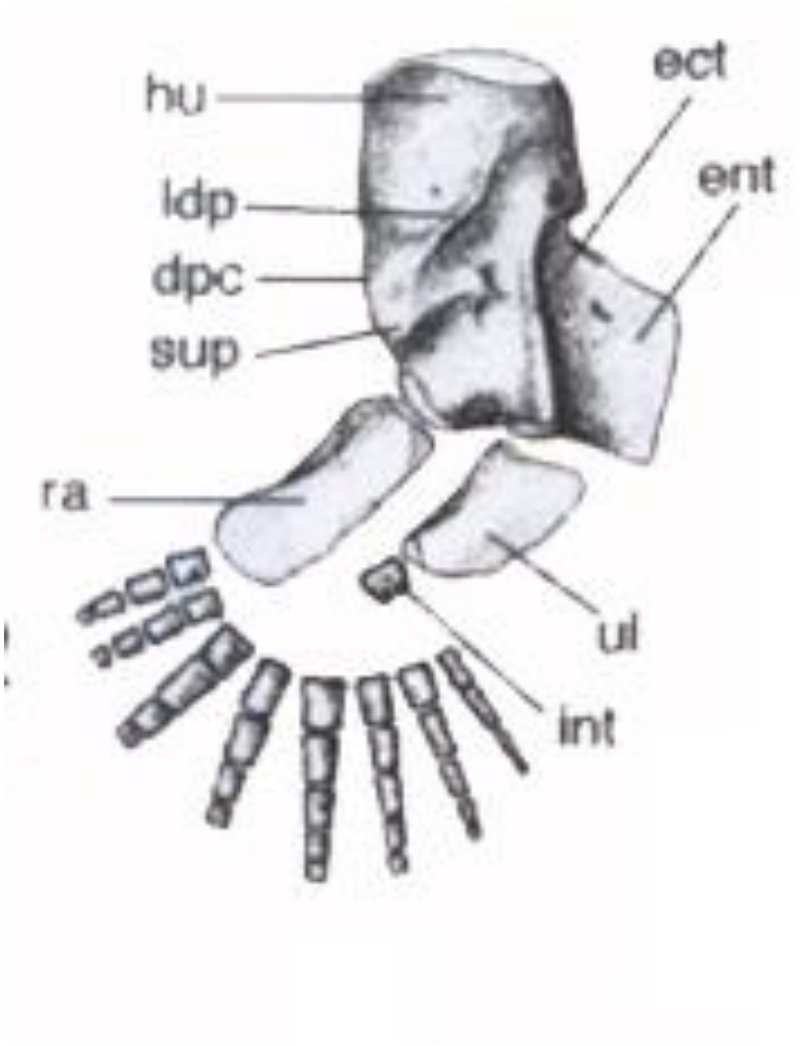

?
?
Glyptolepis
Sauripterus
Eusthenopteron
Panderichthys
Tiktaalik
Acanthostega
Tulerpeton
1

Limb in the Devonian tetrapod *Acanthostega:*

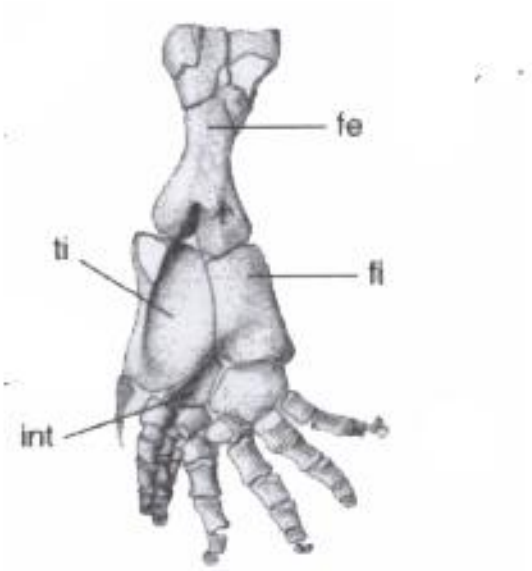
Polydactylous – eight digits present. A very "fin-like" hand.

No dermal fin rays.

Where would the "axis" be??



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*).
Where is the axis???

Some authors distinguish between the origin of new body parts – novelties, and new functions – innovations. Some assert 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 gene could be phylogenetically older than the novel character.

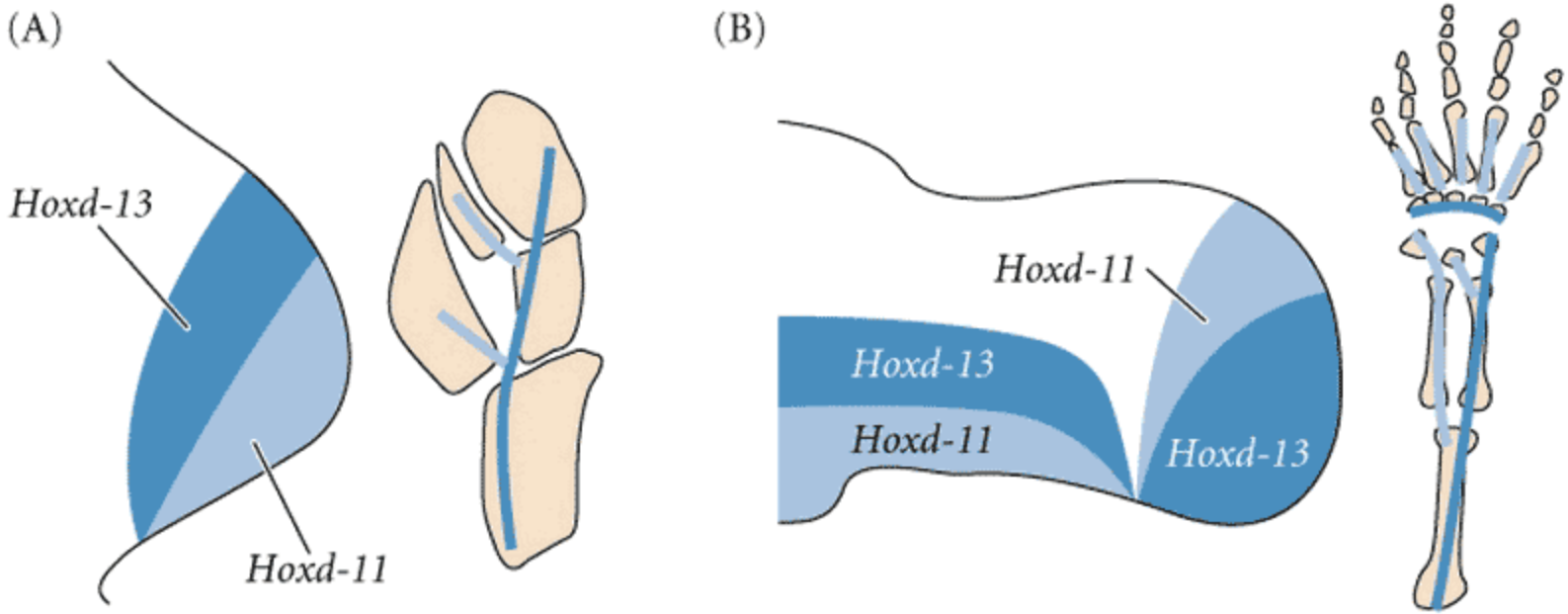
- Gene essential in derived species could have acquired a new function after character evolved.

Some authors 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 more 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.

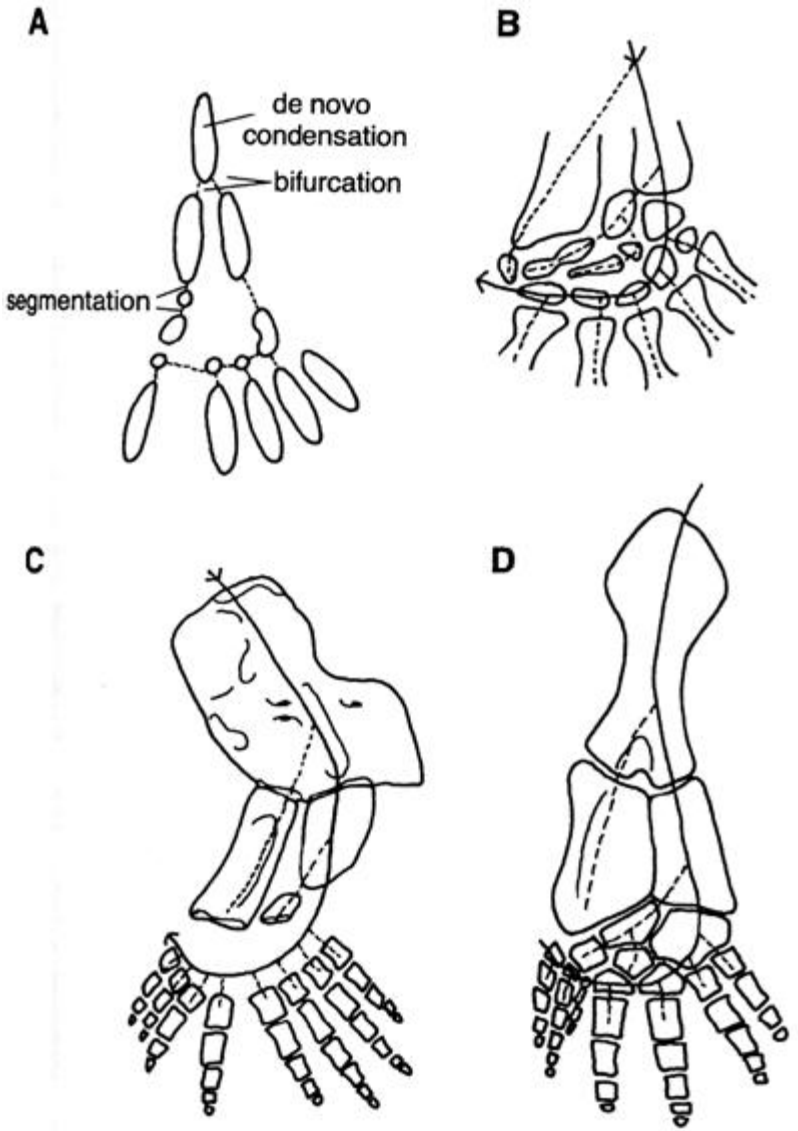


Differences in *Hoxd-11* and *Hoxd-13* expression in fish and tetrapod embryonic appendages. (A) Fin of a fish, wherein *Hoxd-11* expression is distal to *Hoxd-13* expression. The fin axis extends distally. (B) In tetrapods, *Hoxd-13* expression becomes distal to *Hoxd-11* expression, and the limb axis 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

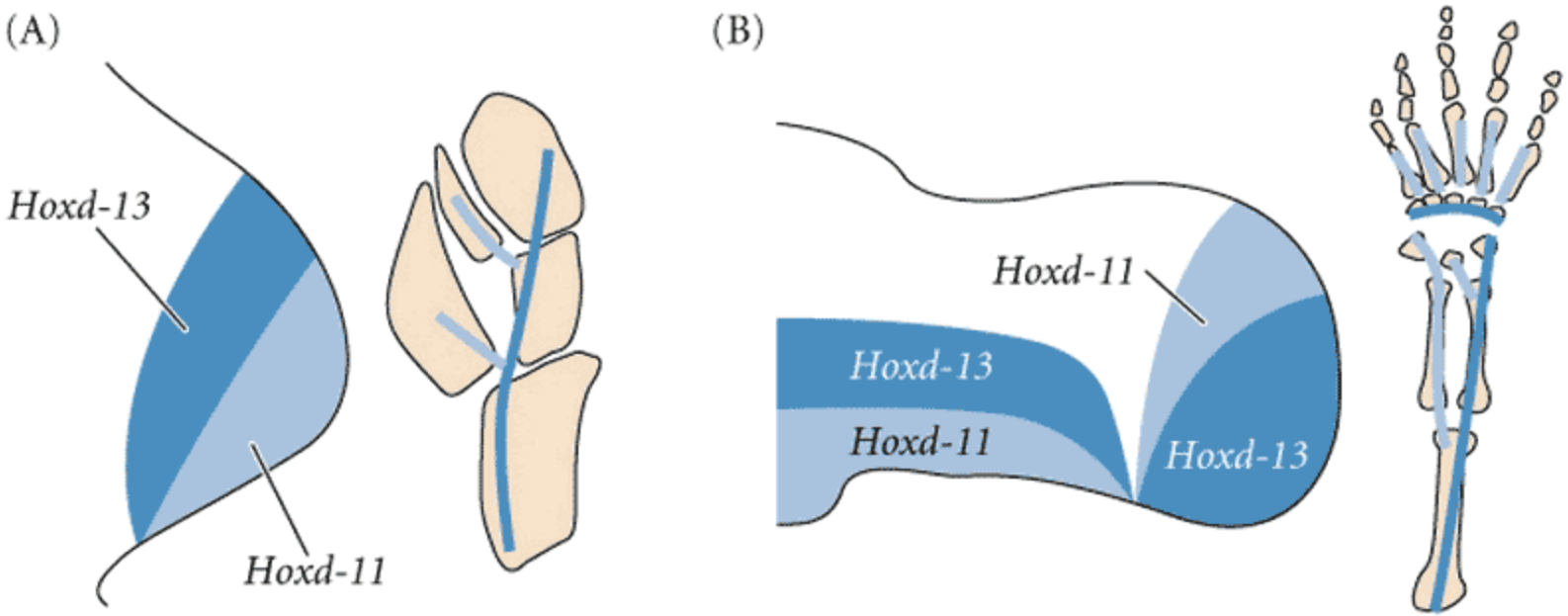
DIGITAL ARCH MODEL



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.



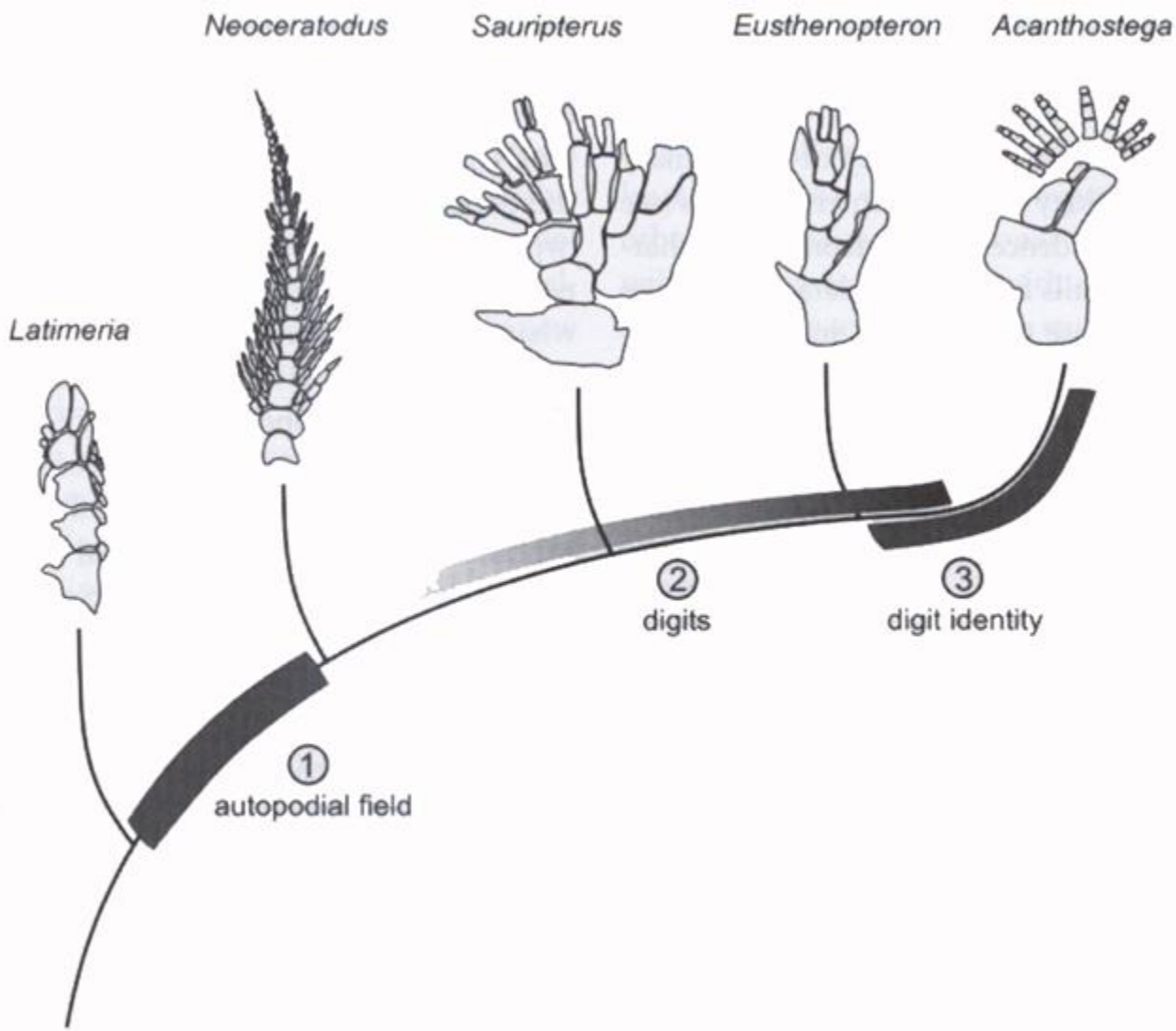
HOWEVER: Note that expression of *Hoxd-13* essentially mirrors pattern of the digital arch model!

NEOMORPHIC AUTOPODIUM MODEL

Some authors 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 genetric events:

1. Evolution of an Autopodial Field. Autopodial field is a morphogenetic field under 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*.

*So, the passing of a metapterygial axis through the middle digit was an artificial coincidence.


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

NEOMORPHIC AUTOPODIUM MODEL

Although some authors 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*.

Example of apoptosis in final limb organization and morphology.