Origin of Amphibians

Unit II, Paper- Zoo-301

By

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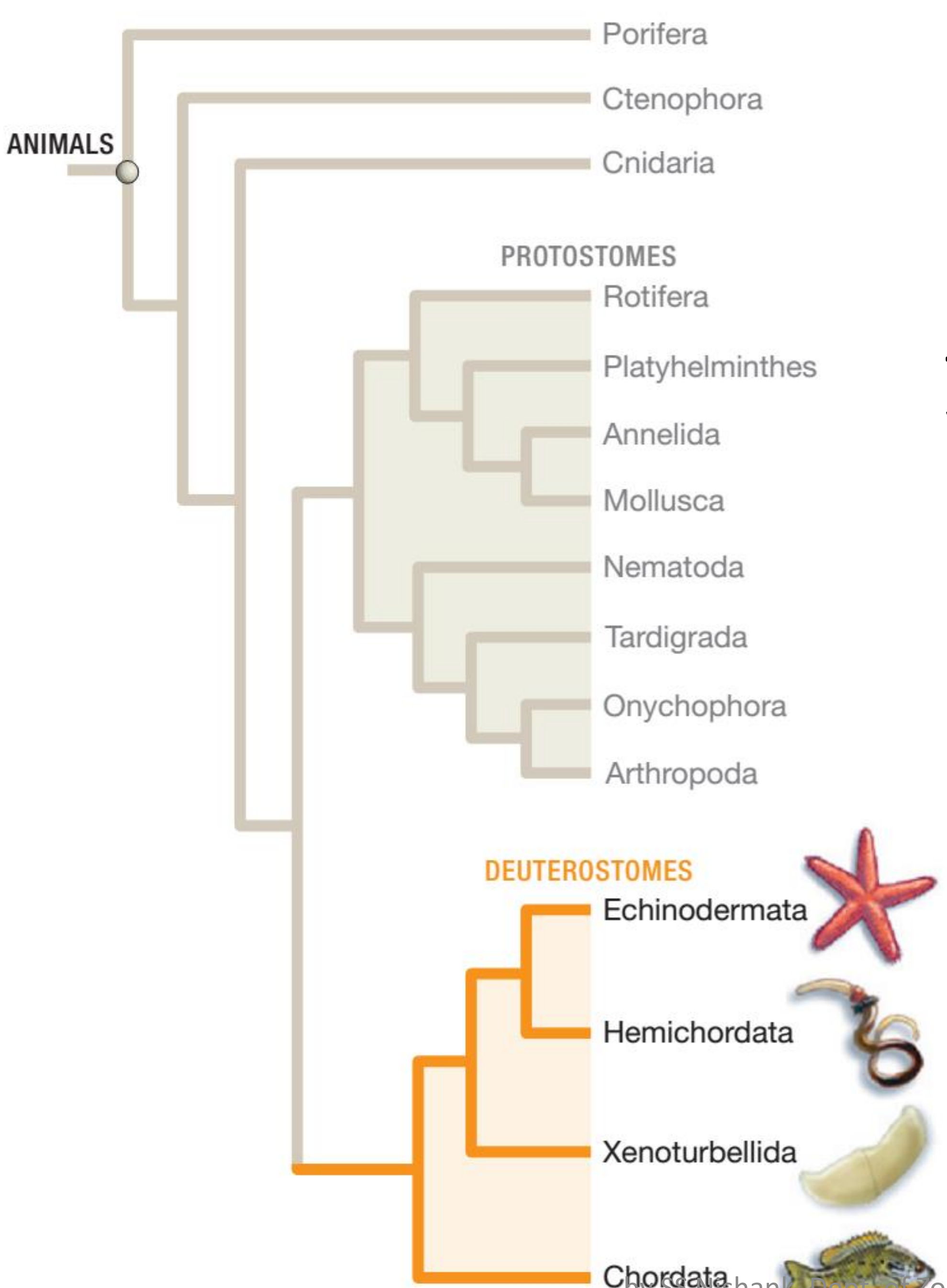
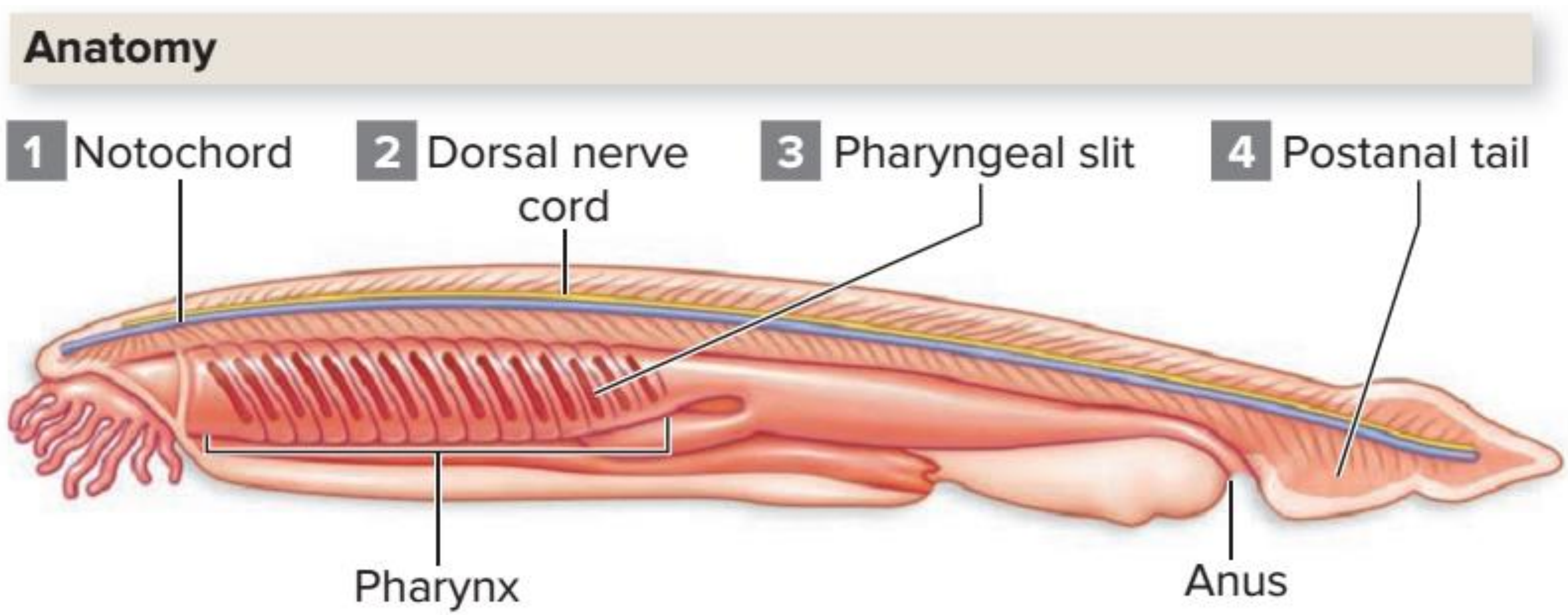


There Are Four Phyla of Deuterostomes.
Vertebrates are in the phylum Chordata.

Four Key Features Distinguish Chordates

- Notochord
- Dorsal, hollow nerve cord parallel to the notochord
- Pharyngeal slits (or pouches) in most chordate embryos,
- Postanal tail: A muscular tail extends past the anus in all chordate embryos.



Characteristics of Phylum Chordata

1. **Postanal tail; notochord; endostyle** or **thyroid gland; bone** and **cartilage** in vertebrates
2. Living in marine, freshwater, and terrestrial habitats; many capable of flight
3. Free-living, but a very few fishes are ectoparasitic
4. Bilateral symmetry; segmented, but segmentation inconspicuous in many
5. Triploblastic
6. **Coelom well developed**
7. Epidermis present in all; dermis in vertebrates; keratinized or bony structures often present in vertebrate integument; glands often diverse and abundant in vertebrates
8. Digestive system complete; muscular gut in vertebrates; **pharyngeal pouches** present early in development, erupting to outside as gill slits in aquatic forms
9. Smooth, skeletal, and cardiac muscle tissue present; segmented myomeres in fishes and amphibians
10. **Nerve cord hollow and dorsal;** distinct, **three-lobed brain** present in vertebrates
11. Protochordates with simple, unpaired photoreceptors and statocysts; vertebrates with well-developed paired sensory organs for vision, chemoreception, hearing, balance, electroreception, and vibration sensitivity
12. Asexual reproduction by parthenogenesis in some fishes, amphibians, and lizards
13. Sexes usually separate; hermaphroditism in sea squirts and some fishes; fertilization internal or external; oviparous or viviparous; distinct larval stage in some; crocodilians, birds, mammals, and some fishes and amphibians with parental care of young
14. Paired, glomerular kidneys and ducts in vertebrates
15. Respiration primarily via gills, lungs, and skin; swim bladder present in many fishes, functioning in buoyancy
16. Closed circulation; **chambered hearts** and red blood cells in vertebrates; distinct aortic arches in all except sea squirts

Evolution that took place Among Chordates are

- The four distinguishing characters of vertebrates are cranium, vertebrae, bone & neural crest cells
- Presence of Cranium: Hagfishes and vertebrates form two clades of craniates, animals that have a cranium that surrounds and protects the brain.
- Vertebrae: Vertebrae are a series of small bone or cartilage structures that make up the vertebral column, or backbone. Vertebrae protect the spinal cord and provide attachment points for muscles, giving the animal a greater range of movement.
- Jaws : Jaws are the bones that frame the entrance to the mouth.
- Thus this led to birth of vertebrates

Vertebrates Probably Arose from an Invertebrate Chordate Ancestor through the Duplication of Genes That Regulate Development

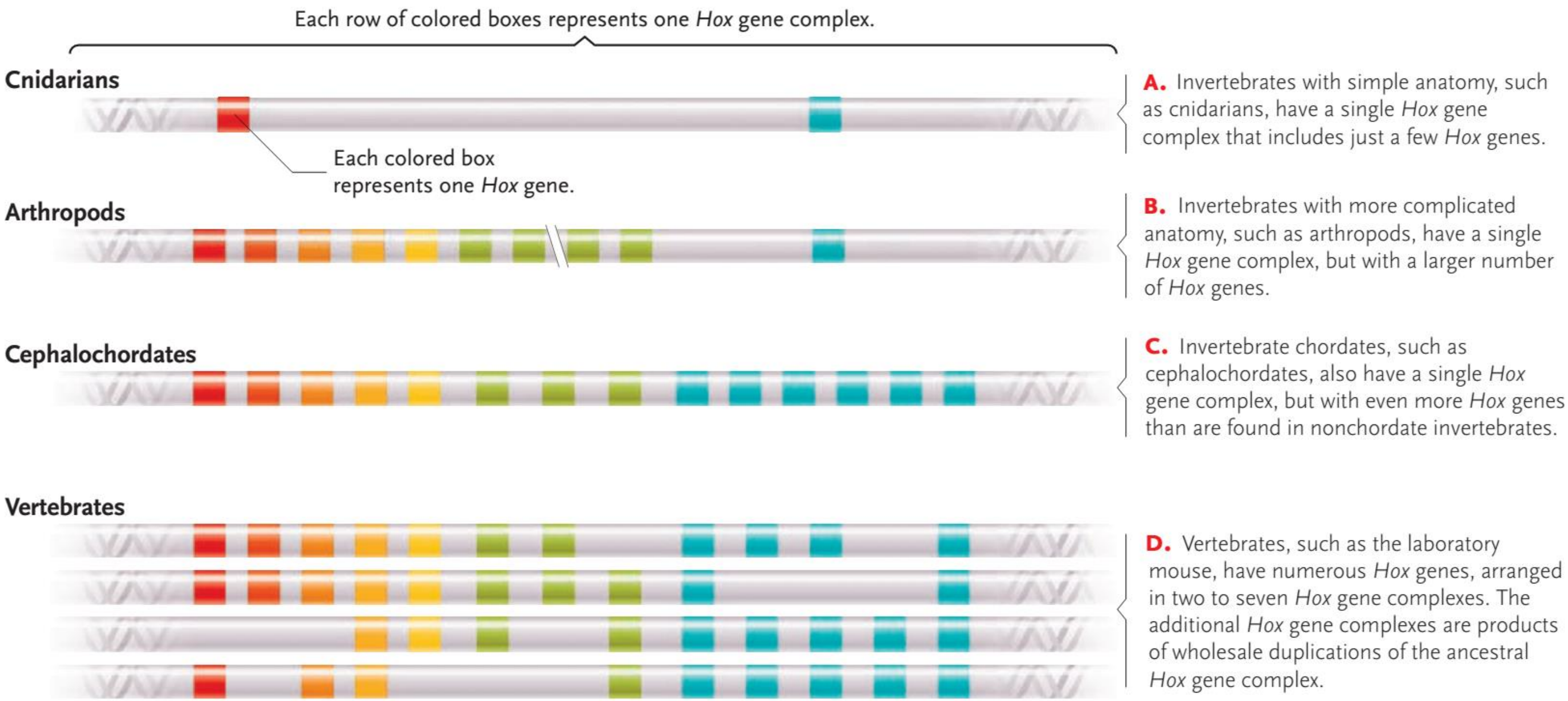
The evolution of vertebrates from an **invertebrate chordate (Cephalochordates & Urochordates)** ancestor was marked by the emergence of neural crest, bone, and other typically vertebrate traits.

What genetic changes were responsible for these remarkable developments?

Biologists now hypothesize that an increase in the number of homeobox—structure determining—genes may have made the development of more complex anatomy possible.

Animal groups with the simplest structure, such as cnidarians, have two Hox genes. Those with more complex anatomy, such as insects, have 10. Chordates have as many as 13 or 14. Thus, lineages with many Hox genes generally have more complex anatomy than do those with fewer Hox genes.

The *Hox* genes in different animal groups appear to be homologous, indicated here by their color and position in the *Hox* gene complex.



SUMMARY Vertebrates have many more individual *Hox* genes than most invertebrates do because the entire *Hox* gene complex was duplicated in the vertebrate lineage. The additional copies of *Hox* genes probably evolved to specify the development of uniquely vertebrate characteristics, such as the cranium, vertebral column, and neural crest cells.

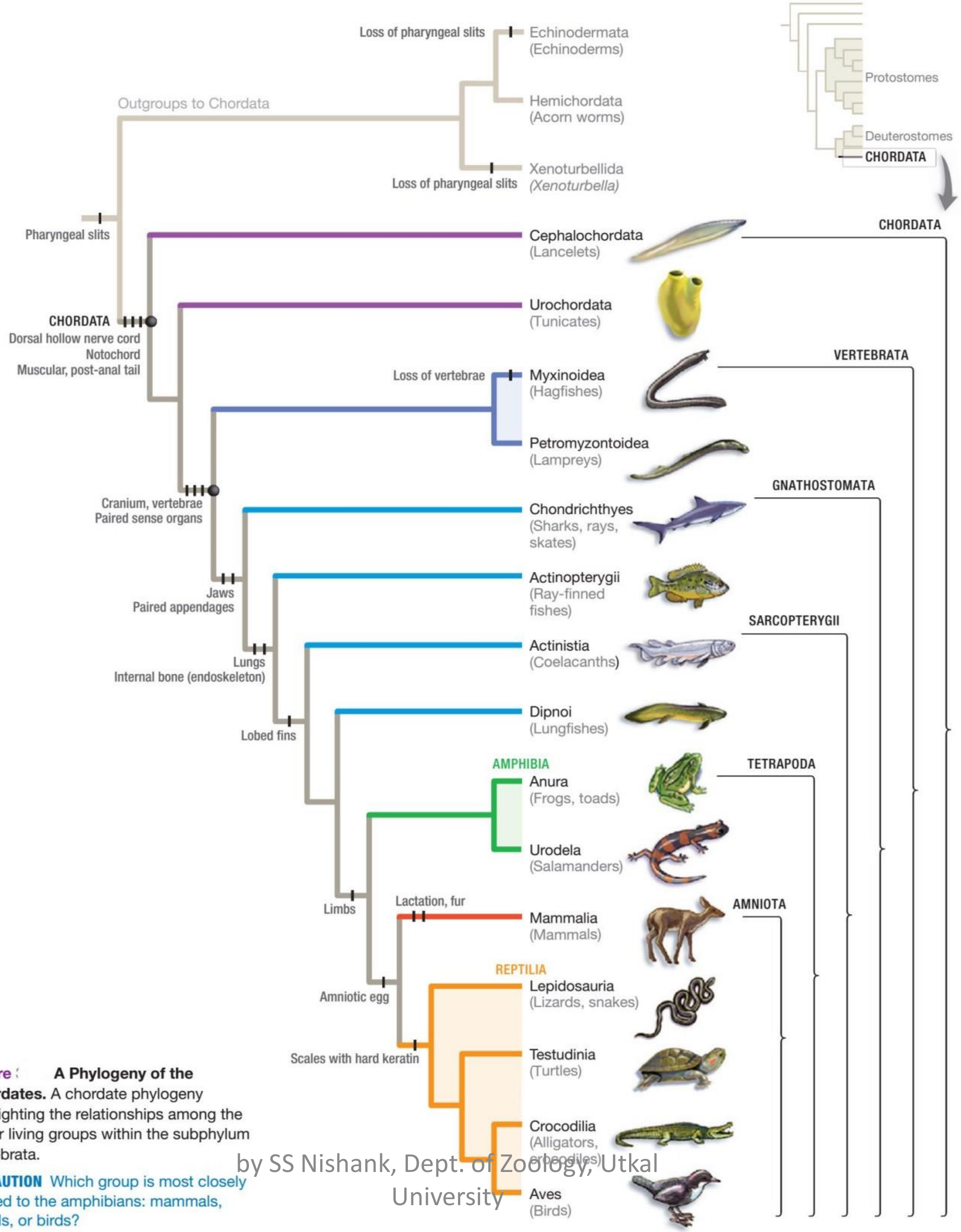
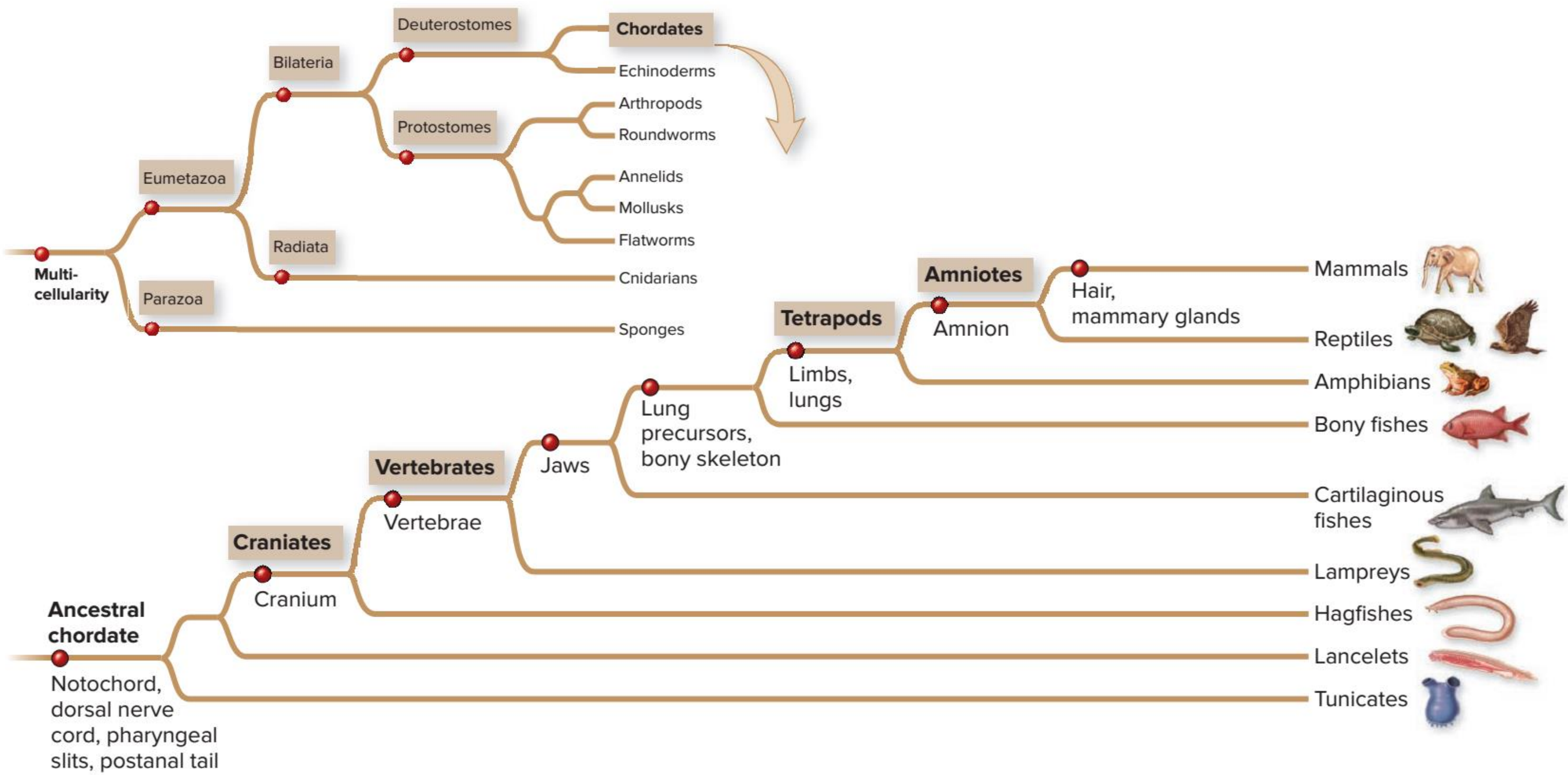
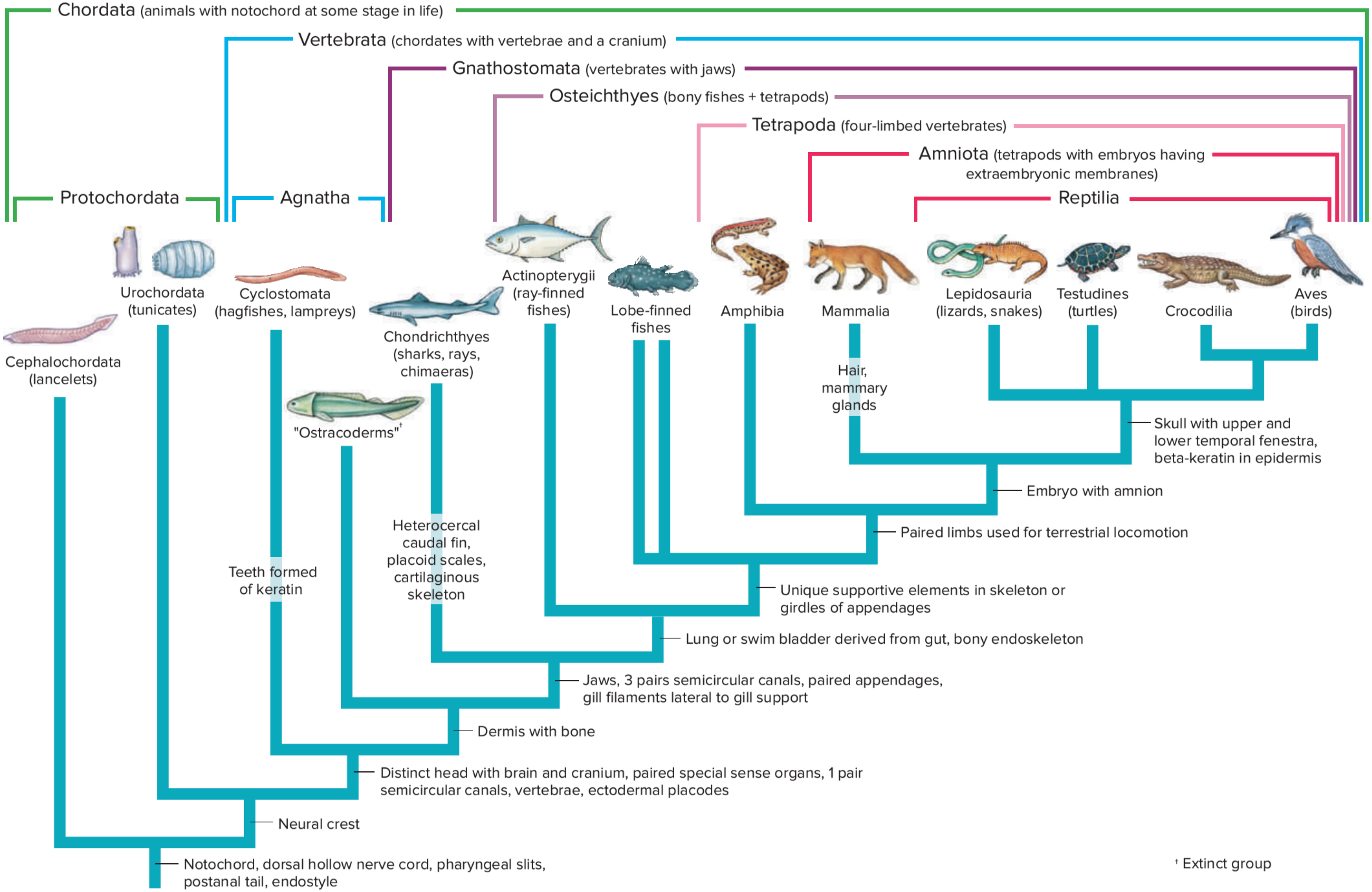


Figure **A Phylogeny of the Chordates.** A chordate phylogeny highlighting the relationships among the major living groups within the subphylum Vertebrata.

✔ **CAUTION** Which group is most closely related to the amphibians: mammals, lizards, or birds?



Deuterostomes
Chordates
Bilateria
Echinoderms
Arthropods
Protostomes
Roundworms
Eumetazoa
Annelids
Mollusks
Flatworms
Radiata
Multi-
cellularity
Cnidarians
Parazoa
Sponges
Amniotes
Mammals
Hair,
mammary glands
Tetrapods
Amnion
Reptiles
Limbs,
lungs
Amphibians
Lung
precursors,
bony skeleton
Bony fishes
Vertebrates
Jaws
Cartilaginous
fishes
Vertebrae
Craniates
Lampreys
Cranium
Ancestral
chordate
Hagfishes
Lancelets
Notochord,
dorsal nerve
cord, pharyngeal
slits, postanal tail
Tunicates

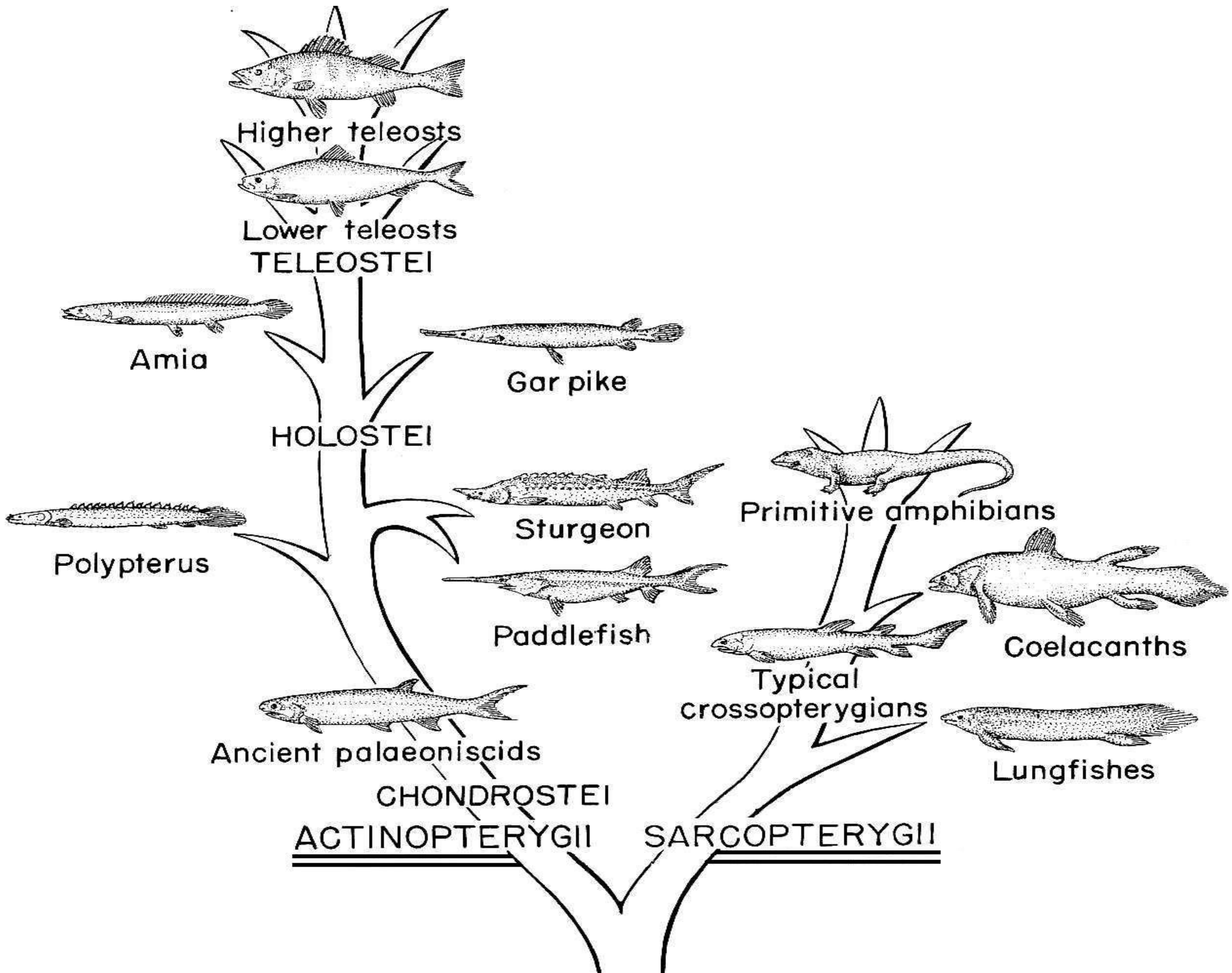

Chordata (animals with notochord at some stage in life)
Vertebrata (chordates with vertebrae and a cranium)
Gnathostomata (vertebrates with jaws)
Osteichthyes (bony fishes + tetrapods)
Tetrapoda (four-limbed vertebrates)
Amniota (tetrapods with embryos having extraembryonic membranes)
Reptilia
Protochordata
Agnatha
Cephalochordata (lancelets)
Urochordata (tunicates)
Cyclostomata (hagfishes, lampreys)
"Ostracoderms"†
Chondrichthyes (sharks, rays, chimaeras)
Actinopterygii (ray-finned fishes)
Lobe-finned fishes
Amphibia
Mammalia
Lepidosauria (lizards, snakes)
Testudines (turtles)
Crocodilia
Aves (birds)
Hair, mammary glands
Teeth formed of keratin
Heterocercal caudal fin, placoid scales, cartilaginous skeleton
Skull with upper and lower temporal fenestra, beta-keratin in epidermis
Embryo with amnion
Paired limbs used for terrestrial locomotion
Unique supportive elements in skeleton or girdles of appendages
Lung or swim bladder derived from gut, bony endoskeleton
Jaws, 3 pairs semicircular canals, paired appendages, gill filaments lateral to gill support
Dermis with bone
Distinct head with brain and cranium, paired special sense organs, 1 pair semicircular canals, vertebrae, ectodermal placodes
Neural crest
Notochord, dorsal hollow nerve cord, pharyngeal slits, postanal tail, endostyle
† Extinct group

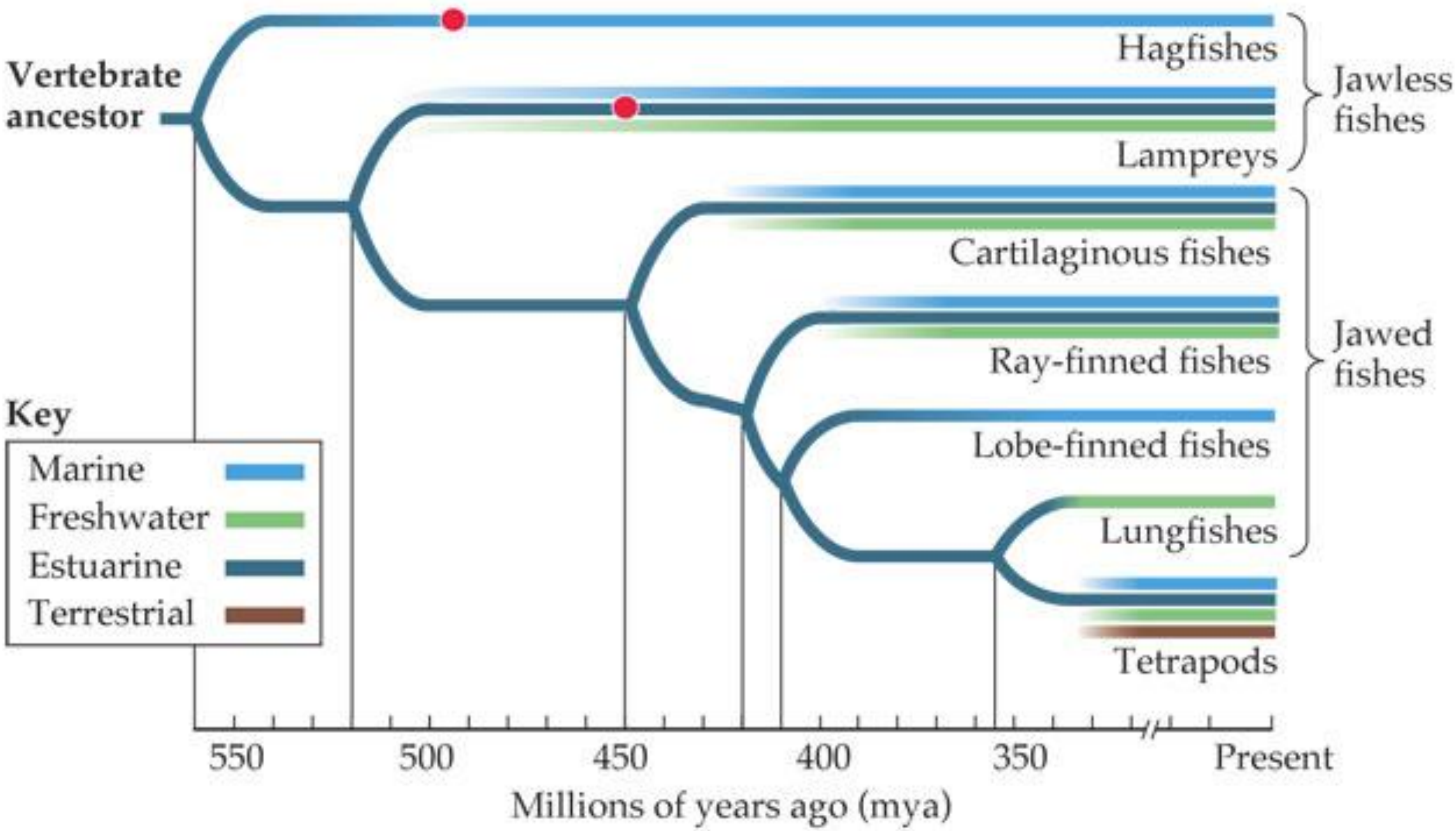
Key Lineages of Jawed Fishes

Chordata > Vertebrata >		Known Species	Feeding	Movement	Reproduction
	**Chondrichthyes** **Sharks, rays, skates** Cartilaginous skeleton, jaws, and paired lateral fins	**1200** Marine (Freshwater) 10 cm–13 m	Some suspension feed on plankton, but most are predators; sharks are referred to as the “top predator” because they are at the top of the food web	Sharks swim by undulating their bodies from side to side and beating their tails; rays and skates swim by flapping their large pectoral fins	Internal fertilization; some are oviparous, some ovoviviparous, and some viviparous; a placenta evolved independently in certain shark lineages
	**Actinopterygii** **Ray-finned fishes** Bony skeleton, fins supported by long, bony rods arranged in a ray pattern; scales	**30,500** Marine Freshwater 8 mm–14 m	Can suck food toward their mouths, grasp it with their protrusible jaws, process it with teeth on jaws and with pharyngeal jaws in throat	Swim by undulating side to side and by flapping fins; many have a gas-filled swim bladder that prevents sinking	Most rely on external fertilization and are oviparous; others have internal fertilization and are viviparous; some have parental care; many undergo metamorphosis
	**Actinistia** **Coelacanths** Four fleshy, lobed fins supported by bones; thought to have gone extinct 65 mya, discov-ered alive in 1938	**2** Marine 1.5–2 m	Has a unique hinge in its skull that enables it to open its mouth extremely wide to consume large fish and cephalopods	Generally swim slowly and passively using four lobed fins in alternating pattern resembling use of limbs in tetrapods	Sexual reproduction; internal fertilization; ovoviviparous (retain embryos within eggs for a year or more before birth of fully developed young)
	**Dipnoi** **Lungfishes** Four lobed fins; use lungs to breathe air when oxygen levels drop in their shallow aquatic habitats	**6** Freshwater 0.4–2 m	Omnivorous, eating algae and plant material as well as animals; teeth fuse to form tooth plates for crushing and chewing	Swim by undulating their bodies; some also use their lobed fins to walk along the bottom of ponds	Sexual reproduction; external fertilization; oviparous; eggs hatch into larvae that resemble juvenile salamanders

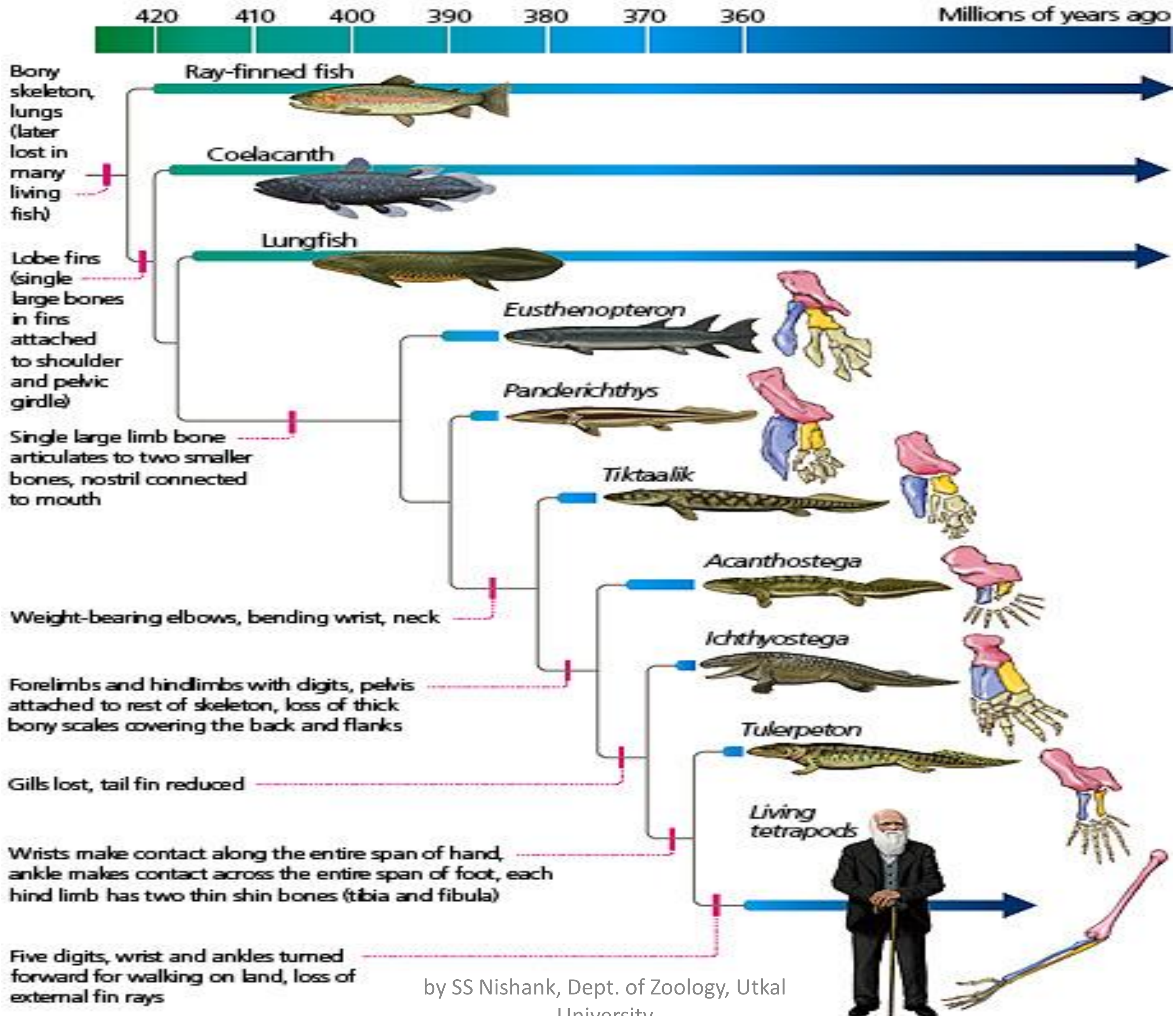
Tetrapods: Origin of the Limb

- Although coelacanths and lungfishes represent independent lineages, they are sometimes grouped together in a grade called lobe-finned fishes.
- The first vertebrates that had limbs and were capable of moving on land date to about 365 million years ago, late in the Devonian. These were the first of the tetrapods—animals with four limbs.

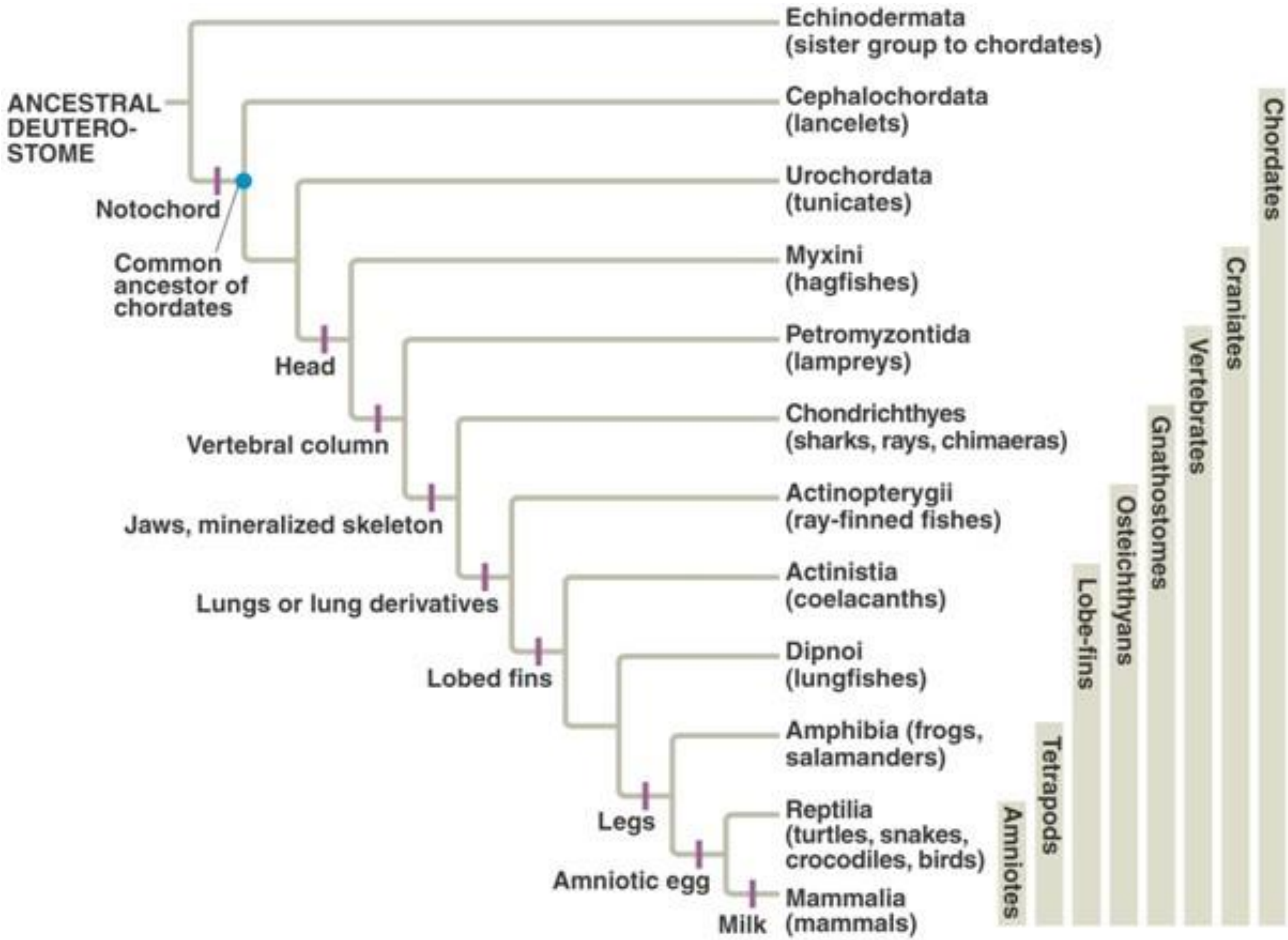

Higher teleosts
Lower teleosts
TELEOSTEI
Amia
Gar pike
HOLOSTEI
Primitive amphibians
Sturgeon
Polypterus
Coelacanths
Paddlefish
Typical crossopterygians
Ancient palaeoniscids
Lungfishes
CHONDROSTEI
ACTINOPTERYGII
SARCOPTERYGII



LIFE: THE SCIENCE OF BIOLOGY, Seventh Edition, Figure 34.8 A Current Phylogeny of the Vertebrates



420
410
400
390
380
370
360
Millions of years ago
Bony skeleton, lungs (later lost in many living fish)
Ray-finned fish
Coelacanth
Lungfish
Lobe fins (single large bones in fins attached to shoulder and pelvic girdle)
Eusthenopteron
Panderichthys
Single large limb bone articulates to two smaller bones, nostril connected to mouth
Tiktaalik
Acanthostega
Weight-bearing elbows, bending wrist, neck
Ichthyostega
Forelimbs and hindlimbs with digits, pelvis attached to rest of skeleton, loss of thick bony scales covering the back and flanks
Tulerpeton
Gills lost, tail fin reduced
Living tetrapods
Wrists make contact along the entire span of hand, ankle makes contact across the entire span of foot, each hind limb has two thin shin bones (tibia and fibula)
Five digits, wrist and ankles turned forward for walking on land, loss of external fin rays


ANCESTRAL DEUTERO-STOME
Notochord
Common ancestor of chordates
Head
Vertebral column
Jaws, mineralized skeleton
Lungs or lung derivatives
Lobed fins
Legs
Amniotic egg
Milk
Echinodermata (sister group to chordates)
Cephalochordata (lancelets)
Urochordata (tunicates)
Myxini (hagfishes)
Petromyzontida (lampreys)
Chondrichthyes (sharks, rays, chimaeras)
Actinopterygii (ray-finned fishes)
Actinistia (coelacanths)
Dipnoi (lungfishes)
Amphibia (frogs, salamanders)
Reptilia (turtles, snakes, crocodiles, birds)
Mammalia (mammals)
Chordates
Craniates
Vertebrates
Gnathostomes
Osteichthyans
Lobe-fins
Tetrapods
Amniotes

Cause of transition to land

1. To get back into the water under arid conditions
2. "Limbs" initially for burrowing in the mud
3. Competition and/or predation with other aquatic forms
4. To escape oxygen-depleted water
5. Feeding on terrestrial or semi-terrestrial food sources
6. Increase in body temperature
   a. Increase in rate of digestion
   b. Speed development
7. Spawning on land
8. Limbs evolved originally for amplexus in the water

key challenges faced by vertebrates when they moved on to land ?

- air breathing
- weight & locomotion support
- new way of feeding
- sensing of prey & predators
- sensing of water balance
- reproduction

Living Amphibians Have Five Distinguishing Features

- 1. **Legs.** Frogs and most salamanders have four legs and can move about on land quite well.
- 2. **Lungs.** Most amphibians possess a pair of lungs, Amphibians breathe by lowering the floor of the mouth to suck in air, then raising it back to force the air down into the lungs.
- 3. **Cutaneous respiration.** Frogs, salamanders, and caecilians all supplement the use of lungs by respiring through their skin
- 4. **Pulmonary veins.** After blood is pumped through the lungs, two large veins called pulmonary veins return the aerated blood to the heart for repumping.
- 5. **Partially divided heart.** The blood circulation is thus divided into two separate paths: pulmonary and systemic.

Chordata > Vertebrata > Amphibia >		Known Species	Feeding	Movement	Reproduction
	**Anura** **Frogs, toads** Stout-bodied; lacking tails as adults; large eyes	**7400** Freshwater Terrestrial 0.8–32 cm	Adults are carnivores; most are sit-and-wait predators that use their long, extensible tongues to capture prey	Four limbs; on land, frogs and toads kick their hind legs to jump or hop; in water, they kick their hind legs to swim	Sexual reproduction; usually external fertilization in water; aquatic tadpoles usually metamorphose into land-dwelling adults
	**Urodela** **Salamanders** Slender-bodied; tails in both larvae and adults; short limbs; large eyes	**675** Freshwater Terrestrial 1.5–180 cm	Most adults are carnivores; terrestrial species use their extensible tongues to capture prey; aquatic forms grab prey with their jaws	Four limbs; on land, salamanders walk; in water, they undulate their bodies to swim	Sexual reproduction; usually internal fertilization in water; aquatic larvae metamorphose into aquatic or terrestrial adults
	**Gymnophiona** **Caecilians** Slender-bodied; no limbs; small, skin-covered eyes detect light	**200** Freshwater Terrestrial 11–150 cm	Terrestrial caecilians prey on earthworms and other soil-dwelling animals; aquatic forms eat invertebrates and small fishes	Lack limbs, so resemble worms or snakes; burrow underground in wet tropical regions; in water, swim by undulating their bodies	Sexual reproduction; internal fertilization; most are viviparous; some have larvae while others have direct development

Early tetrapodomorphs

Tetrapodomorphs includes all taxa that are more closely related to modern amphibians, reptiles, and mammals than to lungfish

Eusthenopteron:

- It was a large sized (up to 1.8 m) predatory fish that inhabited shallow marine or estuarine waters in the Late Devonian (385-380 million years ago).
- Eusthenopteron is notable because its teeth have extensive folding of enamel (labyrinthodont dentition) like those of other early tetrapods.
- More important, its pectoral and pelvic fins contain bones homologous to the radius,ulna, tibia, and fibula of modern tetrapods .
- Eusthenopteron was probably fully aquatic

Early tetrapodomorphs

***Panderichthys* :**

- It was a was contemporaneous fish in Late Devonian (-385 mya) with *Eusthenopteron* and displayed more tetrapod-like features
- Its body was dorsolaterally flattened and lacked dorsal and anal fins, and the tail fin was greatly reduced.
- Its pectoral girdle was more robust than that of *Eusthenopteron*, and *Panderichthys* may have walked on the bottom of shallow water bodies.
- Its eyes were located dorsally on a rather crocodile-like skull, and *Panderichthys* may have foraged at the water surface.
- the middle-ear archlecture of Panderichthys shows modifications that may represent the early transition to a tetrapod-like middle ear

Early tetrapodomorphs

***Tiktaalik* :**

- This fish showed the transition from water to land in early tetrapodomorphs.
- Although distinctly a fish that inhabited shallow water bodies, *Tiktaalik* possessed a suite of morphological characters that represents a transitional stage between aquatic and terrestrial modes of living.
- *Tiktaalik l*acks the bony sheath (operculum) that covers the gills in other fish.rfbis change is functionally important because loss of the operculum eliminates the rigid connection between the body and head, creating a flexible neck. Thus, *Tiktaalik* could probably raise its head out of the water and turn it from side to side.
- Perhaps more important, the pectoral and pelvic girdles were stronger than those of other tetrapodomorph fish, thus allowing *Tiktaalik* to prop itself up on its fins, use them for aquatic propulsion, and maybe even make brief terrestrial forays along the water's edge

Early tetrapods : is containing the ancestor of Acanthostega and all descendants of this common ancestor: modern-day amphibians, reptiles, and mammals, including extinct lineages such as Ichthyostega.

Acanthostega and Ichthyostega :

- These animals that lived during the Late Devonian (-365 mya), were far more like our own terrestrially adapted skeletons than the skeletons of fish.
- They had well-developed pectoral and pelvic girdles and distinct neck regions that allowed movement of the head independent of the trunk.
- They also possessed limbs with bony digits—seven on the hindlimb of Ichthyostega (the forelimb of *Ichthyostega* is unknown) and eight on both the forelimb and hindlimb of *Acanthostega*.
- Ichthyostega had additional skeletal modifications that suggest partially terrestrial habits. For example, the pectoral and pelvic girdles of Ichthyostega were far more robust than those of Acanthostega, the elbow was bendable, the vertebral column was reinforced by strong connections between vertebrae (zygopophyses), and the ribs were expanded and overlapping, thereby forming a distinct rib cage.

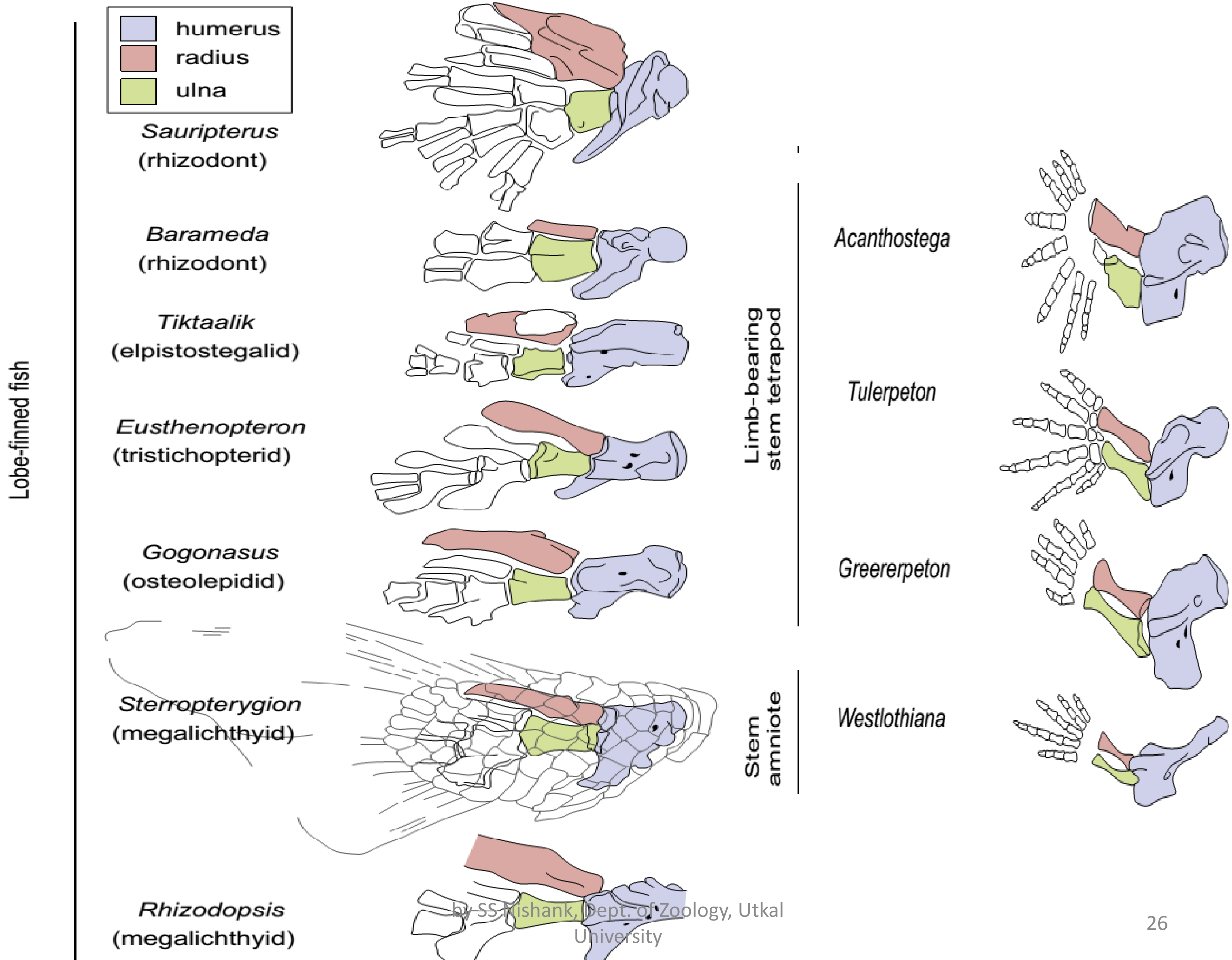
Early tetrapods : is containing the ancestor of Acanthostega and all descendants of this common ancestor: modern-day amphibians, reptiles, and mammals, including extinct lineages such as Ichthyostega.

Acanthostega and Ichthyostega :

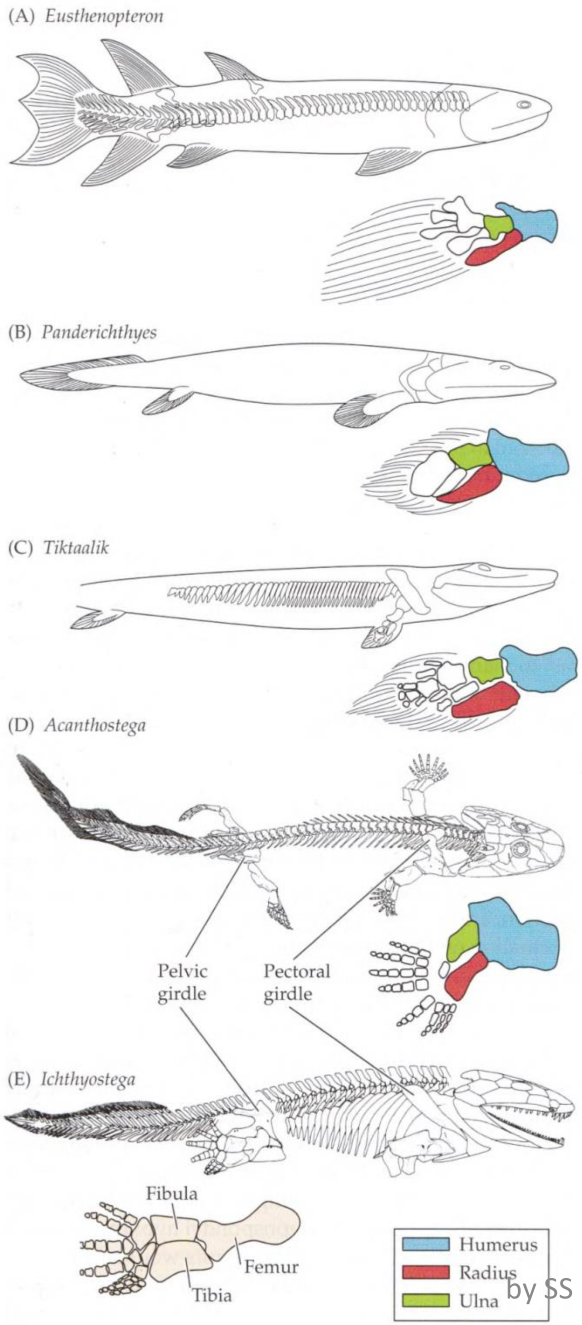
•All of these features suggest that Ichthyostega could drag 让self out of the water with its forelimbs (the hindlimbs were smaller and more paddlelike) and support its weight in terrestrial environments, although it not possible to know how long it could remain out of the water.

•Like lungfish today; these genera probably had lungs, but they also retained fishlike internal gills and were primarily aquatic.

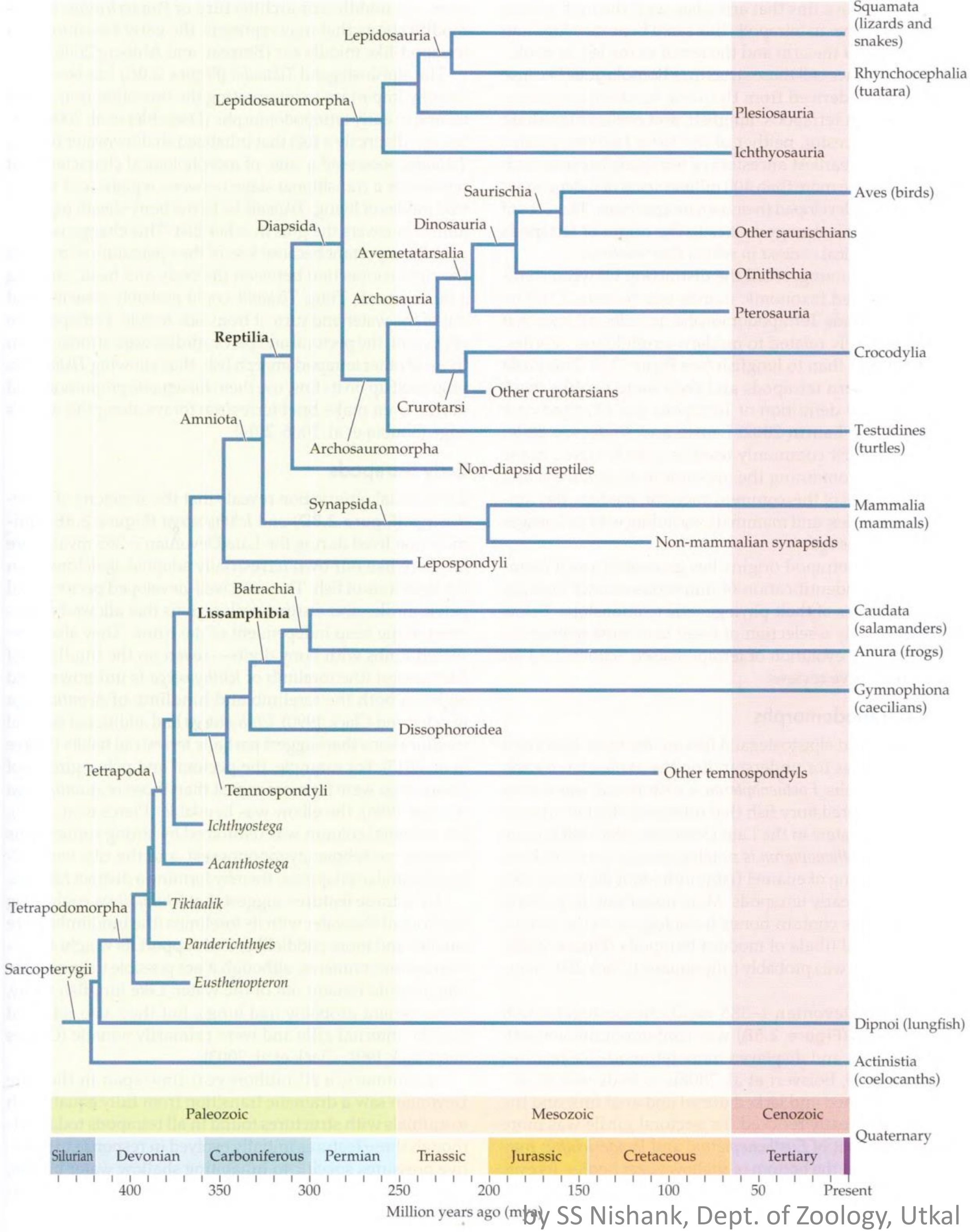
•In summary, a 20-million-year time span in the Late Devonian saw a dramatic transition from fully aquatic fish to animals with structures found in all tetrapods today. Although these features initially evolved in response to selective pressures specific to inhab辻ing shallow water bodies, they provided the basic building blocks that eventually allowed tetrapods to invade and diversify on land.



humerus
radius
ulna
Sauripterus
(rhizodont)
Barameda
(rhizodont)
Tiktaalik
(elpistostegalid)
Eusthenopteron
(tristichopterid)
Gogonasus
(osteolepidid)
Sterropterygion
(megalichthyid)
Rhizodopsis
(megalichthyid)
Lobe-finned fish
Limb-bearing stem tetrapod
Stem amniote
Acanthostega
Tulerpeton
Greererpeton
Westlothiana



Reconstructed skeletons and limbs of extinct tetrapodomorphs and tetrapods.
The reconstructed dorsal view of the forelimb of each species is shown, except for *Ichthyostega* (E), whose hindlimb is shown (the forelimb is unknown for this genus). Homologous bones are color-coded.



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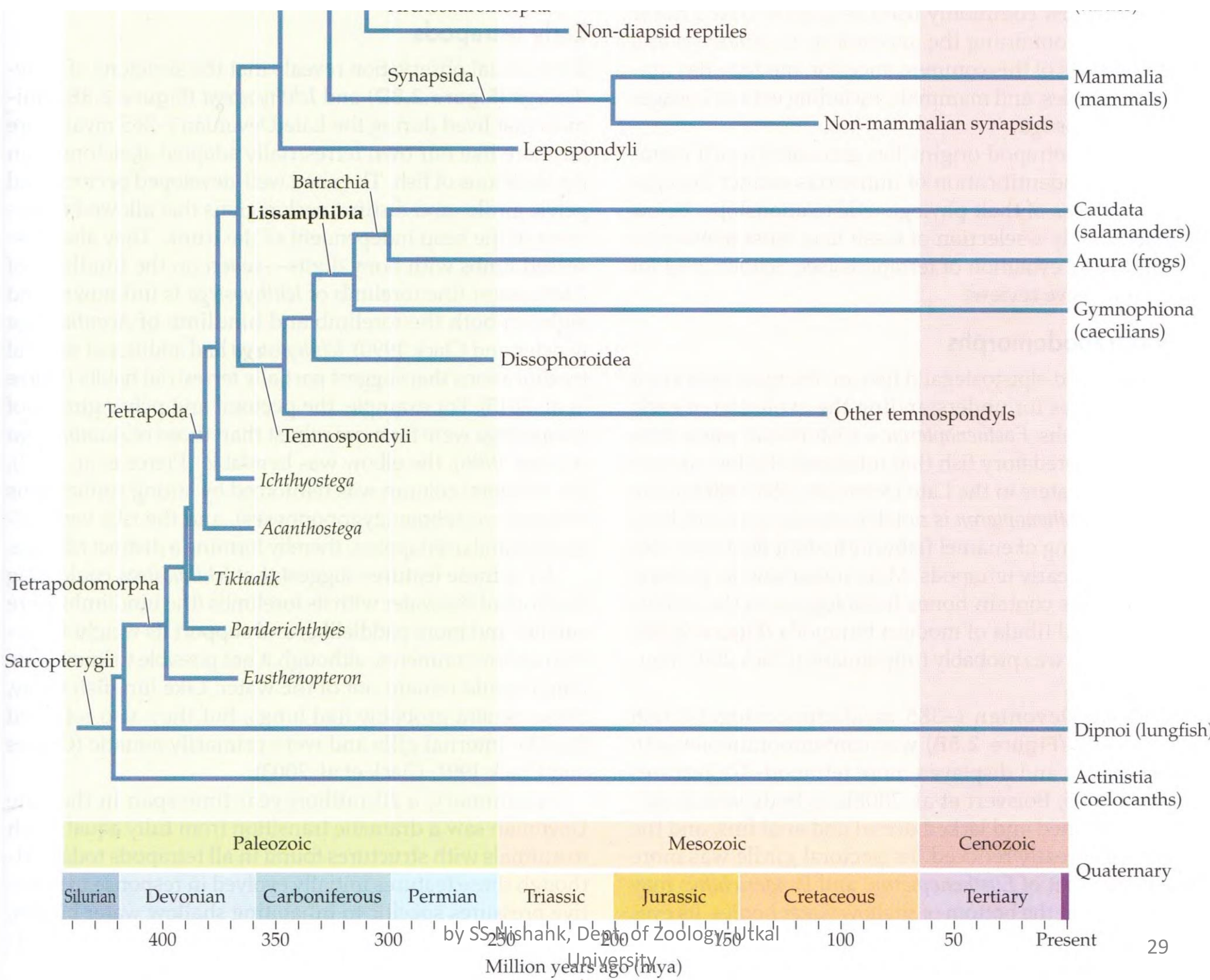
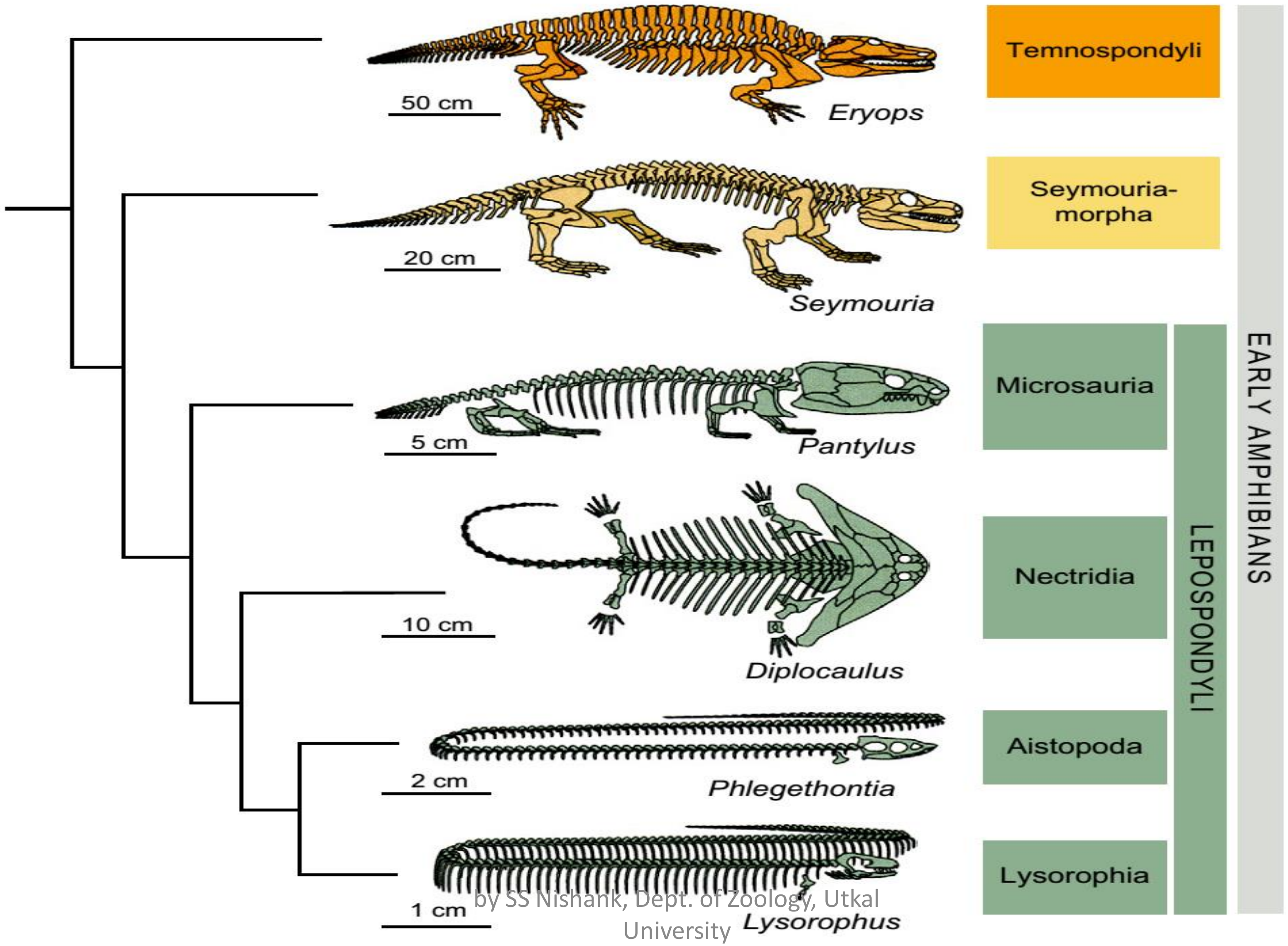


Non-diapsid reptiles
Synapsida
Mammalia
(mammals)
Non-mammalian synapsids
Lepospondyli
Batrachia
Lissamphibia
Caudata
(salamanders)
Anura (frogs)
Gymnophiona
(caecilians)
Dissophoroidea
Tetrapoda
Other temnospondyls
Temnospondyli
Ichthyostega
Acanthostega
Tetrapodomorpha
Tiktaalik
Panderichthyes
Sarcopterygii
Eusthenopteron
Dipnoi (lungfish)
Actinistia
(coelocanths)
Paleozoic
Mesozoic
Cenozoic
Quaternary
Silurian
Devonian
Carboniferous
Permian
Triassic
Jurassic
Cretaceous
Tertiary
400
350
300
250
200
150
100
50
Present
Million years ago (mya)

Amphibians of the Late Paleozoic and Early Mesozoic

- Most amphibians of the Paleozoic and early Mesozoic can be categorized into three major clades, the **Temnospondyli,** the **Seymouriamorpha**, and the **Lepospondyli**.
- The more than 300 species of **temnospondyls** were medium to large (1–6 m) salamander-like tetrapods living in streams, lakes, and swamps. Most were aquatic, but some became more or less terrestrial. They appeared in Early Carboniferous and flourished during the Carboniferous, Permian, and Triassic.
- A few survived into the Cretaceous. By the Late Permian, most terrestrial temnospondyls had disappeared, but semiaquatic and aquatic temnospondyls continued to diversify.
- A Permian temnospondyl, *Prionosuchus*, looked like a giant salamander with a long, gavial-like snout, and was the largest amphibian ever described, reaching 9 m in total length. Others, such as the eryopoids included aquatic to terrestrial, small to large amphibians.
- The heavy bodied *Eryops* is characteristic of this group, although it was larger (nearly 2 m TL/total length) than most eryopoids.

Early Amphibians



Amphibians of the Late Paleozoic and Early Mesozoic

- Development was gradual in temnospondyls, with no indication of the kinds of transformations seen in modern amphibians. Modern amphibians (Lissamphibia) likely have their origins within the Temnospondyli.
- The less diverse **seymouriamorphs** were represented by the aquatic discosauriscids and the terrestrial seymouriids. Discosaurids were newt-like and are known only from either larval forms or neotenic forms.
- Rounded scales covered the body. They also had lateral line systems. Seymouriids are represented by the genus *Seymouria*, containing three species. These were stocky reptilomorphs with large heads, well-developed jaws, robust bodies, and strong limbs. They were terrestrial, but likely returned to water to breed. Larvae are not known for seymouriids.
- Seymouriamorphs appeared in the early Permian and persisted through nearly the entire Permian. No evidence exists for either metamorphosis or neoteny in seymouriamorphs.

Amphibians of the Late Paleozoic and Early Mesozoic

- The **Lepospondyli** contains four clades, Microsauria, Nectridia, Aistopoda, and Lysorophia. Lepospondyls varied considerably in morphology.
- Some were salamanderlike, some were flat with large, triangular-shaped heads, and some were even limbless. Most species were small (5–10 cm). They were present from the Carboniferous through the Permian.
- The microsaurs were small (most <50 cm TL), salamander-like tetrapods. Microsaurs were the most diverse among lepospondyls, and they varied considerably in morphology. Some species had long, thin bodies, whereas others were rather short and stout. All microsaurs had short legs and short tails. Some lived on dry land, some burrowed, and others retained a larval-type morphology with external gills, and they presumably were aquatic.
- These were heavily ossified amphibians, with ossification occurring early during development. Consequently, even though they resembled salamanders, their life histories were quite different, with metamorphosis unlikely. They are known from the Late Carboniferous through the Early Permian.

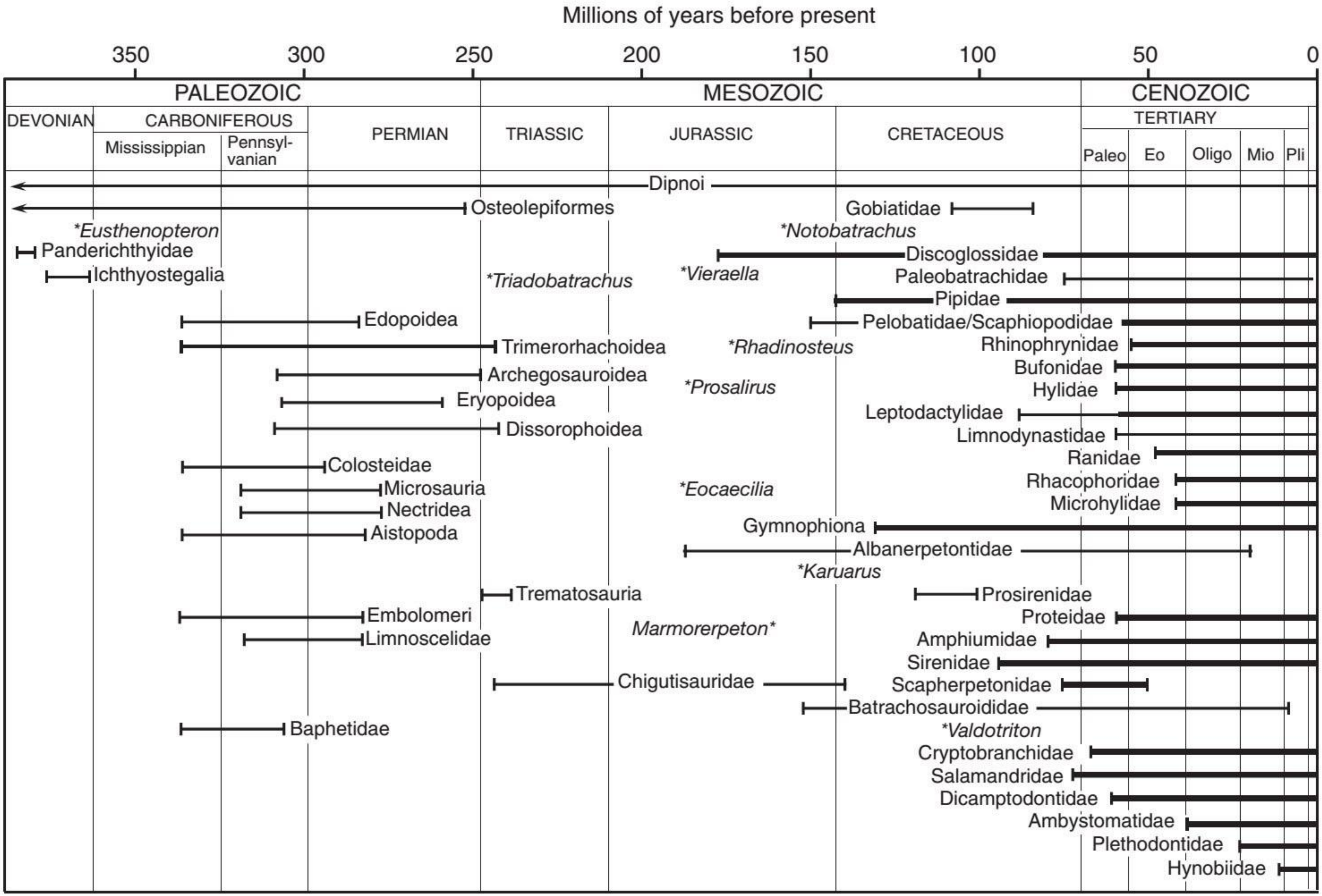


FIGURE Geological occurrence of some early tetrapods, and extinct and living amphibians. Abbreviations for Cenozoic epochs: Paleo, Paleocene; Eo, Eocene; Oligo, Oligocene; Mio, Miocene; Pli, Pliocene; Pleistocene is the narrow, unlabeled epoch on the far right side of the chart. *Taken partly from Carroll, 2009.*

Amphibians of the Late Paleozoic and Early Mesozoic

- Nectrideans were small to medium sized, newt-like amphibians, all less than 0.5 m TL. The heads of some, such as *Diplocaulus*, were arrow-shaped with large, laterally projecting horns. This head shape appears to facilitate rapid opening of the mouth for suction-gape feeding. *Diplocaulus* had a biphasic lifestyle (larva and adult morphs), but morphological changes that occurred were most likely associated with changes in the mode of feeding, not a shift from aquatic to terrestrial life.
- Other nectrideans had more typically shaped heads with strong dentition for snap-and-grasp feeding. Presumably , they were predominantly aquatic and semiaquatic.
- Aistopods were delicate eel-like, limbless amphibians that persisted from the Carboniferous through the Early Permian. Some were very small (5 cm) and others were moderately large (70 cm). Presumably they were aquatic and semiaquatic because they had fragile skulls unlike those of burrowing animals. *Ophiderpeton*, which reached 70 cm, fed on small invertebrates, primarily worms and arthropods.

Amphibians of the Late Paleozoic and Early Mesozoic

- Lysorophians were similar to aistopods in that they were eel or snake-like. This is a low diversity group, with only about five genera in a single family, the Cocytinidae. Limbs are extremely small or absent. They were aquatic, and occurred during the Carboniferous and Permian.
- At the Permian–Triassic boundary, about 252Ma (million years before present), the greatest extinction event in the history of the Earth occurred. Nearly 70% of terrestrial species and 96% of marine species disappeared. This included more than 80% of all known genera disappearing and nearly 60% of known families.
- Following the Great Extinction, reptiles and synapsids had become the dominant terrestrial vertebrates by the Triassic.
- In contrast, amphibians experienced a minor diversity explosion with the appearance of at least seven different groups of presumed temnospondyls, including the first lissamphibian.
- The radiation included small to large temnospondyls with several groups having species in the 1.5–3 m range (e.g., capitosauroids, chigutisauroids, and metoposaurids) and some mastodonsaurids to 6 m TL. All large species appear to have been highly aquatic, and most had crocodile-like body forms

FIGURE Triassic landscape showing early reptiles including the dycinodont *Placerias* (left), a group of theropods in the genus *Coelophysis* (right), several phytosaurs (crocodile-like), and a group of metaposaurs (labyrinthodont amphibians). *By Karen Carr, with permission of the Sam Noble Oklahoma Museum of Natural History.*

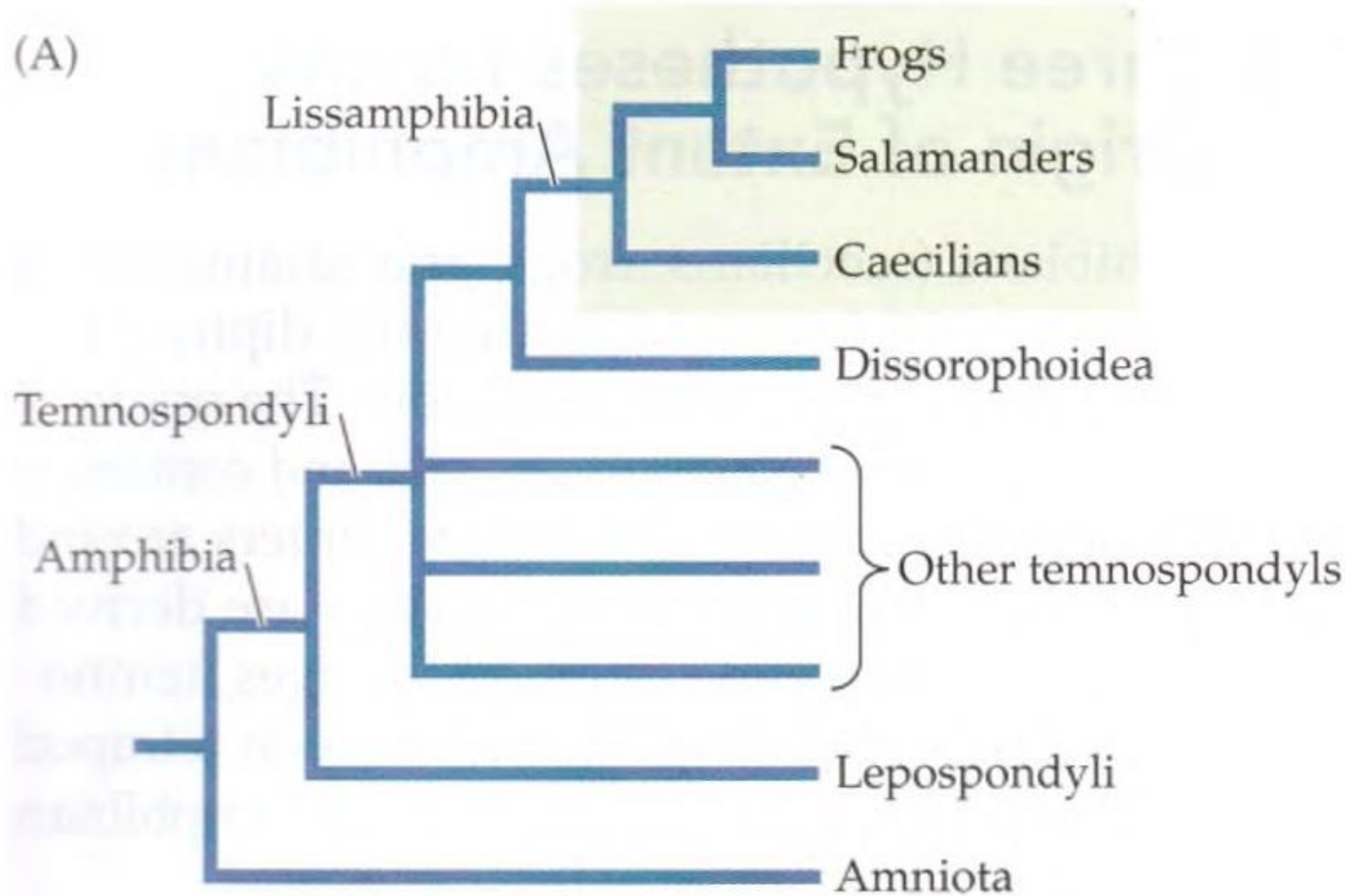
Amphibians of the Late Paleozoic and Early Mesozoic

- The mastodonsaurids were a shortlived group found only in Lower Triassic sediments of northern Eurasia. The 2 m (TL) trematosaurs were another Lower Triassic taxon with triangular to gharial-like heads; some were marine, an anomaly for amphibians.
- Three temnospondyl groups (brachyopoids, capitosauroids, and plagiosaurids) occurred throughout the Triassic.

Three Hypotheses for the Origin of Living Amphibians

***Extant amphibians (caecilians, frogs, and salamanders) form a clade named Lissamphibia*:**

- The origin of Lissamphibia has been debated for decades and continues to produce copious literature.
- The debate centers around whether caecilians, frogs, and salamanders are derived from one or both of two early tetrapod lineages, temnospondyls and lepospondyls
- A. The temnospondyl hypothesis
- B. The lepospondyl hypothesis
- C. The diphyly hypothesis



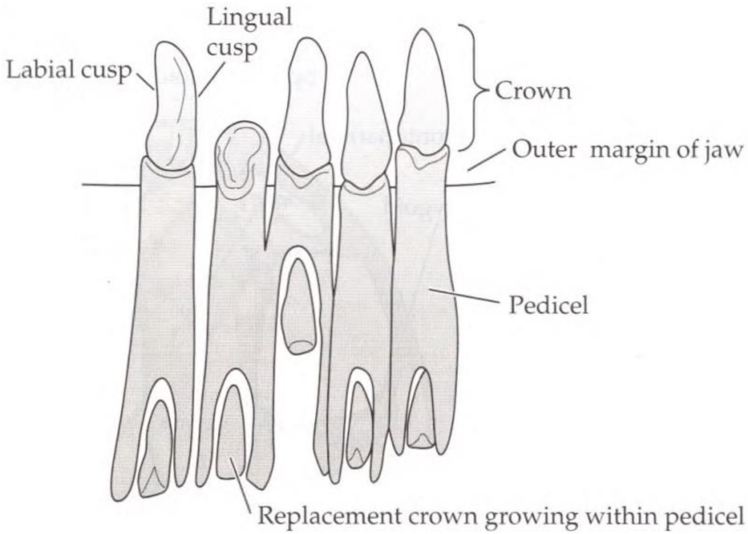
(A) The temnospondyl hypothesis postulates that modern amphibians—salamanders, frogs, and caecilians—form the clade Lissamphibia and are derived from temnospondyl amphibian ancestors, most likely the Dissorophoidea.

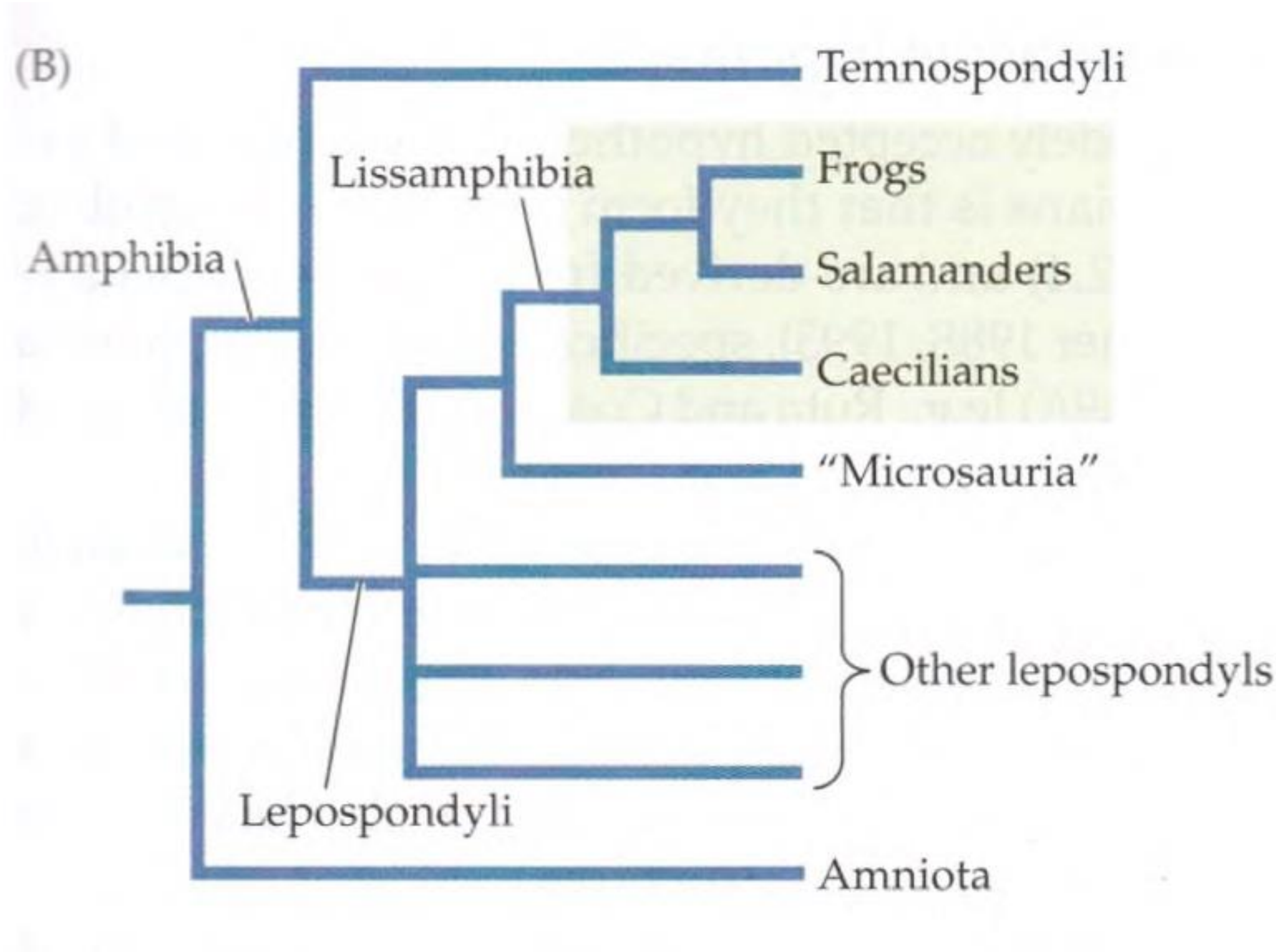
The temnospondyl hypothesis

- The most widely accepted hypothesis for the origin of extant amphibians is that they form a clade (Lissamphibia) and are derived from temnospondyl ancestors, specifically the Dissorophoidea.
- Temnospondyls (from the Greek temn, "cut” + spondyl, "vertebra") are so named because the centrum (body) of their vertebrae consists of two distinct regions that surround the notochord. The intercentrum is a wedge-shaped ventral structure, and the pleurocentra are two wedge-shaped dorsal structures.
- Temnospondyls are represented by almost 200 genera from the Early Carboniferous to the Middle Cretaceous (-330-130 mya).
- They ranged in length from a few centimeters to a few meters. Many species were crocodile-like, with large, flat skulls and dorsally positioned eyes. Mastodonsaurus, which grew to 6 m and had two massive fangs on the mandible, is an extreme example of this phenotype.
- The teeth of temnospondyls are labyrinthodont, a condition seen in other tetrapodomorphs (e.g., Eusthenopteron). Temnospondyls inhabited both freshwater and marine habitats.

The temnospondyl hypothesis

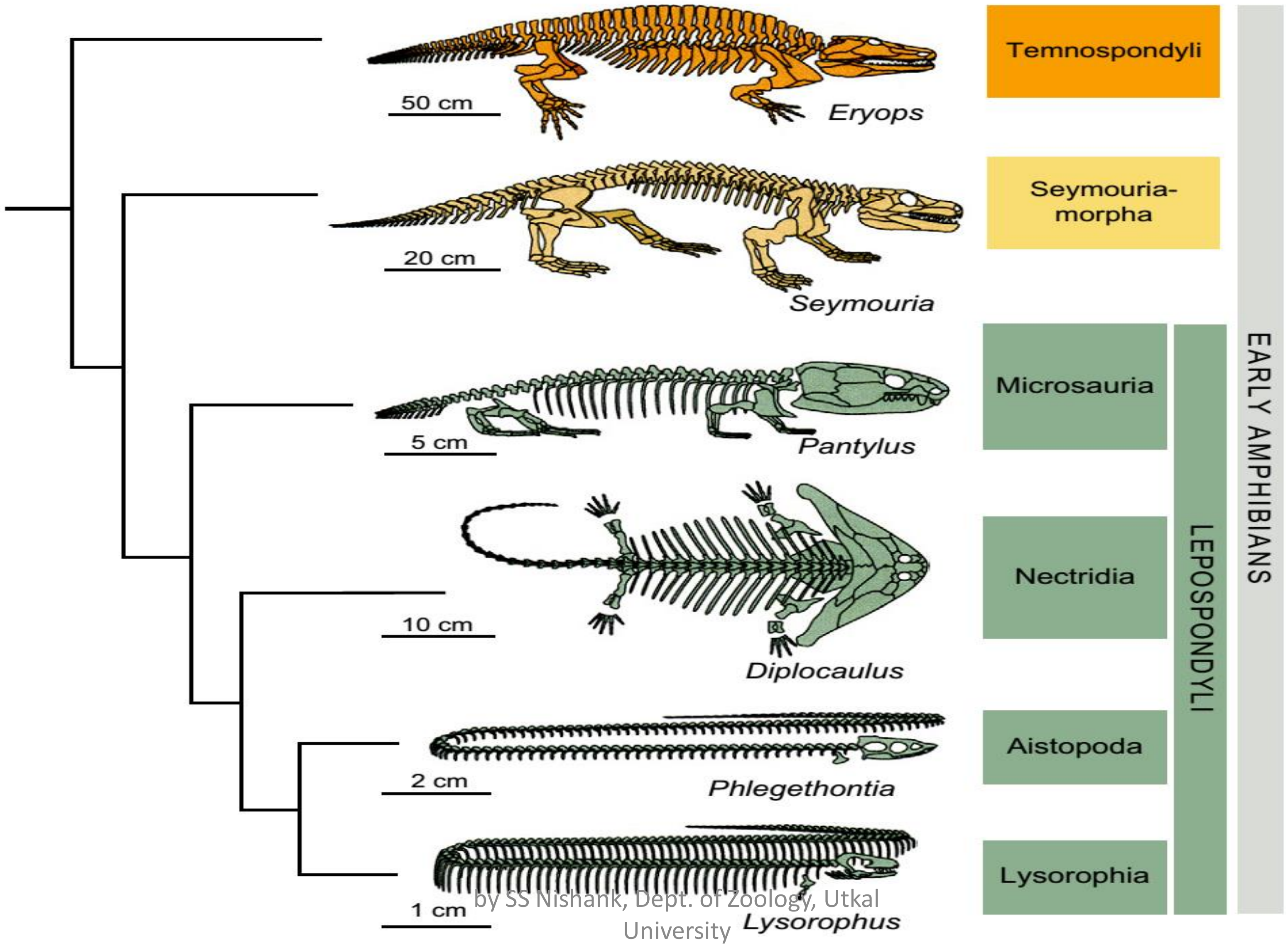
- Numerous characters support a temnospondyl origin of Lissamphibia. Both groups have, among other characters, pedicellate teeth, wide openings in the palate that permit retraction of the eye into the skull, two occipital condyles on the skull that articulate with the first cervical vertebra (the atlas), and short ribs.
- In Pedicellate teeth, the tooth crown sits on a base (pedicel); the two elements are separated by a fibrous connection. The teeth are bicuspid, with one cusp (point) on the lingual (inner) side of the jaw and a second on the labial (outer) side.





(B) The lepospondyl hypothesis states that Lissamphibia is derived from lepospondyl amphibian ancestors, most likely "microsaurs."

Early Amphibians



The lepospondyl hypothesis

- Some phylogenetic studies support the origin of a monophyletic Lissamphibia within lepospondyls, usually within a paraphyletic (a group of organisms descended from a common evolutionary ancestor or ancestral group, but not including all the descendant groups) assemblage of small, lizardlike animals called “microsaurs”
- Unlike the divided three-part vertebrae of temnospondyls, the vertebrae of lepospondyls consist only of a centrum (derived from the pleurocentrum) fused with the neural arch into a single unit.
- Lepospondyls comprise about 60 genera from the Early Carboniferous to the Early Permian (-340-275 mya).
- Aistopods and lysorophids were nearly or entirely limbless, nectrideans were aquatic with strongly compressed tails, and "microsaurs" had a variety of body forms. In contrast to many temnospondyls, lepospondyls were small animals with skulls typically no longer than 5 cm

The lepospondyl hypothesis

- However, one of them—Diplocaulus—is famous for its large (-35 cm) boomerang-shaped head and large body (up to 1.5 m). Probably a flap of skin extended from the head to the sides of the body.
- This unusual structure may have been a hydrofoil to aid swimming, or a way to increase the surface area for cutaneous gas exchange, although these and other hypotheses, such as sexual selection, are not mutually exclusive.
- Both lissamphibians and lepospondyls lack numerous bones of the skull, including the ectopterygoid and postorbital bones, as well as the cleithrum from the pectoral girdle.
- These losses may be interpreted as synapomorphies (*a characteristic present in an ancestral species and shared exclusively (in more or less modified form) by its evolutionary descendants*) that support inclusion of both groups in a clade. A study that included morphological data for both extinct and extant taxa and molecular data for extant taxa also supports the lepospondyl hypothesis.

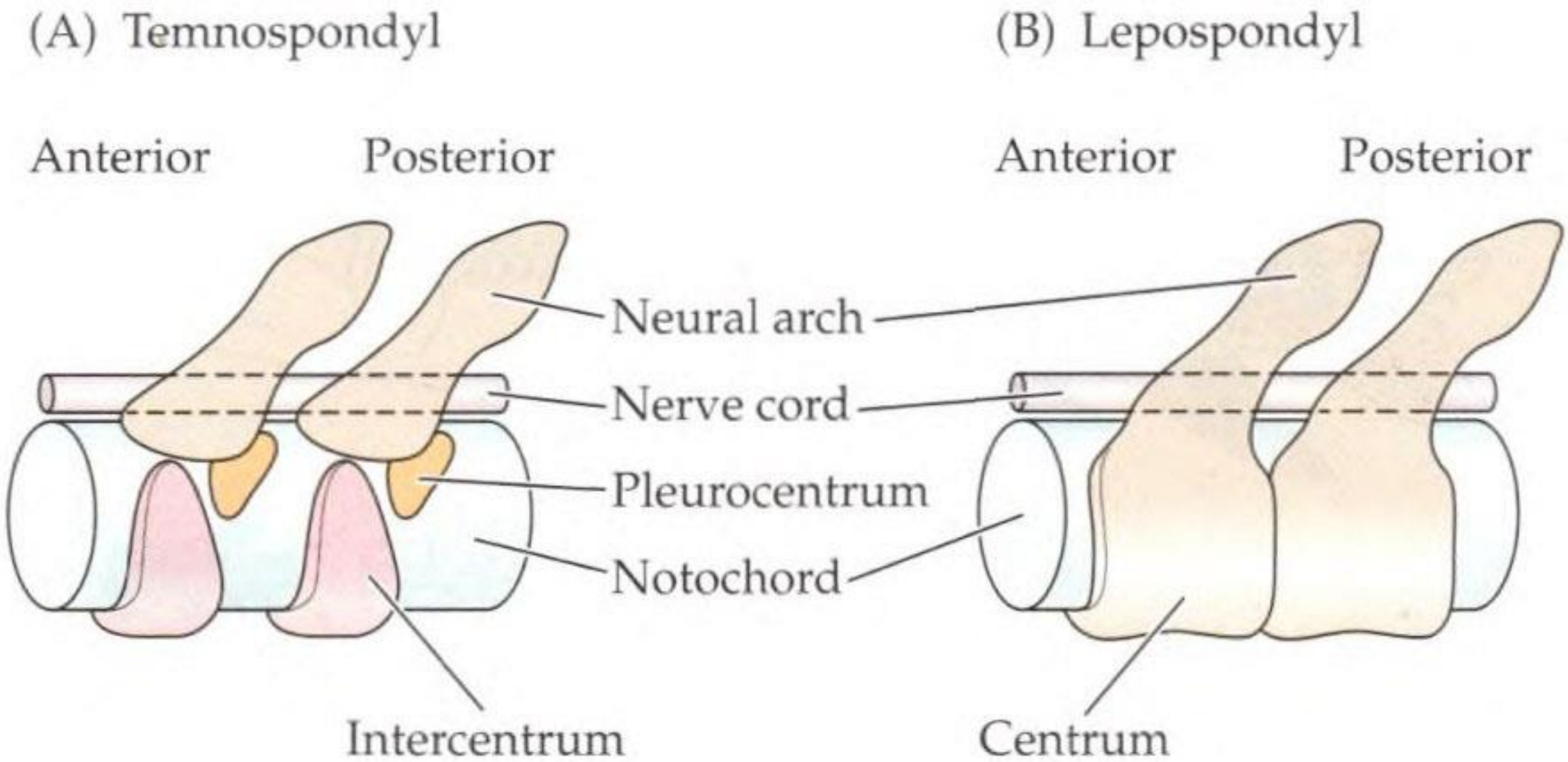


Figure Vertebrae distinguish temnospondyls and lepospondyls. (A) The vertebrae of temnospondyls consist of a wedge-shaped ventral structure, the intercentrum, and two dorsal pleurocentra (the second pleurocentrum is behind the notochord in this view). (B) In lepospondyls, the intercentrum, pleurocentra, and neural arch are fused into a single structure.

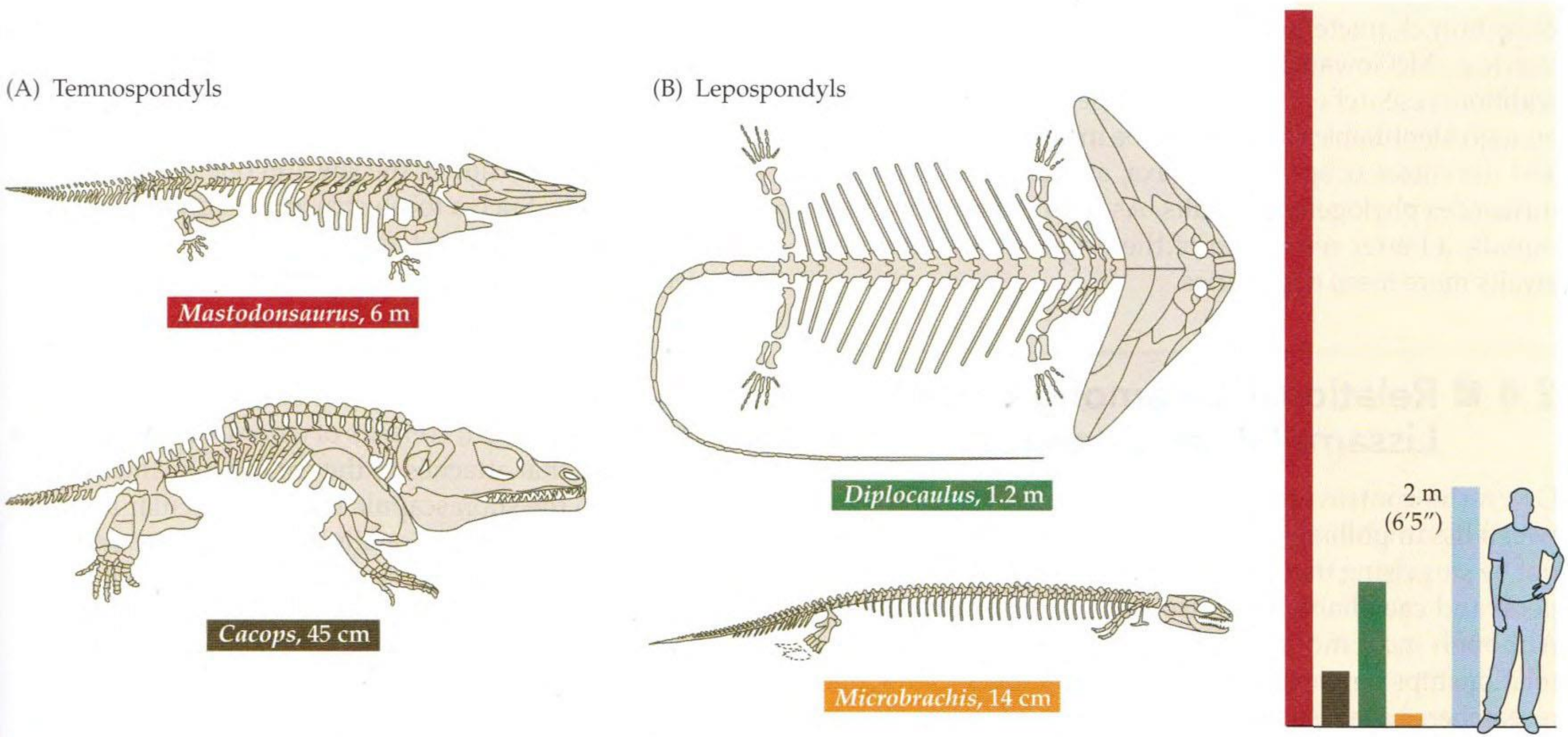
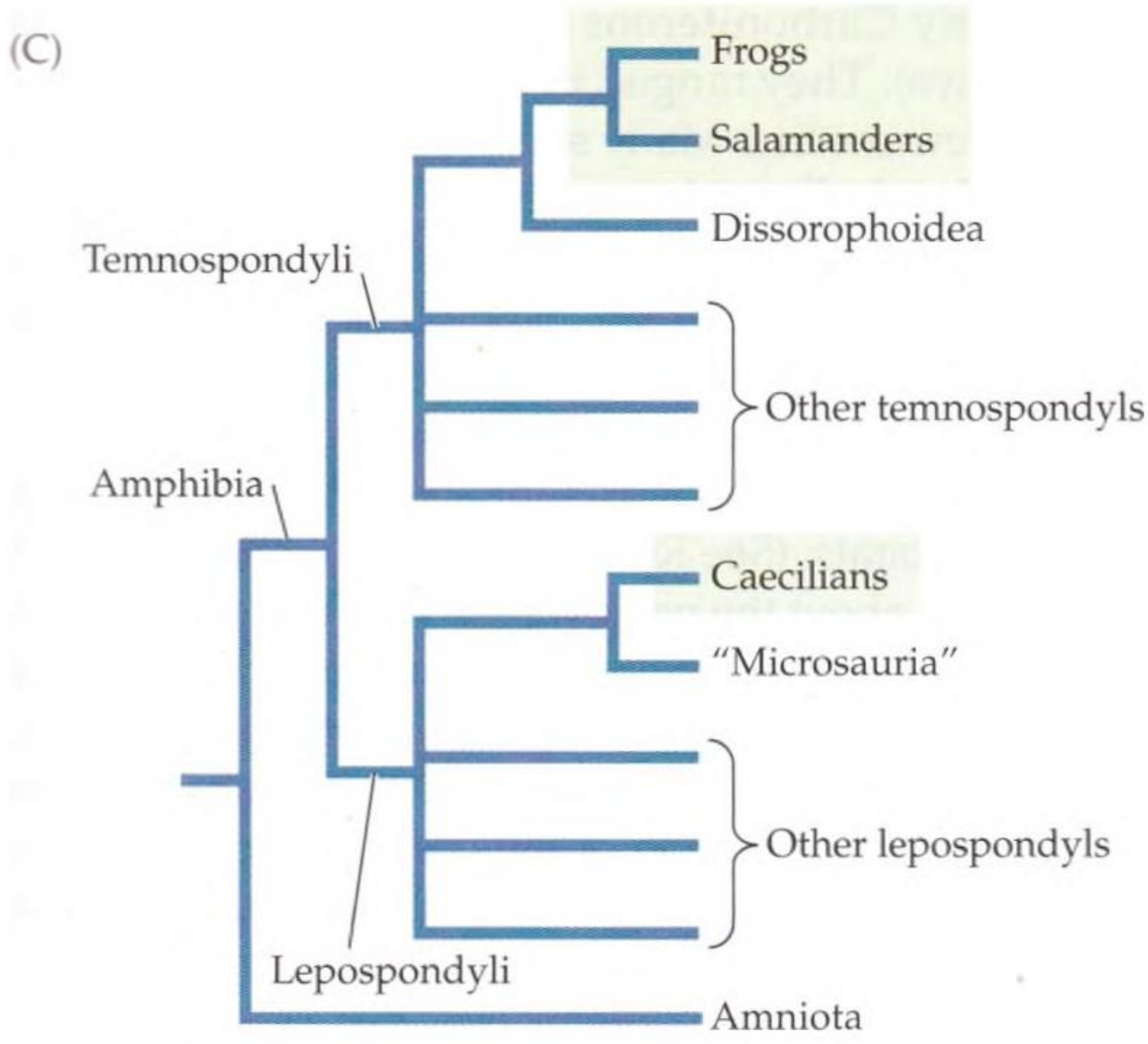


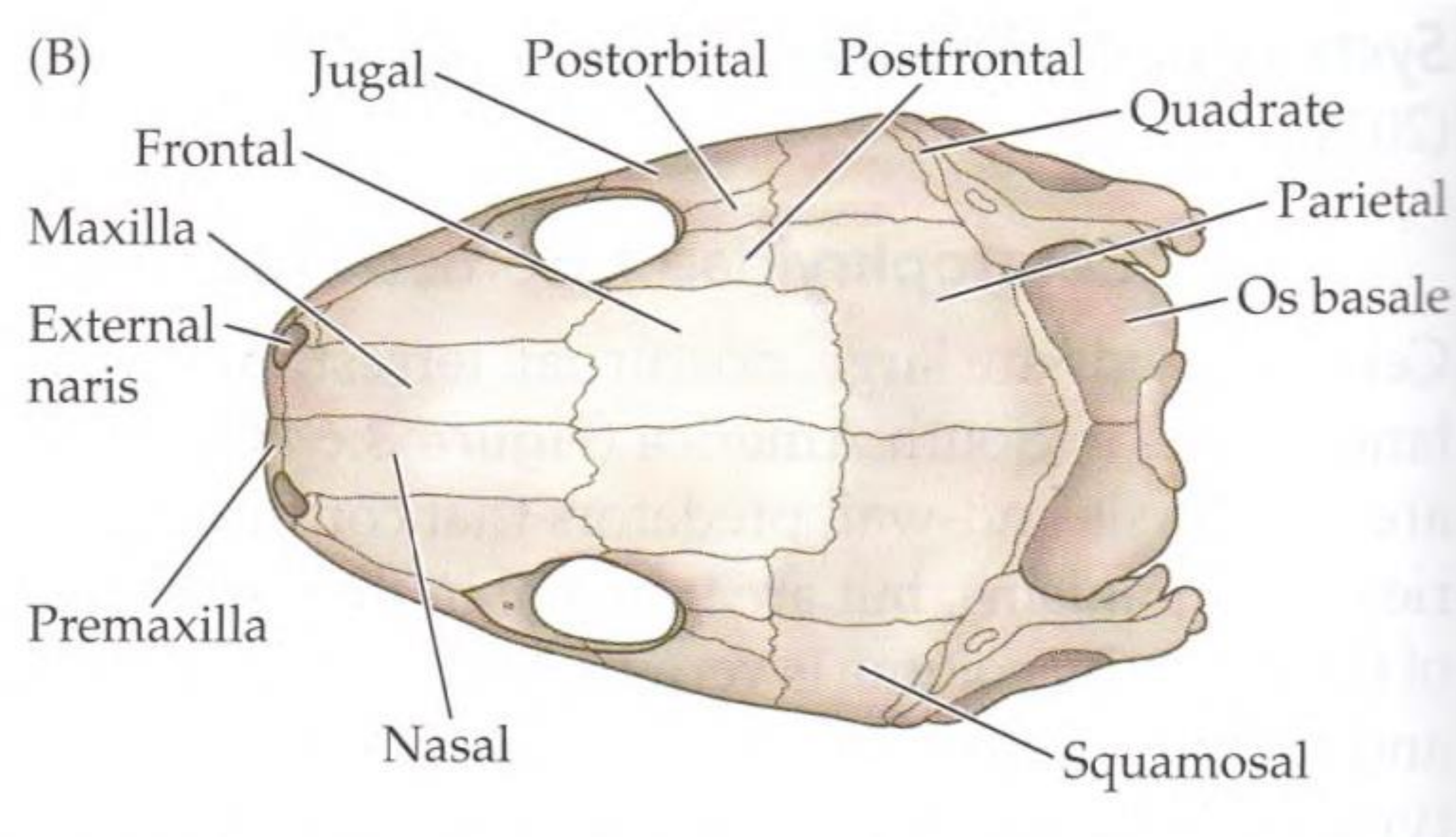
Figure Temnospondyls and lepospondyls of the Late Paleozoic. (A) Two representative temnospondyls. *Mastodonsaurus* was huge and superficially resembled a crocodylian. The much smaller *Cacops* was a more typical size temnospondyl. (B) Two lepospondyls. The unique head shape of *Diplocaulus* may have helped the animal glide through the water. The tiny *Microbrachis* may have appeared similar to some modern salamanders. The graph, keyed to the colored bars beneath the skeletons, shows the relative sizes of the animals compared with a very tall adult human. (After Bolt 1977; Schloch 1999.)

The diphyly hypothesis

- The diphyly (from the Greek di, "two") hypothesis of lissamphibian origin is a hybrid between the temnospondyl and lepospondyl hypotheses and proposes that Lissamphibia is not monophyletic.
- It proposes that frogs and salamanders are derived from dissorophoid temnospondyls and that caecilians are derived from lepospondyl "microsaurs,"
- An important fossil supporting the diphyly hypothesis is that of the caecilian Eocaecilia. Some studies have suggested that Eocaecilia, and therefore modern caecilians, are derived from lepospondyl ancestors
- However, a recent X-ray microtomography analysis of the skull of Eocaecilia has revealed additional characters that reject the diphyly hypothesis and instead support a monophyletic Lissamphibia derived from temnospondyls, a hypothesis also supportedby inner ear structure and other phylogenetic analyses. Thus, the diphyly hypothesis is not widely accepted.



(C) The diphyly hypothesis states that Lissamphibia is not monophyletic and that frogs and salamanders are derived from temnospondyls whereas caecilians are derived from lepospondyls.



The oldest known caecilian. *Eocaecilia micropodia,* from the Early Jurassic, retains ancestral characters such as limbs (A) and skull bones (B) that are not present in extant caecilians

Monophyly of Lissamphibia

- Lissamphibia (caecilians, frogs, and salamanders) is monophyletic and derived from temnospondyl ancestors.
- The earliest fossil that can clearly be assigned to an extant lissamphibian clade is Triadobatrachus from the Earlyrrriassic (-245 mya;
- Triadobatrachus was thus an early ancestor of frogs (although it is unclear whether Triadobatrachus had the ability to jump.

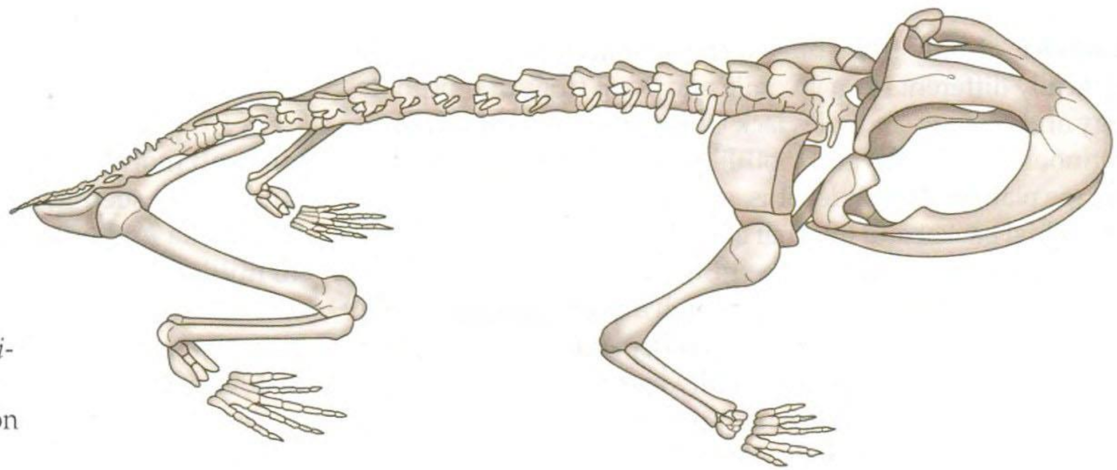


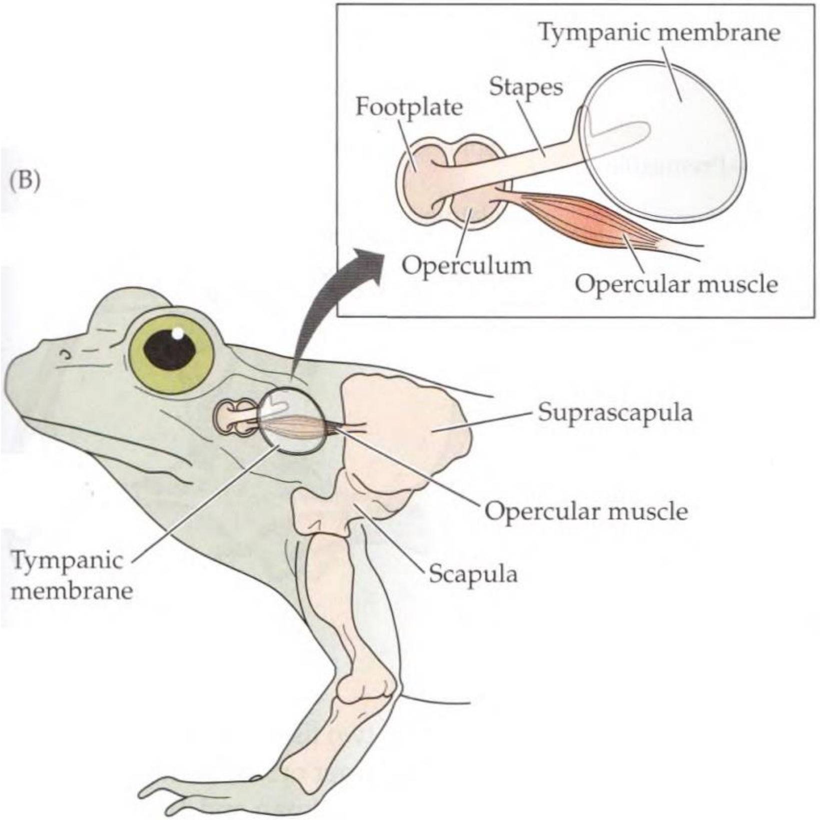
Figure A fossil salientian from the Early Triassic. Skeletal reconstruction of *Triadobatrachus massinoti*. The fossil record of the stem lineage of frogs goes back over 350 million years. (After Rage and Roček 1989.)

Monophyly of Lissamphibia

- Numerous morphological synapomorphies support lissamphibian monophyly. The following characters are some of the derived features that are shared by and in many cases are unique to, extant amphibians:
- 1. The teeth are pedicellate and bicuspid. Each tooth crown sits on a base (pedicel), from which the crown is separated by a fibrous connection. Moreover, the teeth have two cusps, one on the lingual (inner) side of the jaw and one on the labial (outer) side. Such a tooth structure is unique to Lissamphibia and some temnospondyls (see Figure(.
- 2. The sound-conducting apparatus of the middle ear consists of two elements: the stapes (columella), which is the usual element in tetrapods, and the operculum. The operculum (not homologous to the operculum in fish) consists of a bony or cartilaginous structure that attaches to the ear capsule and is connected to the suprascapula via the opercular muscle (see Figure).
- 3. Functionally; this allows ground vibrations to be transmitted from the forelimb to the inner ear.Inside the inner ear are two sensory epithelial patches (not shown), the papilla basilaris, found in other tetrapods, and the papilla amphibiorum, unique to lissamphibians.

Monophyly of Lissamphibia

- 4. The papilla basilaris receives relatively high-frequency sound input via the stapes. The papilla amphibiorum receives relatively low-frequency input via the opercular apparatus. The opercular apparatus is lost in caecilians, perhaps as a result of limb loss, and is reduced in salamanders by the loss of one or more components in various groups.



Monophyly of Lissamphibia

- 5. The stapes is directed dorsolaterally from the fenestra ovalis, a character shared by some of the lissamphibians' presumed Paleozoic relatives.
- 6. The fat bodies develop from the germinal ridge (which also gives rise to the gonads), a developmental origin unique among tetrapods.
- 7. The skin contains both mucus and poison (granular) glands that are broadly similar in structure.
- 8. Specialized receptor cells in the retina of the eye, called green rods, are present in frogs and salamanders. Caecilians apparently lack green rods, perhaps because of their highly reduced eyes.
- 9. A sheet of muscle, the levator bulbi muscle, lies under the eye and permits lissamphib 诅ns to elevate the eye.
- 10. All extant amphibians employ cutaneous and buccopharyngeal respiration.
- 11. The ribs are short, straight, and do not encircle the body. The ribs of Paleozoic stem tetrapods (other than some temnospondyls) are long, robust, and encircle the viscera.

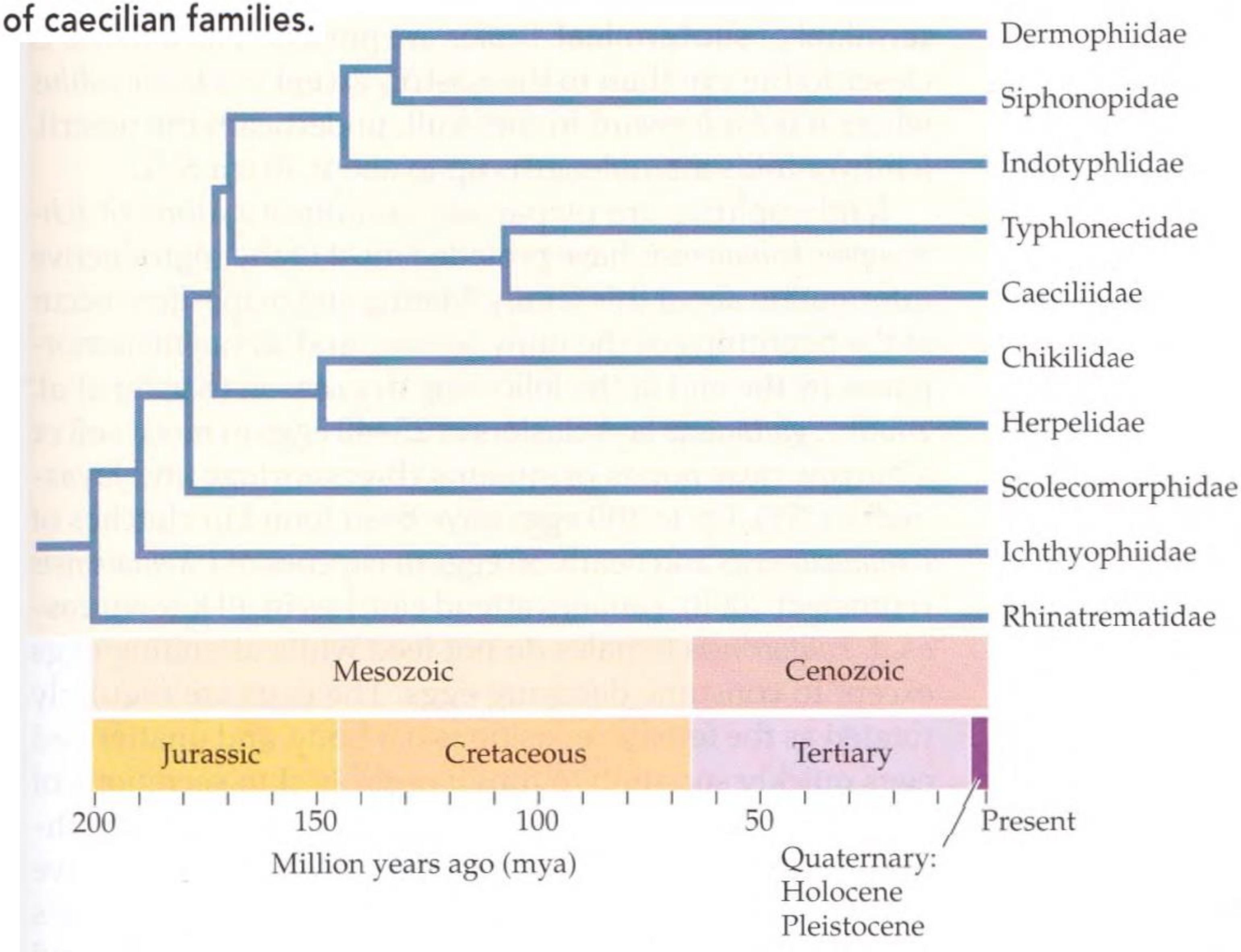
Monophyly of Lissamphibia

- 12. Two occipital condyles at the base of the skull articulate with two cotyles on the first cervical vertebra (the atlas). Most other extant tetrapods have a single occipital condyle, but two condyles are found in some temnospondyls.
- 13. The radius and ulna articulate with a single structure on the humerus called a radial condyle. This character has been lost in caecilians, which are limbless.
- 14. Lissamphibians share similar reductions in skull bones and fenestration patterns compared with Paleozoic tetrapods. These shared derived characters include loss of the supratemporals, intertemporals, tabular, postparietals, jugals, and postorbitals.
- 15. Other elements, such as the pterygoid and parasphenoid bones in the palate, are reduced, producing a similar configuration of bones among the three modern amphibian groups.
- 16. Nonetheless, the skull morphology of caecilians is highly unusual compared with that of frogs and salamanders, reflecting the caecilians' very different life history.

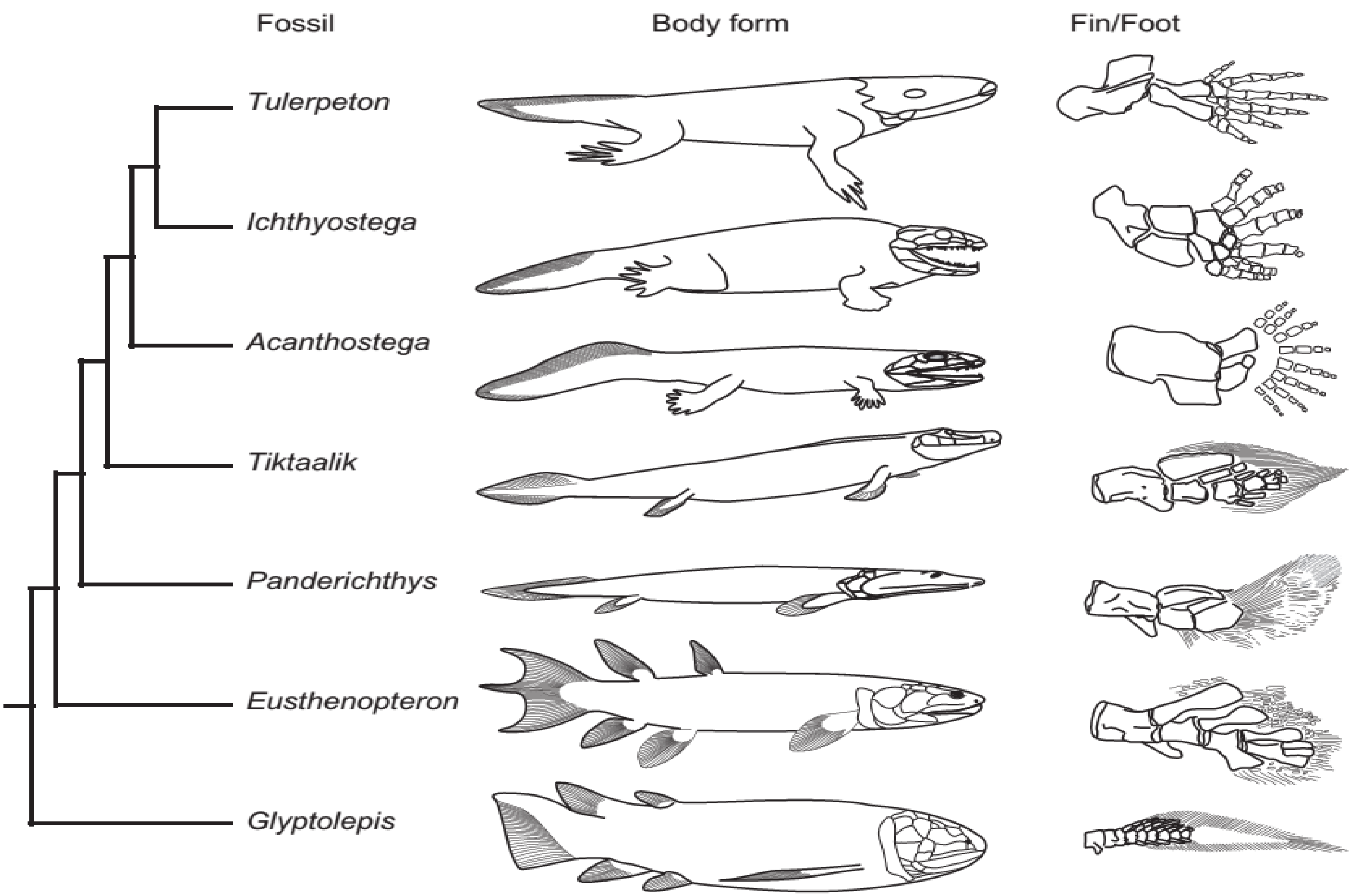
Monophyly of Lissamphibia

- Some of these characters (e.g., characters 6 - 10) are difficult or impossible to evaluate in extinct taxa because soft anatomy is rarely preserved in fossils.
- Moreover, not all of these characters are unique to Lissamphibia. Nonetheless, the preponderance of morphological evidence supports lissamphibian monophyly.
- Although molecular studies cannot sample extinct taxa, no recent molecular phylogenetic analyses reject lissamphibian monophyly.
- In summary, the most comprehensive molecular and morphological analyses support the hypothesis that salamanders and frogs are more closely related to one another than to caecilians.

Phylogeny of caecilian families.



Key fossils linking fishes & land vertebrates



Example of Temnospondyli

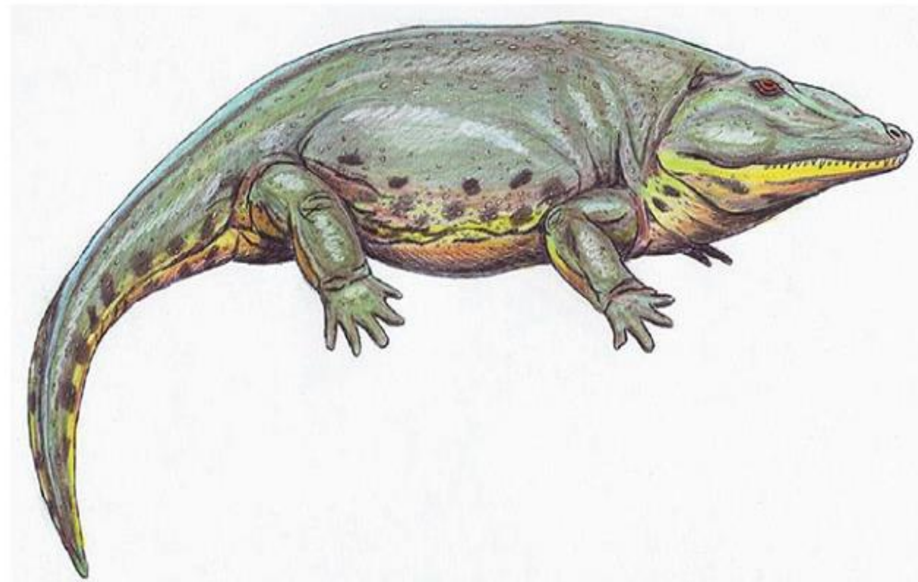
Figure 9.6 The skull of *Mastodonsaurus*. A huge temnospondyl. Image by Ghedoghedo, and placed into Wikimedia.

Example of Temnospondyli

[redacted] *Gerobatrachus*, the so-called frogamander, from the Permian of Texas. It is a possible temnospondyl ancestor of living amphibians. Image by Nobu Tamura, and placed into Wikimedia.

Example of Temnospondyli

[redacted] *Eryops* from the Early Permian of Texas is a poster child for large powerful temnospondyls. It is about 2 meters (6 feet) long, and massively built. Photograph © Joshua Sherurcij, and placed into Wikimedia.



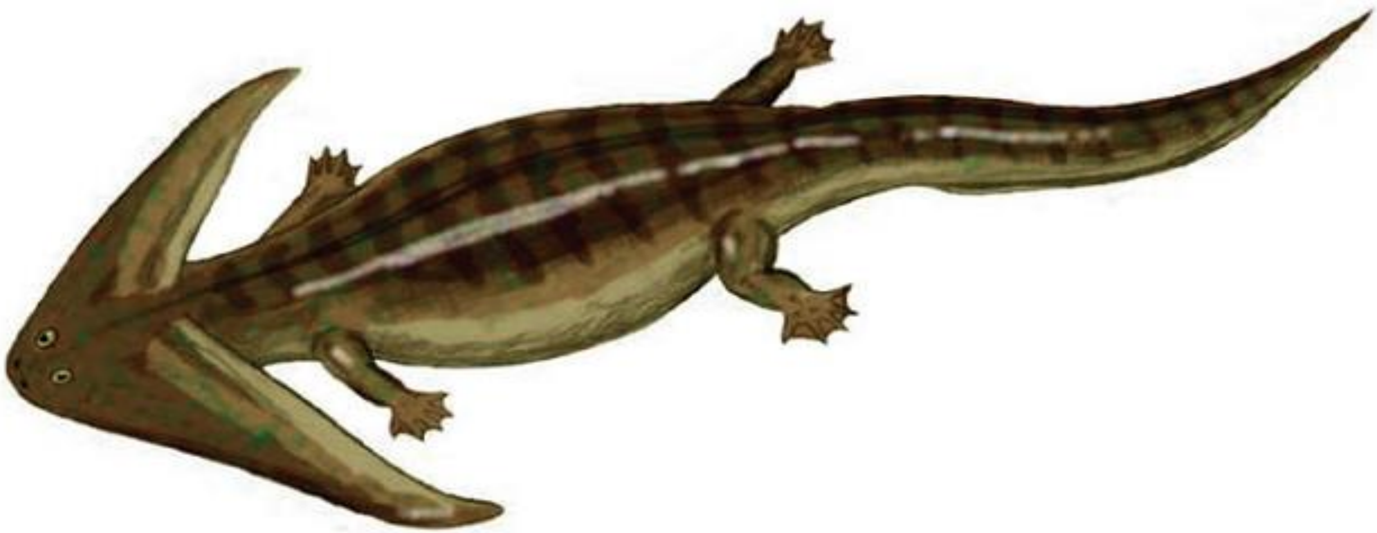
[redacted] *Eryops*, a Permian temnospondyl about 2 m (6 feet) long. This one looks contented and well fed! See Figure 9.3 for the reality of its skeleton. Image by Dmitry Bogdanov, and placed into Wikimedia.

Example of Microsaurs (Lepospondyli)

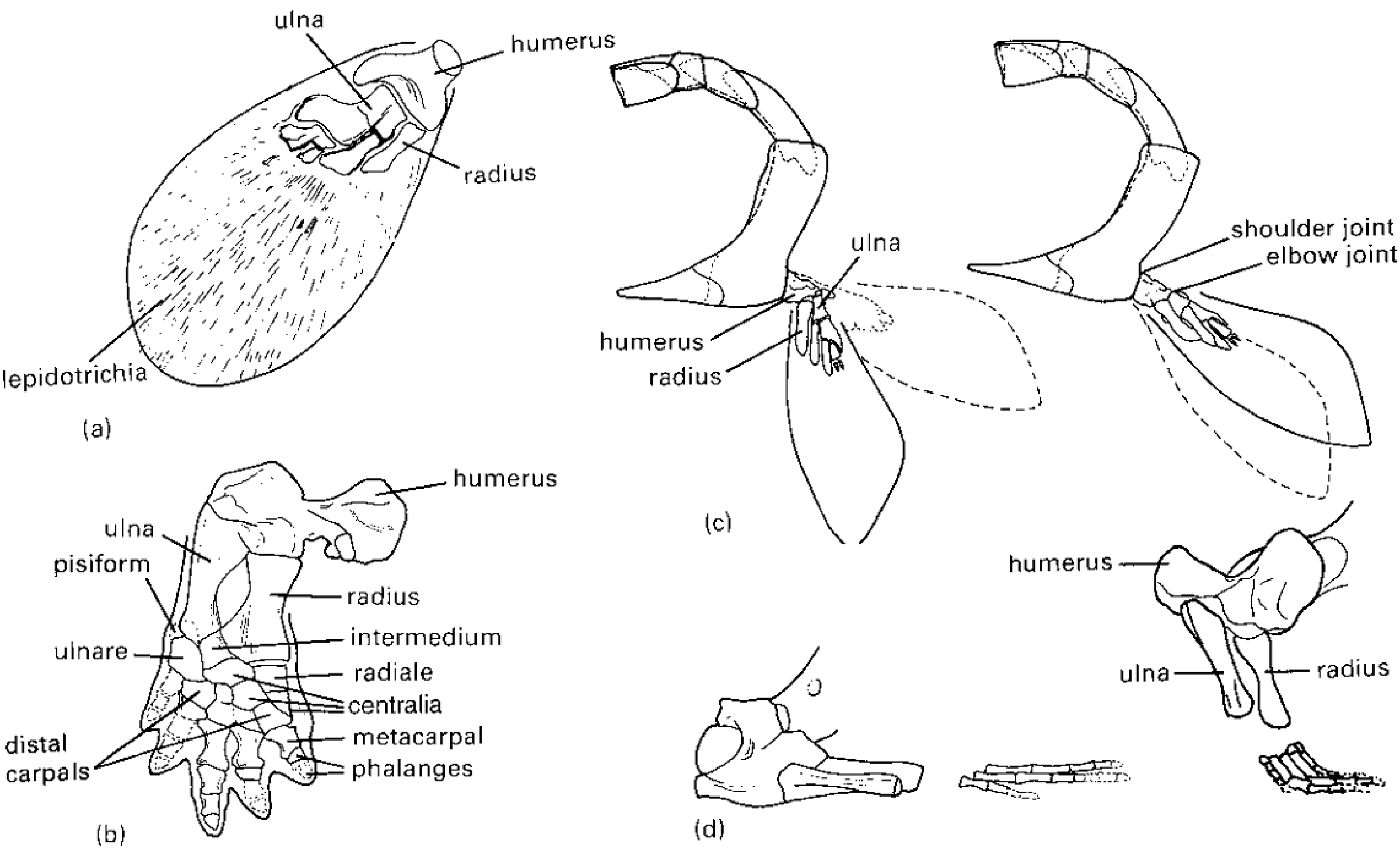
[redacted] *Microbrachis* is a microsaur, about 15 cm (about 6 inches) long, from the Late Carboniferous of the Czech Republic. It still had gills as an adult. Image by Nobu Tamura, and placed into Wikimedia.

Seymouria- Example of Seymourimorpha)

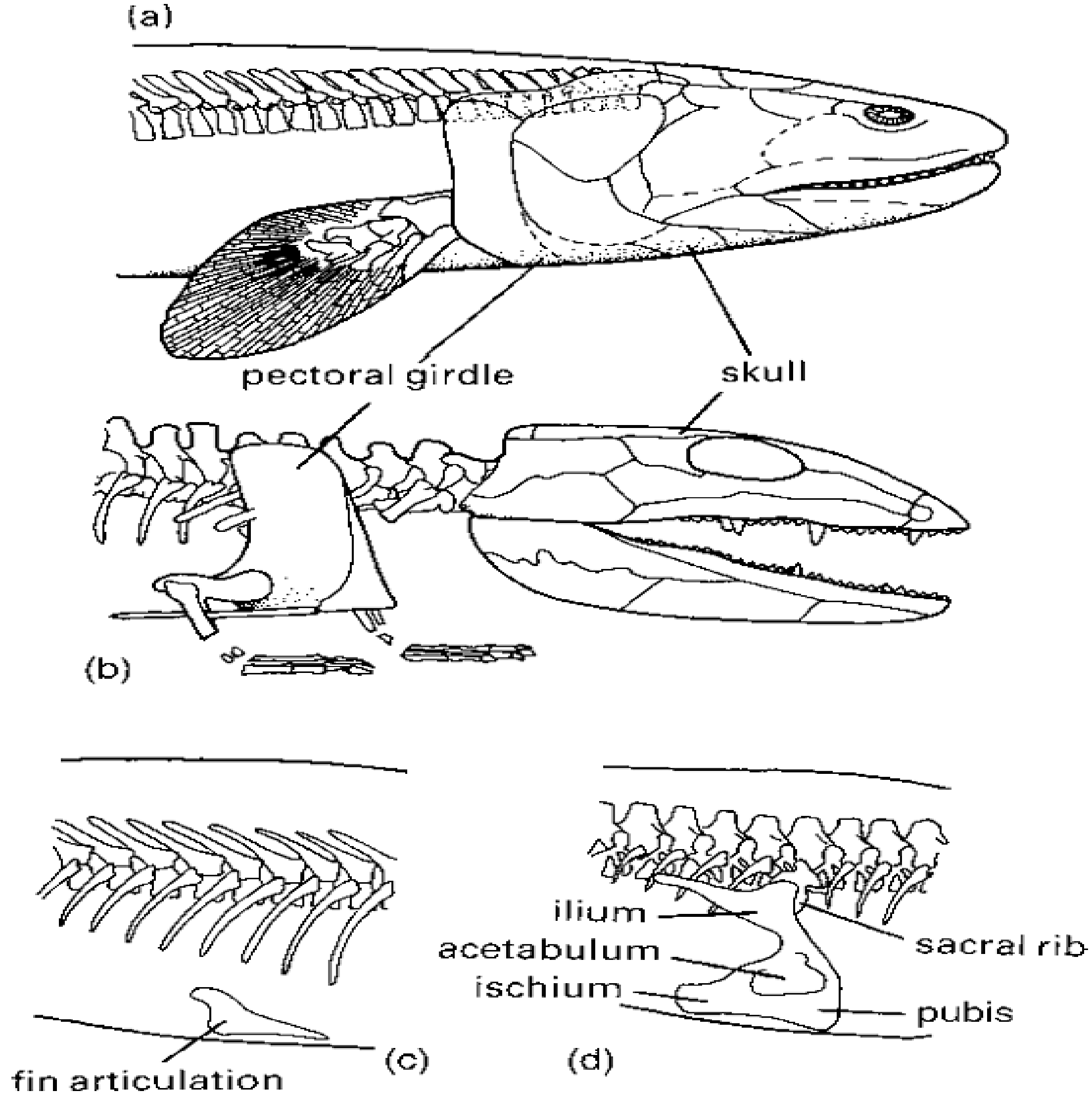
Example of nectridean



[redacted] *Diplocaulus* is a horned nectridean, about a meter long (3 feet) from the Permian of Texas. It is difficult to imagine any other function for the horns than hydrodynamic control during swimming. Image by Nobu Tamura, and placed into Wikimedia.

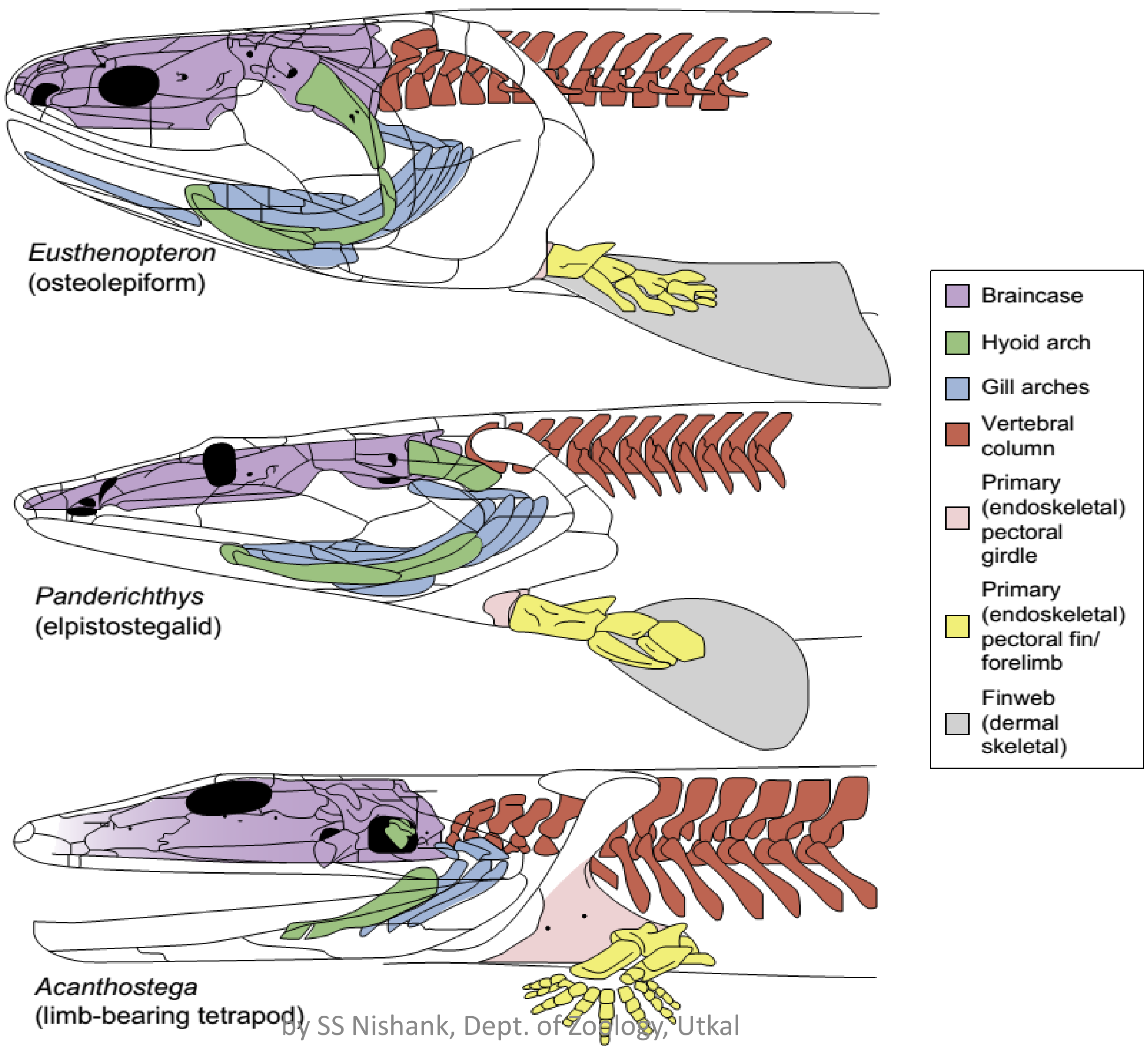


[redacted] The origin of tetrapod limbs and land locomotion: (a) pectoral fin of the tristichopterid fish *Eusthenopteron* showing interpreted identities of the bones; (b) equivalent forelimb of the basal tetrapod *Eryops*; (c) possible movements of the forelimb of *Eusthenopteron*; (d) step cycle of the forelimb of the basal tetrapod *Proterogyrinus*. [Figures (a, b) after various sources; (c) after Andrews and Westoll, 1970a; (d) after Holmes, 1984.]

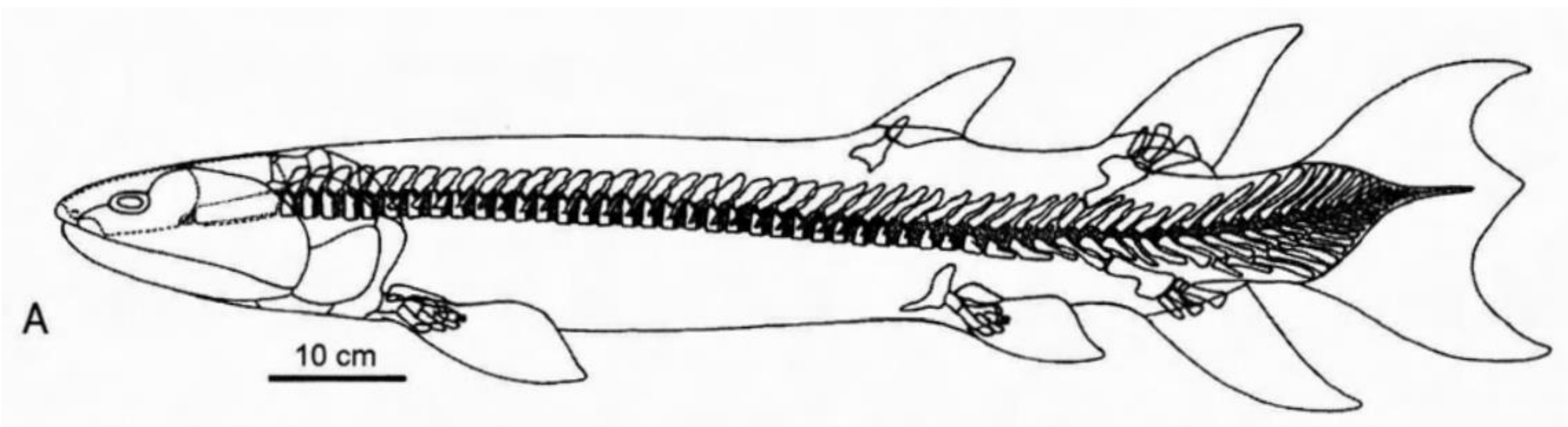


[redacted] The transition from tristichopterid fish (a, c) to basal tetrapod (b, d): (a) and (b) the separation of the skull from the shoulder girdle; (c) and (d) the enlargement of the pelvic girdle and its firm attachment to the vertebral column via the ilium and sacral rib. [Figures (a, c, d), after Stahl, 1974; (b) after Godfrey, 1989.]

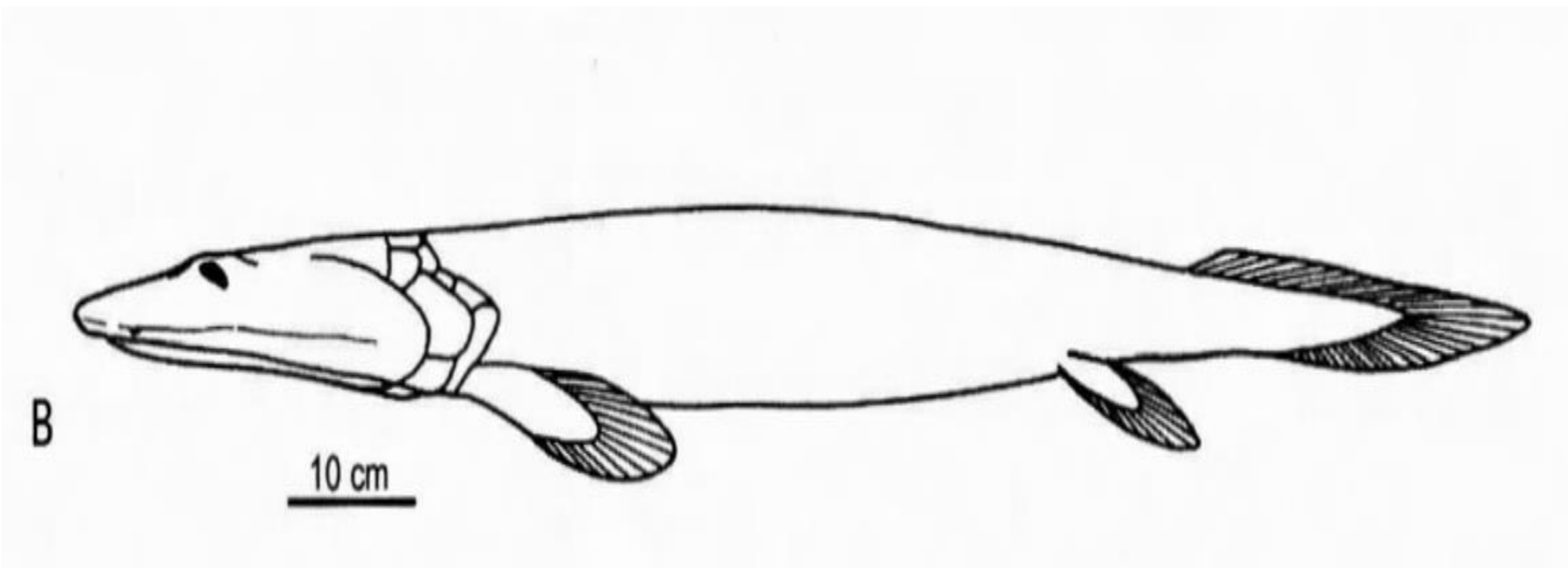
detachment of pectoral girdle from skull & replacement of fin rays by limbs



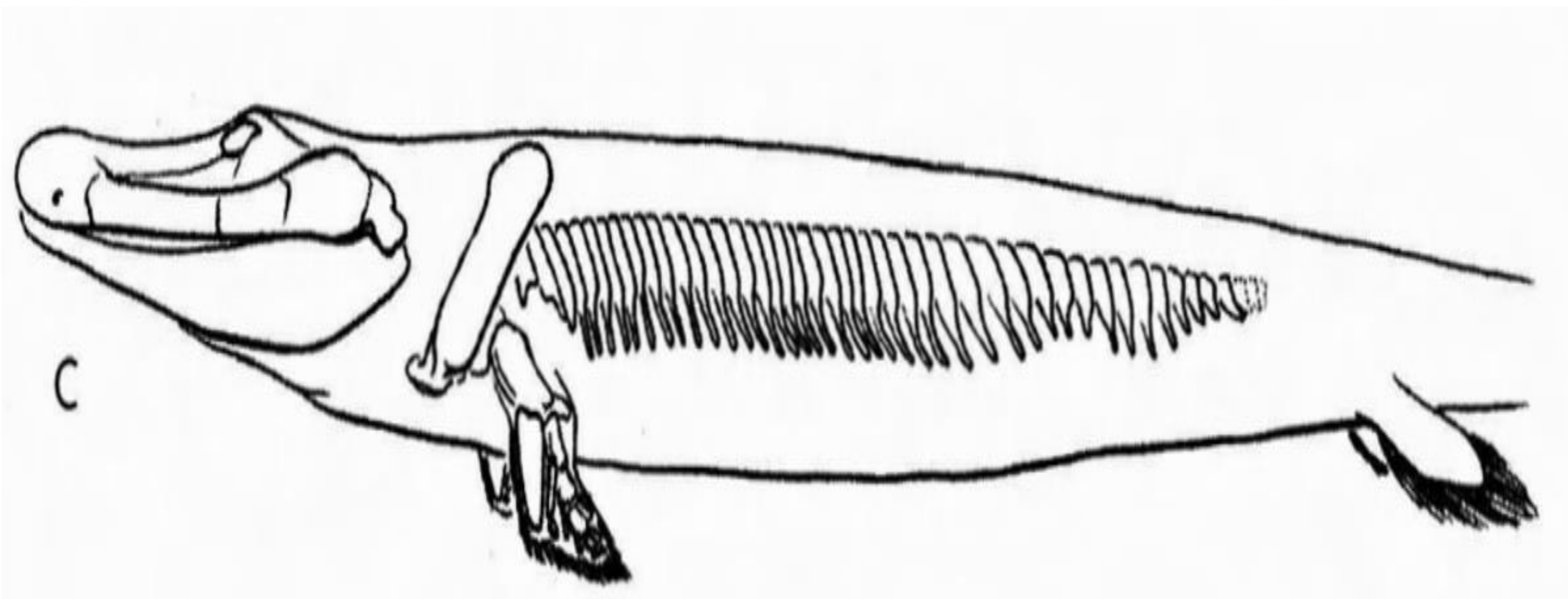
sequence of skeleton changes from obligatory aquatic fish *Eusthenopteron* to



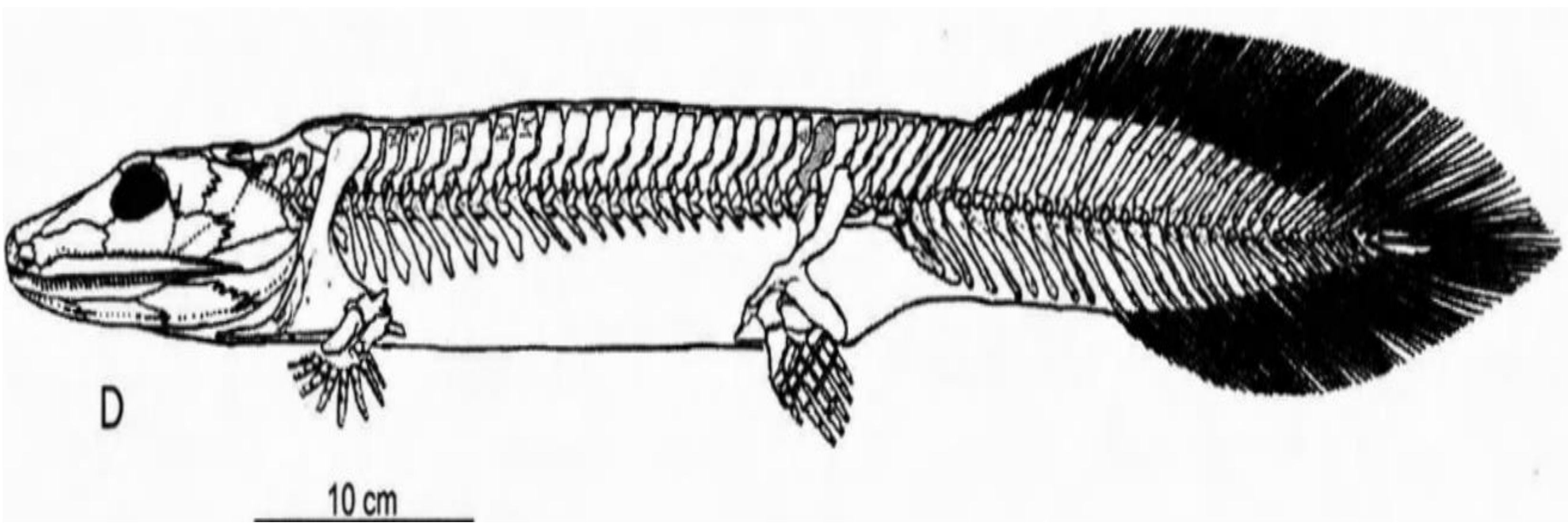
aquatic *Panderichthys* to



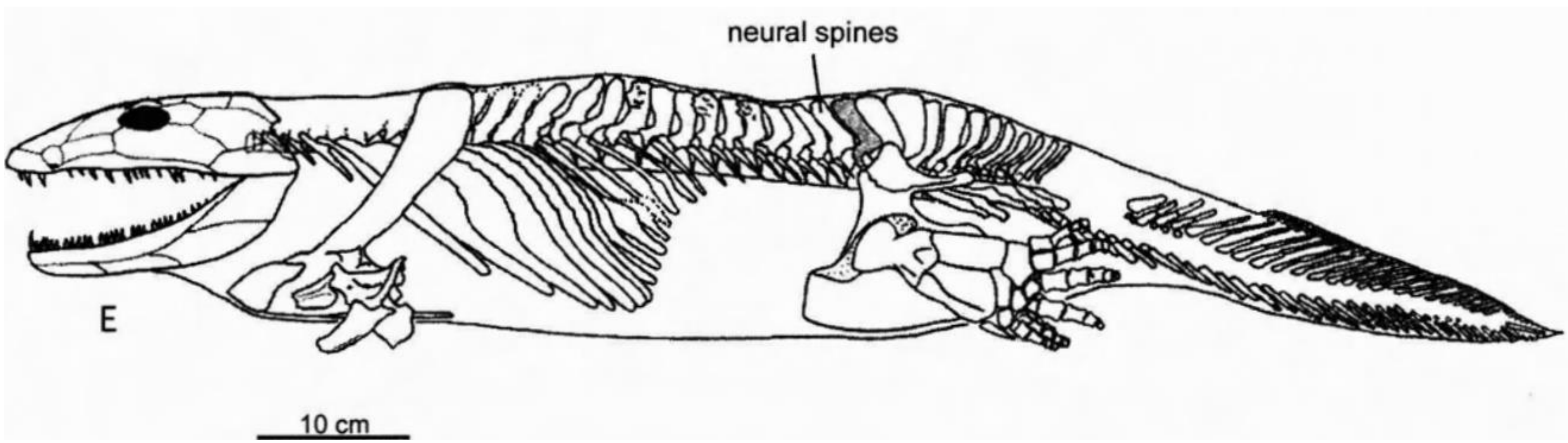
semi aquatic *Tiktaalik* to

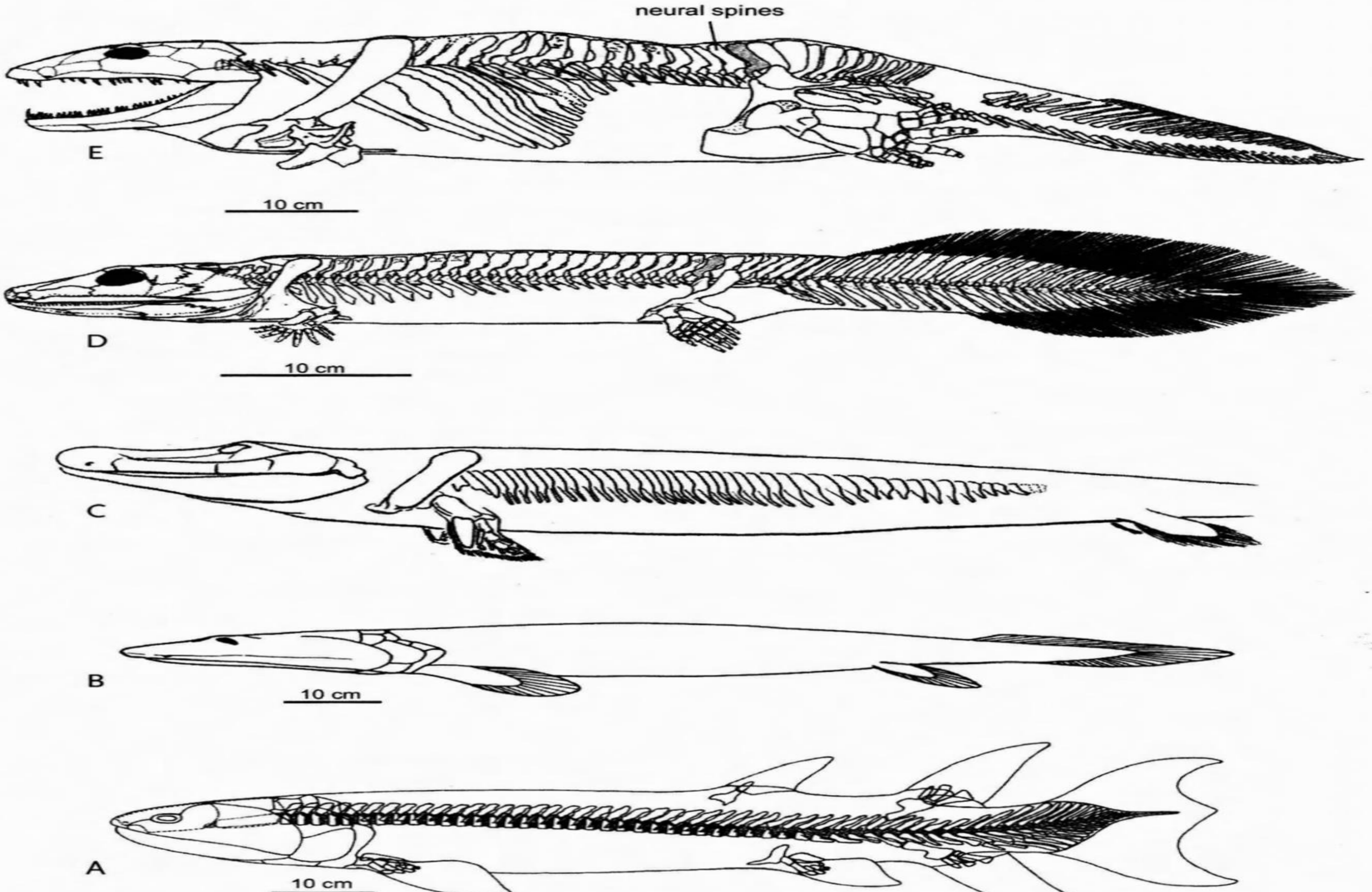


semi aquatic *Acathostega* to



semiaquatic *Ichthyostega*





[redacted]. Sequence of changes in the skeleton leading from the obligatorily aquatic fish *Eusthenopteron* (A) to the facultatively terrestrial amphibians *Acanthostega* (D) and *Ichthyostega* (E). Note that the tails of *Acanthostega* and *Ichthyostega* would be effective in aquatic locomotion. *B*, *Panderichthys*, a choanate fish, in which the loss of the medial dorsal and anal fins would permit locomotion in very shallow water. The very low profile of the skull and the dorsal position of the orbits suggest swimming at the interface of water and air. *C*, Preliminary sketch of *Tiktaalik*, a Late Devonian choanate fish recently discovered in the Canadian Arctic. *A*, modified from Andrews and Westoll, 1970; *B*, from Vorobyeva and Schultze, 1991; *C*, modified from Daeschler et al., 2006; *D* and *E* from Ahlberg et al., 2005.