Overview: Half a Billion Years of Backbones

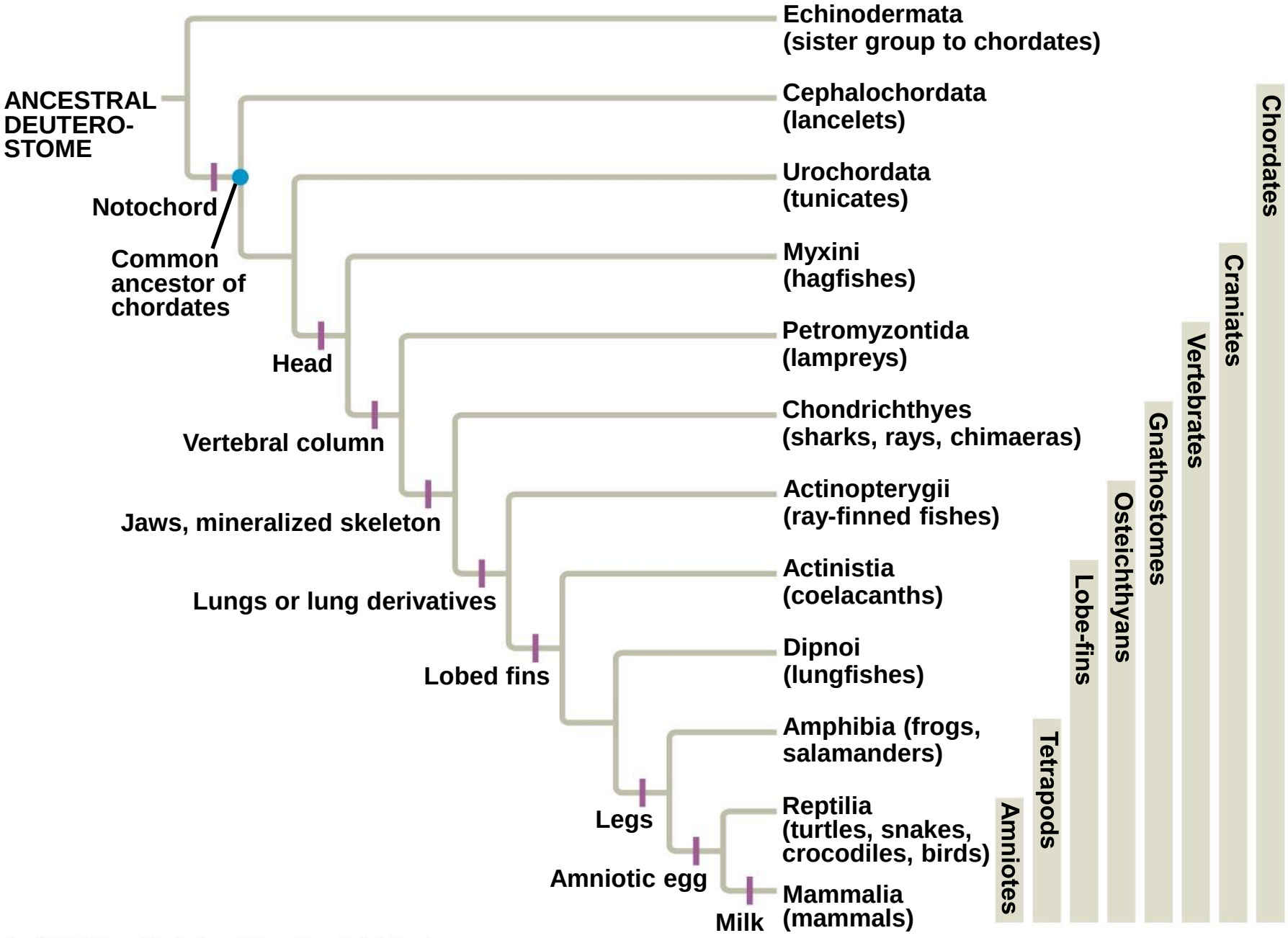
- Early in the Cambrian period, about 530 million years ago, an astonishing variety of animals inhabited Earth's oceans
- One type of animal gave rise to vertebrates, one of the most successful groups of animals

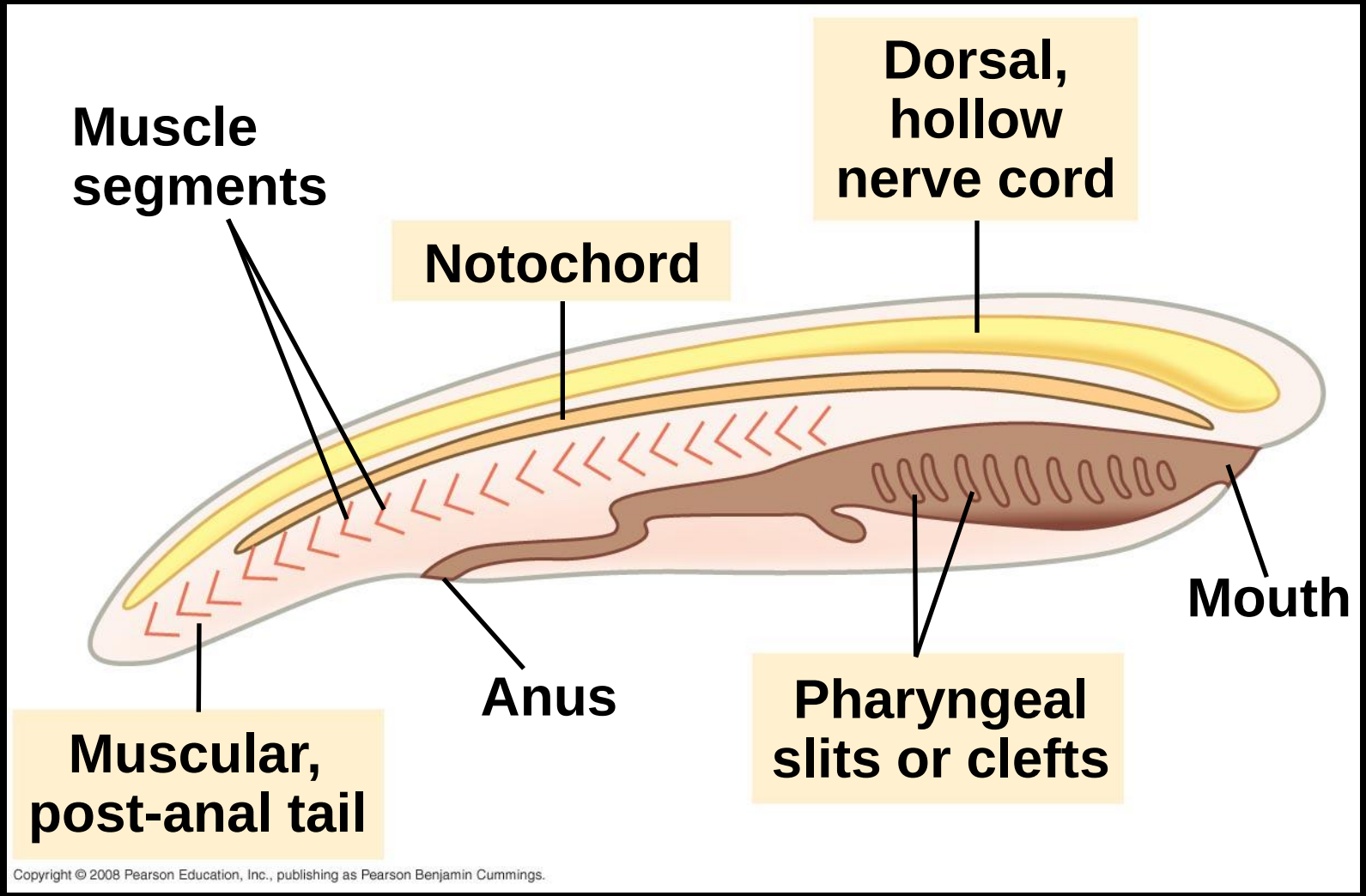
- The animals called **vertebrates** get their name from vertebrae, the series of bones that make up the backbone
- There are about 52,000 species of vertebrates, including the largest organisms ever to live on the Earth
- Vertebrates have great *disparity*, a wide range of differences within the group

Concept 34.1: Chordates have a notochord and a dorsal, hollow nerve cord

- Vertebrates are a subphylum within the phylum Chordata
- **Chordates** are bilaterian animals that belong to the clade of animals known as Deuterostomia
- Two groups of invertebrate deuterostomes, the urochordates and cephalochordates, are more closely related to vertebrates than to other invertebrates

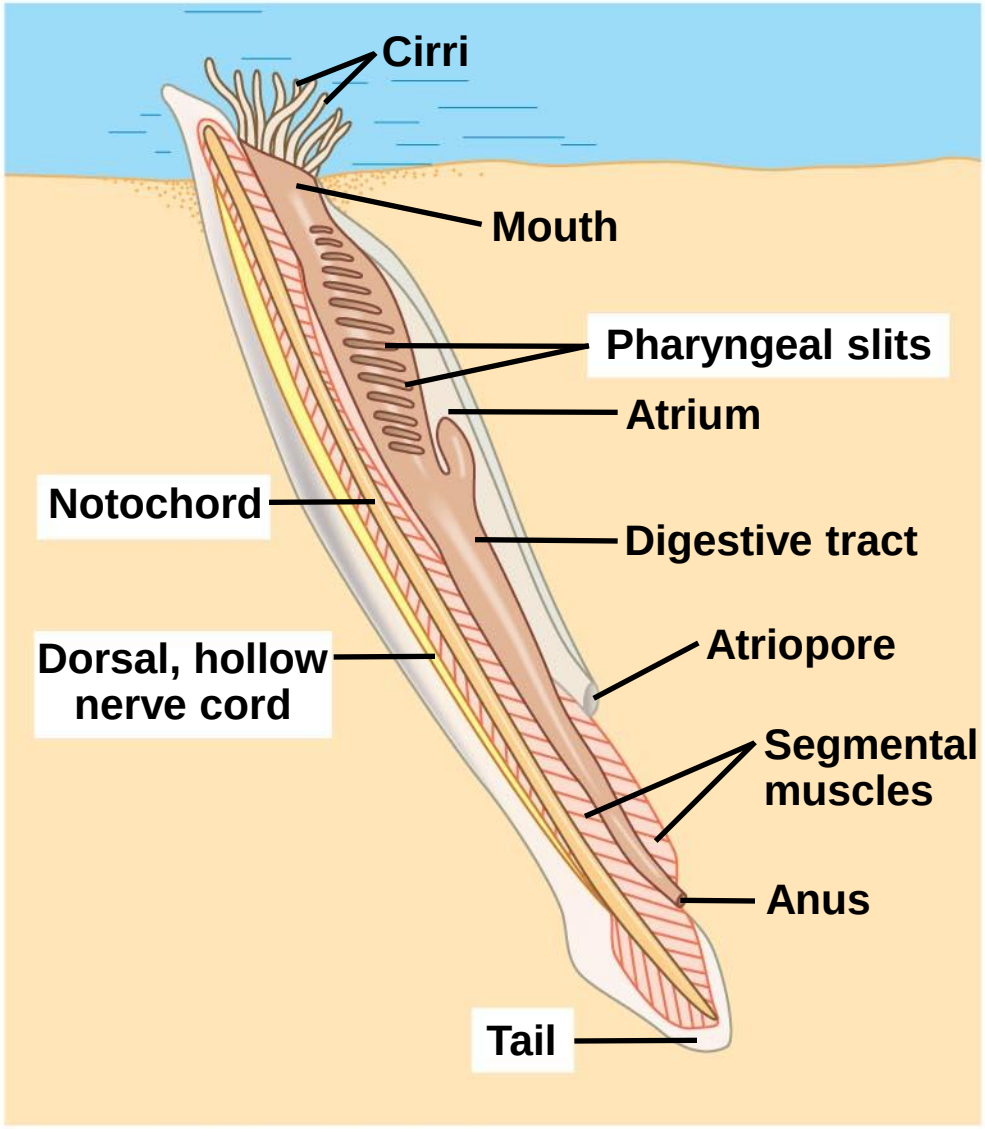
Fig. 34-2

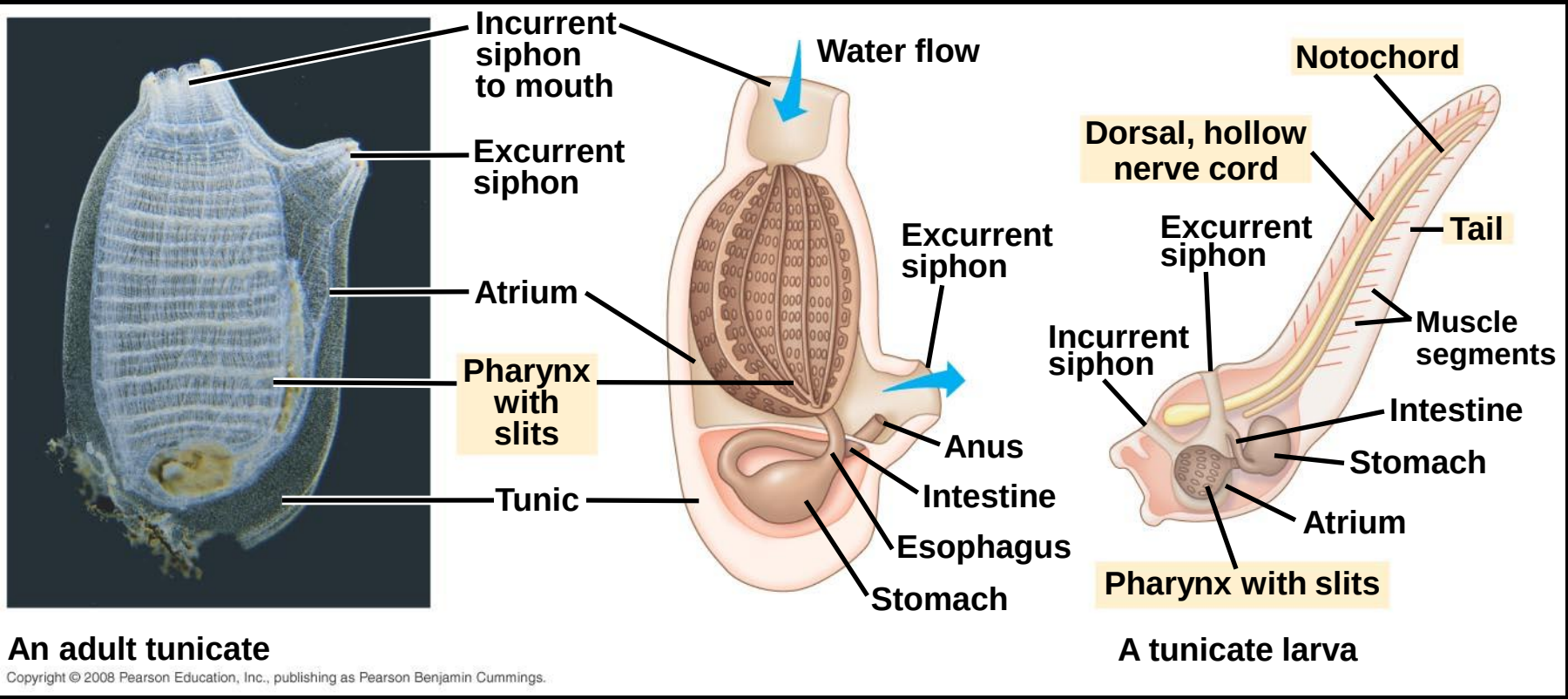




Notochord

- The **notochord** is a longitudinal, flexible rod between the digestive tube and nerve cord
- It provides skeletal support throughout most of the length of a chordate
- In most vertebrates, a more complex, jointed skeleton develops, and the adult retains only remnants of the embryonic notochord

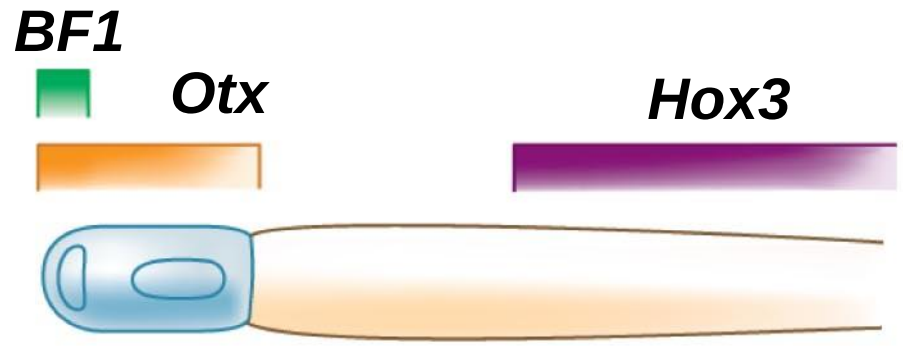




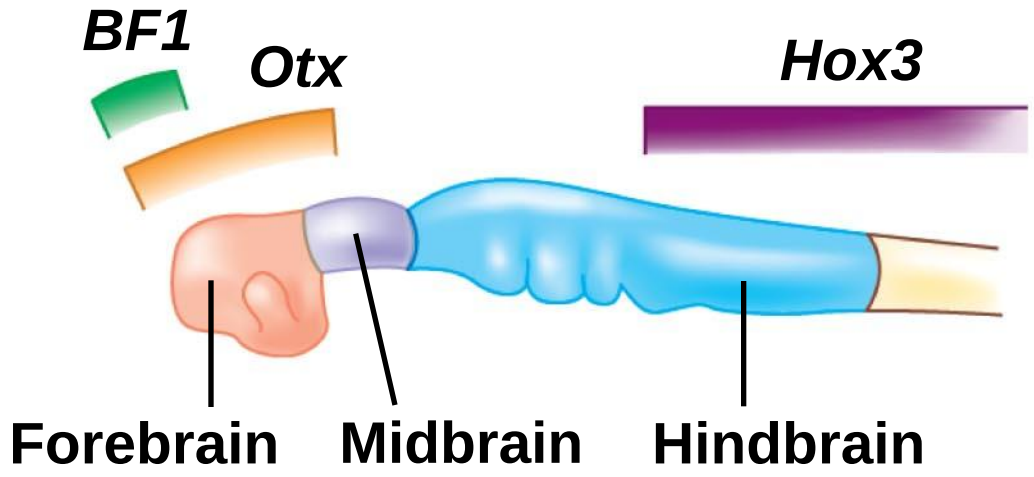
Early Chordate Evolution

- Ancestral chordates may have resembled lancelets
- Genome sequencing of tunicates has identified genes shared by tunicates and vertebrates
- Gene expression in lancelets holds clues to the evolution of the vertebrate form

Nerve cord of lancelet embryo



Brain of vertebrate embryo (shown straightened)

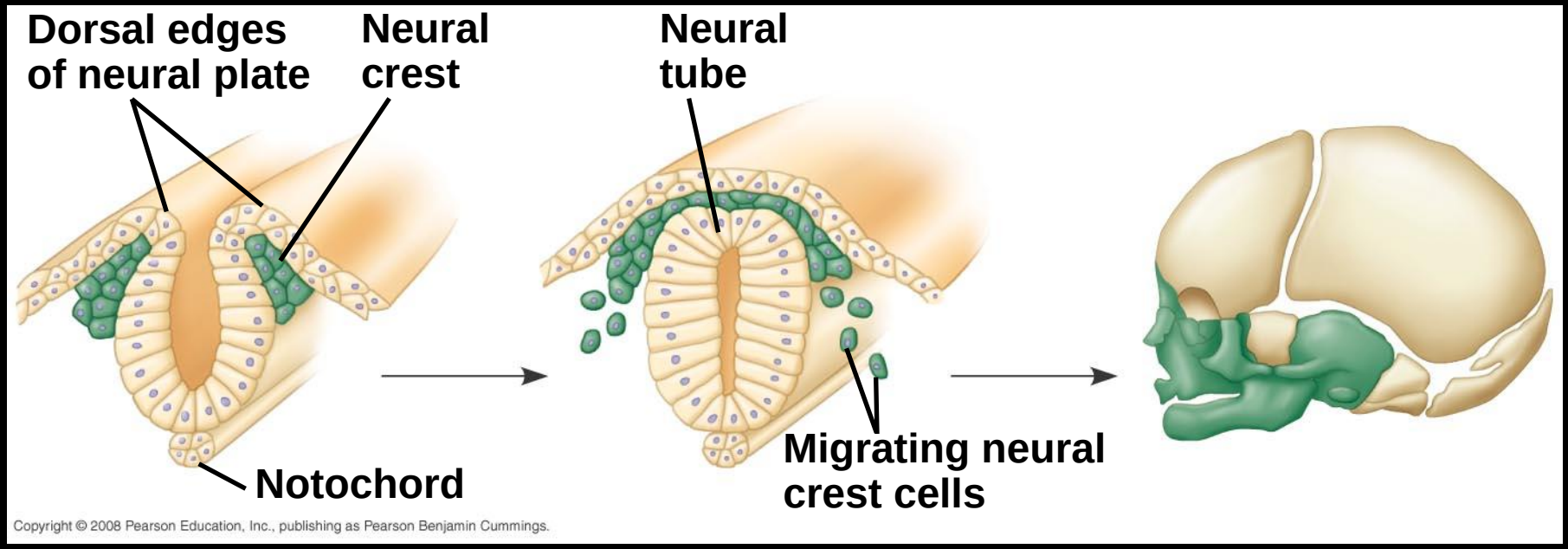


Concept 34.2: Craniates are chordates that have a head

- The origin of a head opened up a completely new way of feeding for chordates: active predation
- **Craniates** share some characteristics: a skull, brain, eyes, and other sensory organs

Derived Characters of Craniates

- Craniates have two clusters of *Hox* genes; lancelets and tunicates have only one cluster
- One feature unique to craniates is the **neural crest**, a collection of cells near the dorsal margins of the closing neural tube in an embryo
- Neural crest cells give rise to a variety of structures, including some of the bones and cartilage of the skull



- In aquatic craniates the pharyngeal clefts evolved into gill slits
- Craniates have a higher metabolism and are more muscular than tunicates and lancelets
- Craniates have a heart with at least two chambers, red blood cells with hemoglobin, and kidneys

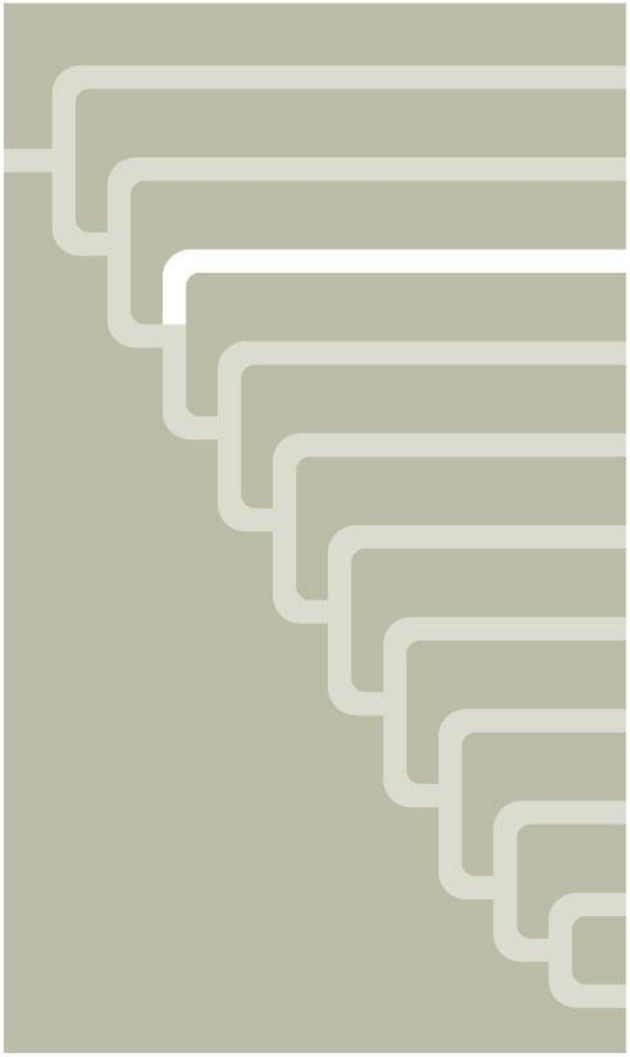
The Origin of Craniates

- Fossils from the Cambrian explosion 530 million years ago document the transition to craniates
- The most primitive of the fossils are those of the 3-cm-long *Haikouella*
- *Haikouella* had a well-formed brain, eyes, and muscular segments, but not a skull

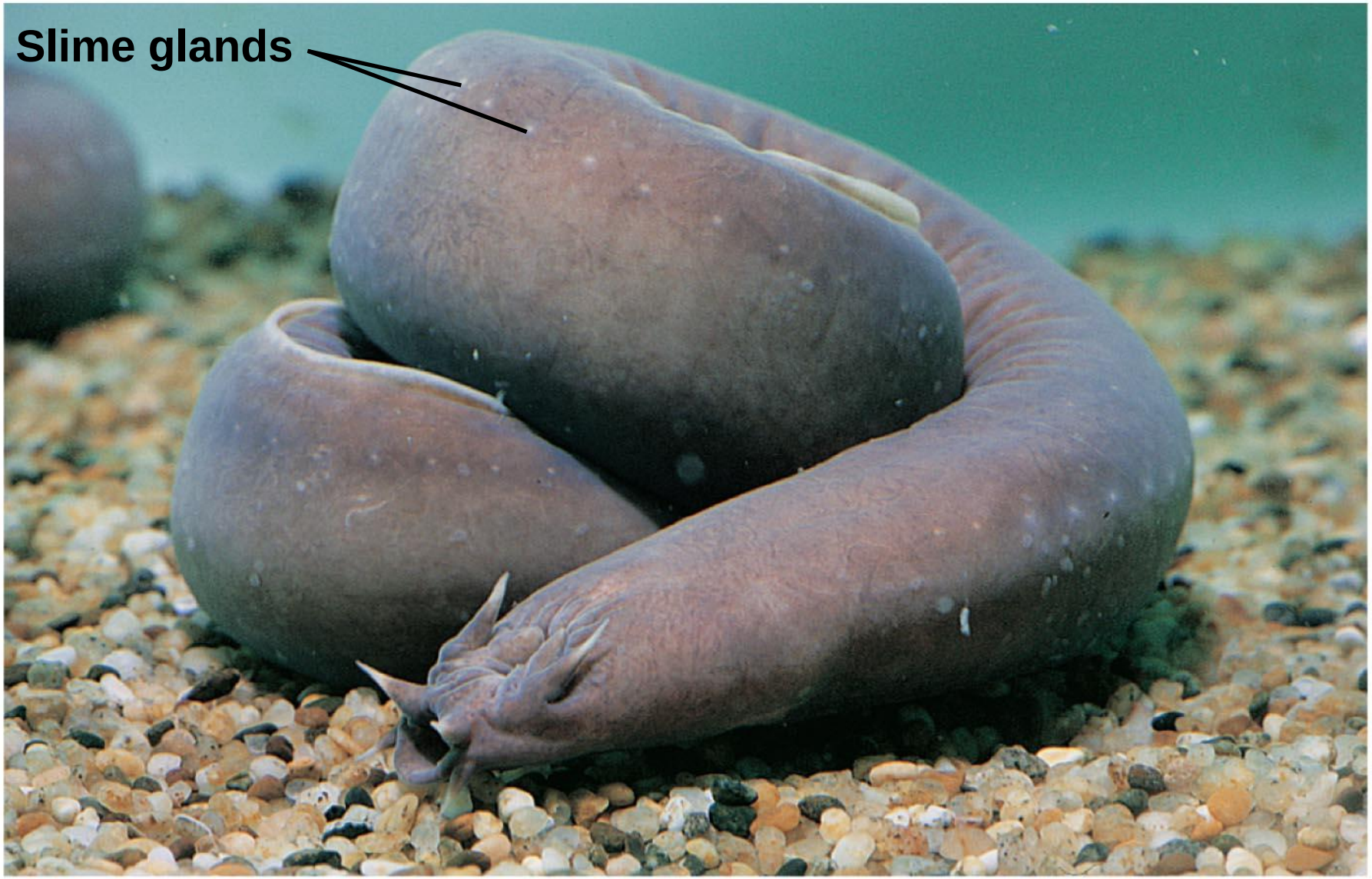
- In other Cambrian rocks, paleontologists have found fossils of even more advanced chordates, such as *Myllokunmingia*
- *Myllokunmingia* had a skull and was a true craniate

Hagfishes

- The least derived surviving craniate lineage is Myxini, the hagfishes
- Hagfishes have a cartilaginous skull and axial rod of cartilage derived from the notochord, but lack jaws and vertebrae



Cephalochordata
Urochordata
Myxini
Petromyzontida
Chondrichthyes
Actinopterygii
Actinistia
Dipnoi
Amphibia
Reptilia
Mammalia



Concept 34.3: Vertebrates are craniates that have a backbone

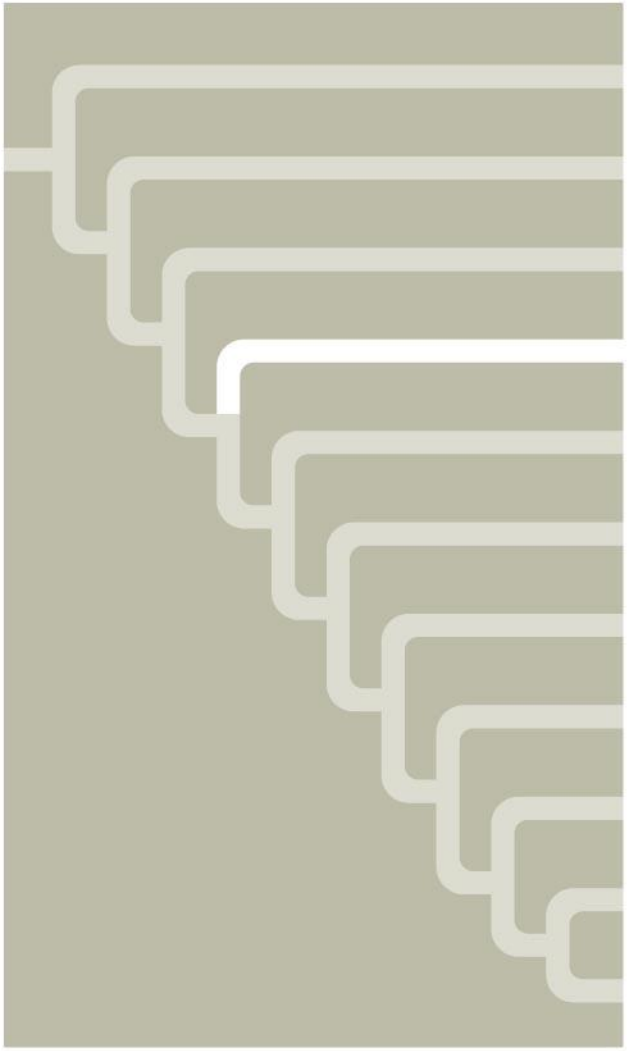
- During the Cambrian period, a lineage of craniates evolved into vertebrates
- Vertebrates became more efficient at capturing food and avoiding being eaten

Derived Characters of Vertebrates

- Vertebrates underwent a second gene duplication involving the *Dlx* family of transcription factors
- Vertebrates have the following derived characters:
  - Vertebrae enclosing a spinal cord
  - An elaborate skull
  - Fin rays, in the aquatic forms

Lampreys

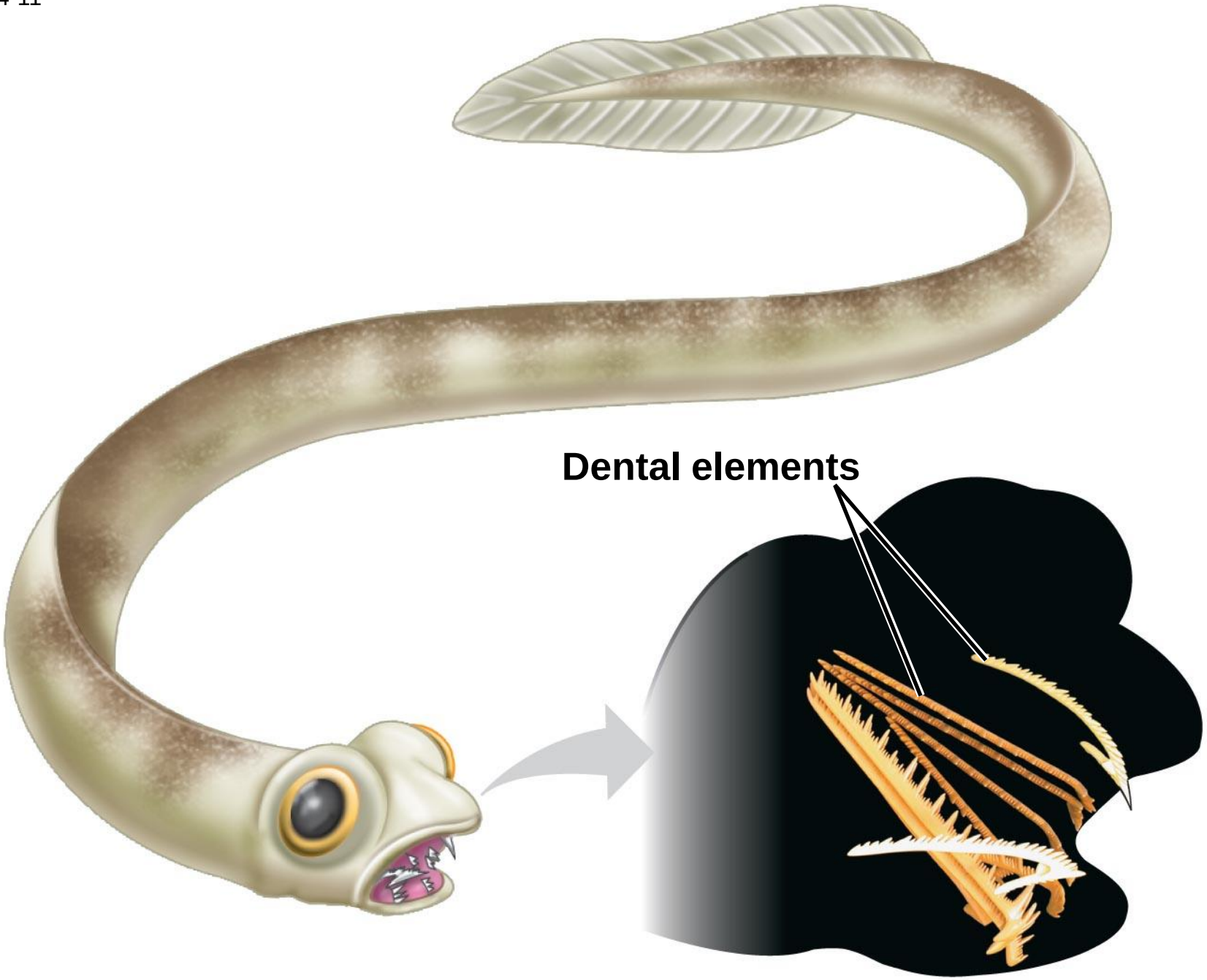
- Lampreys (Petromyzontida) represent the oldest living lineage of vertebrates
- They are jawless vertebrates inhabiting various marine and freshwater habitats
- They have cartilaginous segments surrounding the notochord and arching partly over the nerve cord



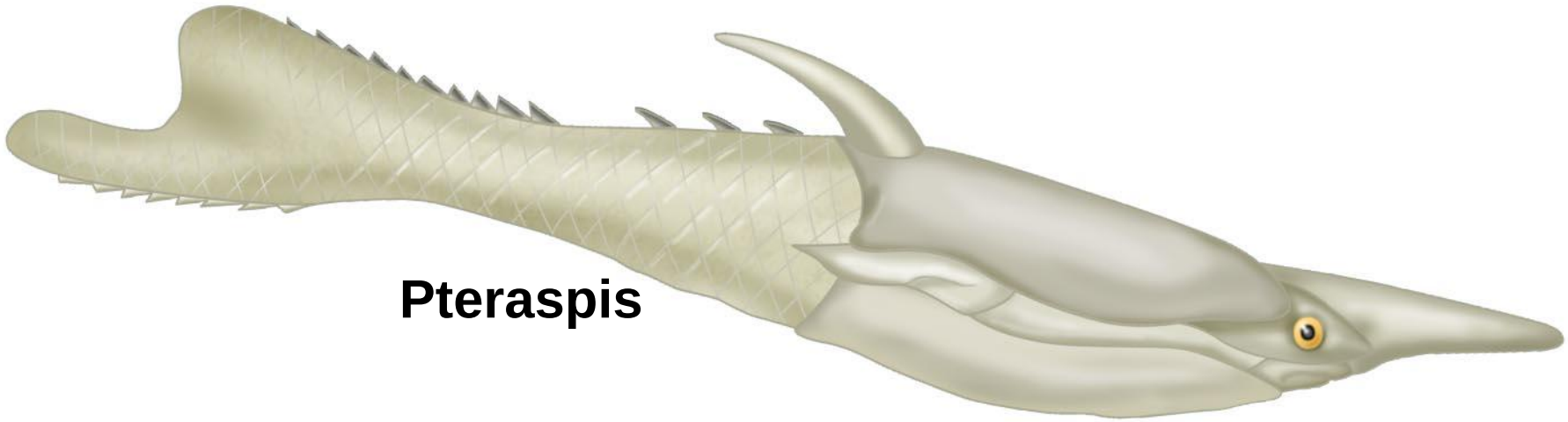
Cephalochordata
Urochordata
Myxini
Petromyzontida
Chondrichthyes
Actinopterygii
Actinistia
Dipnoi
Amphibia
Reptilia
Mammalia

Fossils of Early Vertebrates

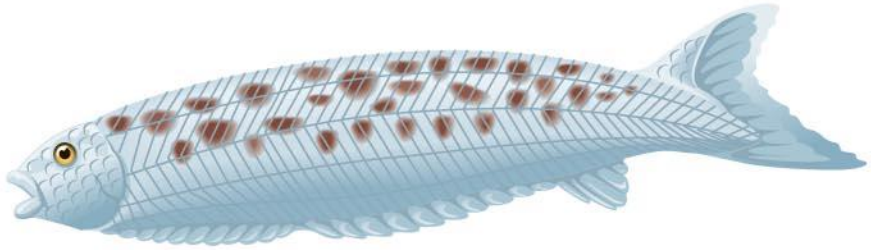
- **Conodonts** were the first vertebrates with mineralized skeletal elements in their mouth and pharynx



- Other armored, jawless vertebrates had defensive plates of bone on their skin



Pteraspis



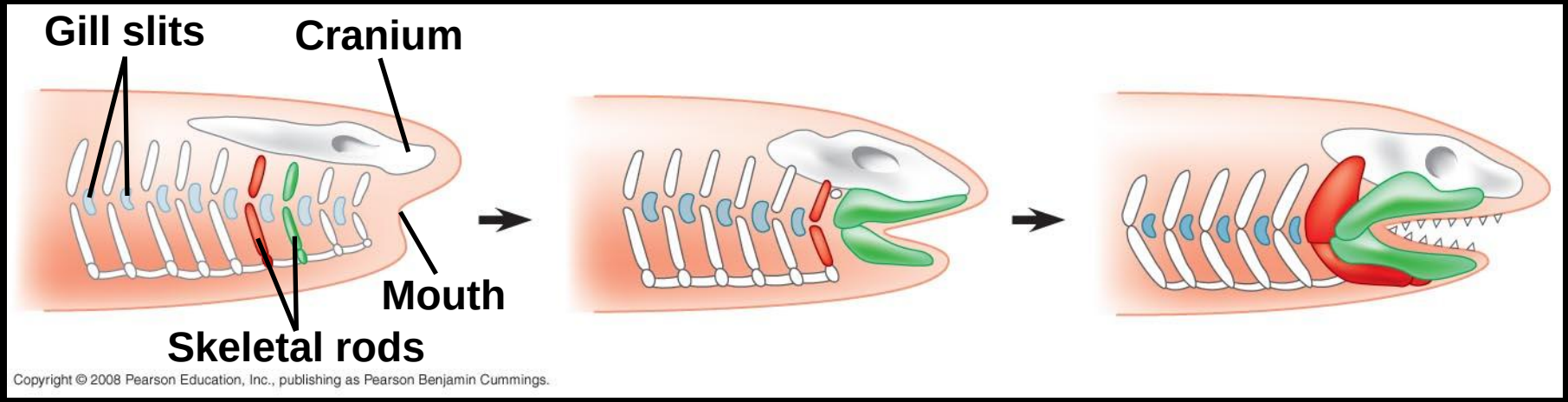
Pharyngolepis

Origins of Bone and Teeth

- Mineralization appears to have originated with vertebrate mouthparts
- The vertebrate endoskeleton became fully mineralized much later

Concept 34.4: Gnathostomes are vertebrates that have jaws

- Today, jawed vertebrates, or **gnathostomes**, outnumber jawless vertebrates

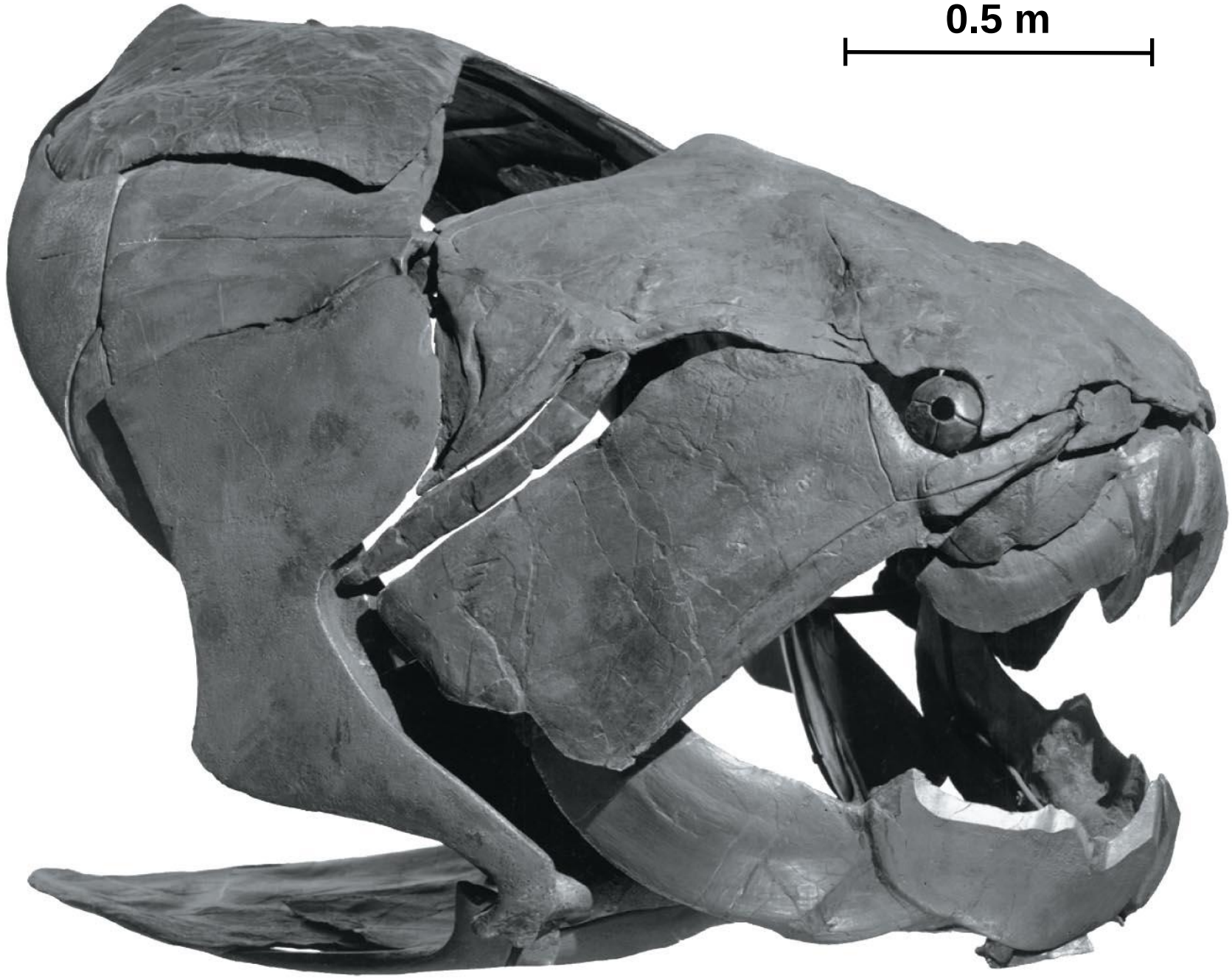


- Other characters common to gnathostomes:
  - An additional duplication of *Hox* genes
  - An enlarged forebrain associated with enhanced smell and vision
  - In aquatic gnathostomes, the **lateral line system**, which is sensitive to vibrations

Fossil Gnathostomes

- The earliest gnathostomes in the fossil record are an extinct lineage of armored vertebrates called **placoderms**

Fig. 34-14



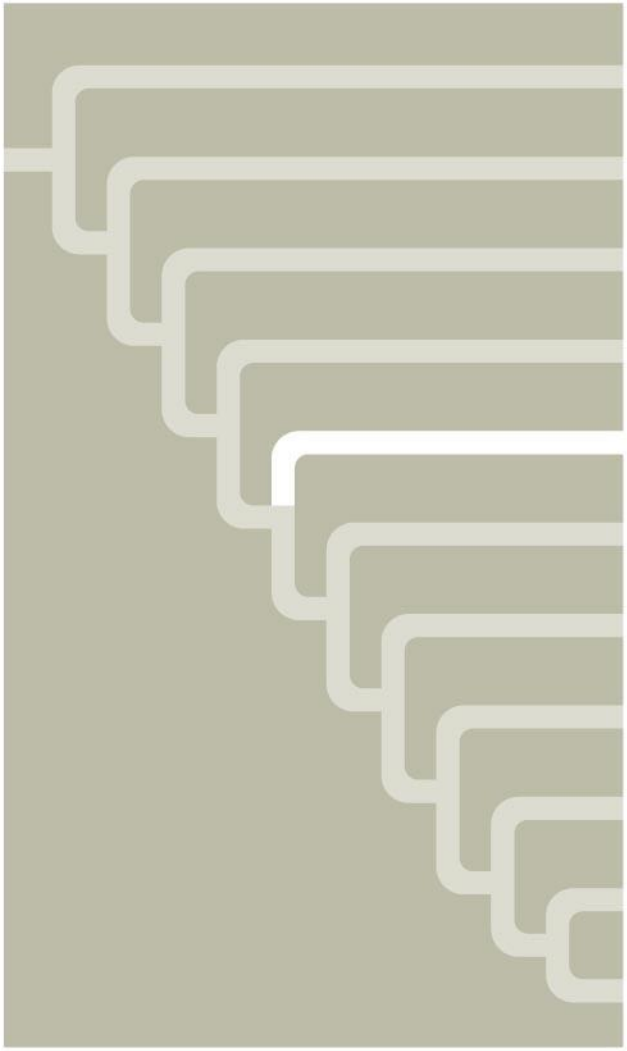
- Another group of jawed vertebrates called acanthodians radiated during the Devonian period

Chondrichthyans (Sharks, Rays, and Their Relatives)

- **Chondrichthyans** (Chondrichthyes) have a skeleton composed primarily of cartilage
- The cartilaginous skeleton evolved secondarily from an ancestral mineralized skeleton
- The largest and most diverse group of chondrichthyans includes the sharks, rays, and skates

PLAY Video: Shark Eating Seal

PLAY Video: Manta Ray



Cephalochordata
Urochordata
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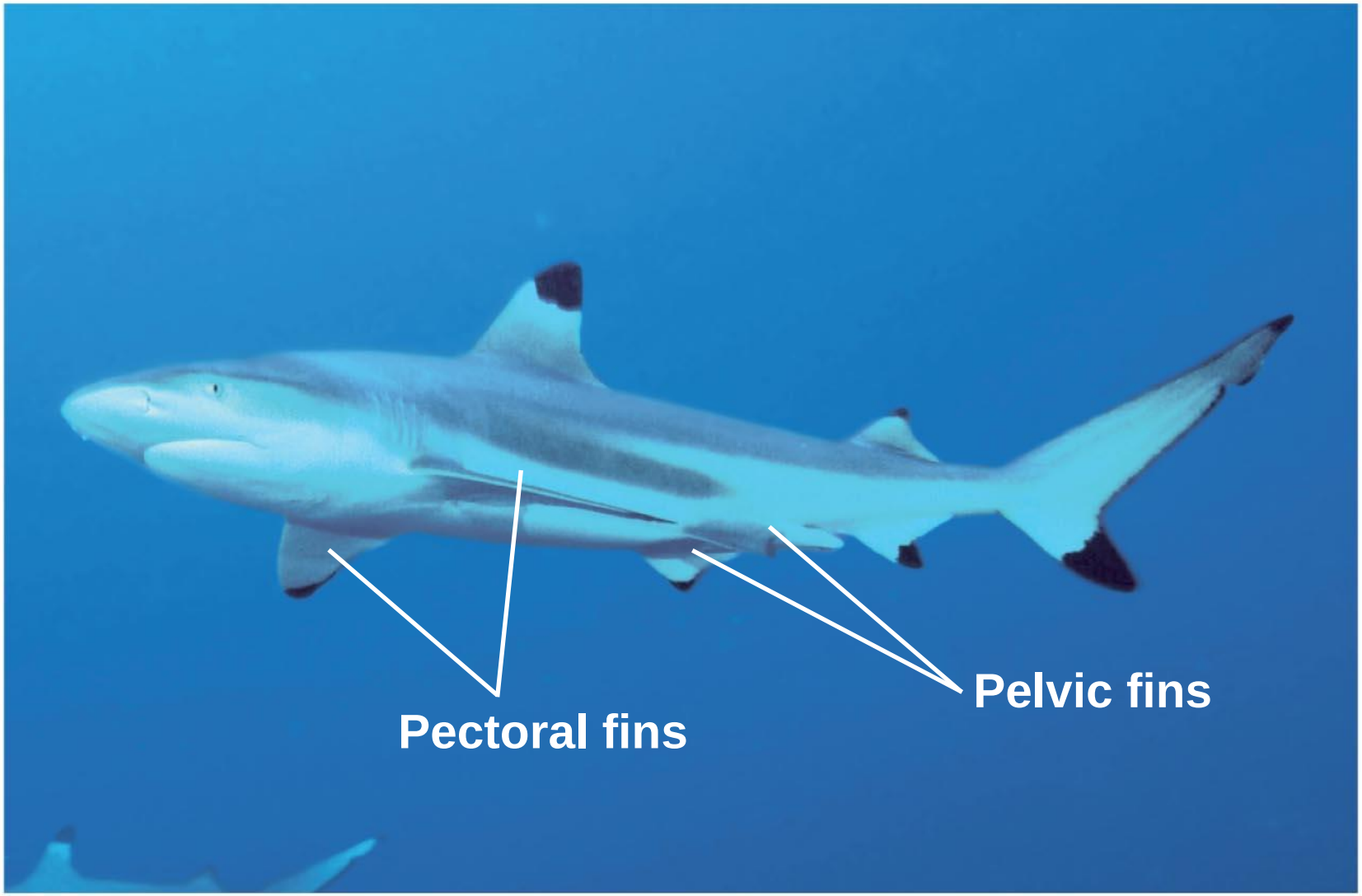
Mammalia



(a) Blacktip reef shark (*Carcharhinus melanopterus*)

(b) Southern stingray (*Dasyatis americana*)

- Most sharks
  - Have a streamlined body and are swift swimmers
  - Are carnivores
  - Have a short digestive tract; a ridge called the *spiral valve* increases the digestive surface area
  - Have acute senses

- Shark eggs are fertilized internally but embryos can develop in different ways:
  - **Oviparous**: eggs hatch outside the mother's body
  - **Ovoviviparous**: the embryo develops within the uterus and is nourished by the egg yolk
  - **Viviparous**: the embryo develops within the uterus and is nourished through a yolk sac placenta from the mother's blood

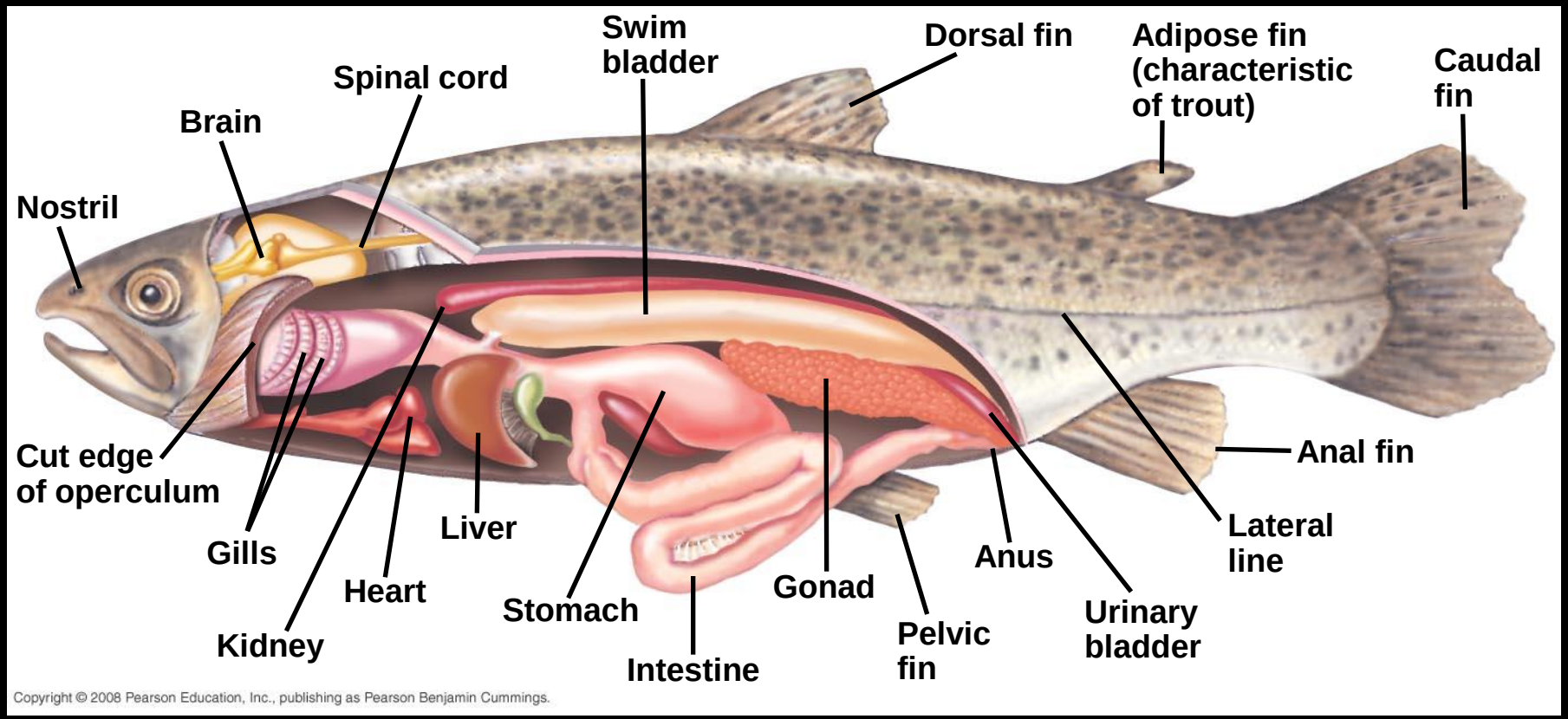
Ray-Finned Fishes

- Class Actinopterygii, the **ray-finned fishes**, includes nearly all the familiar aquatic osteichthyans
- The fins, supported mainly by long, flexible rays, are modified for maneuvering, defense, and other functions

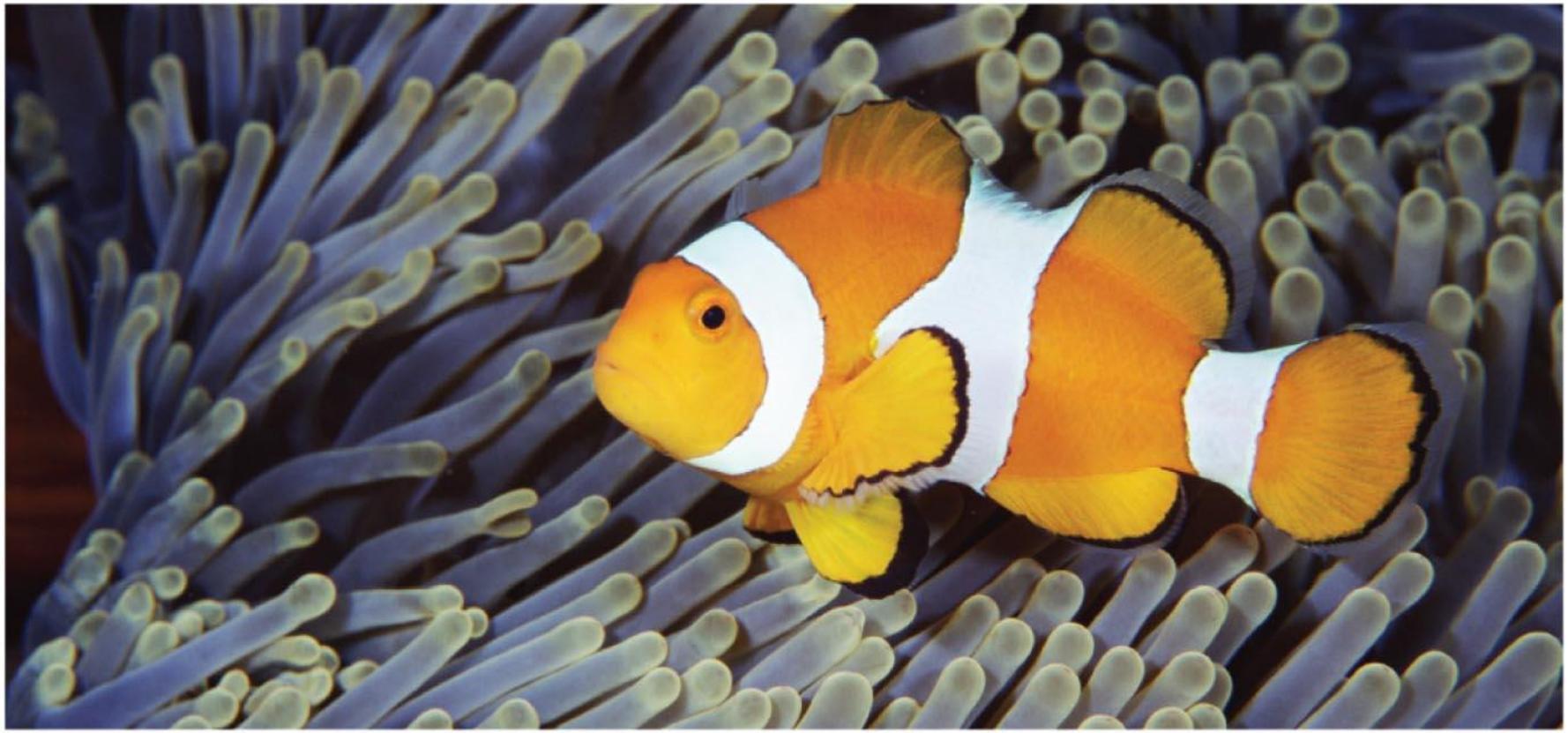
PLAY Video: Clownfish and Anemone

PLAY Video: Coral Reef

PLAY Video: Seahorse Camouflage



(a) Yellowfin tuna (*Thunnus albacares*)



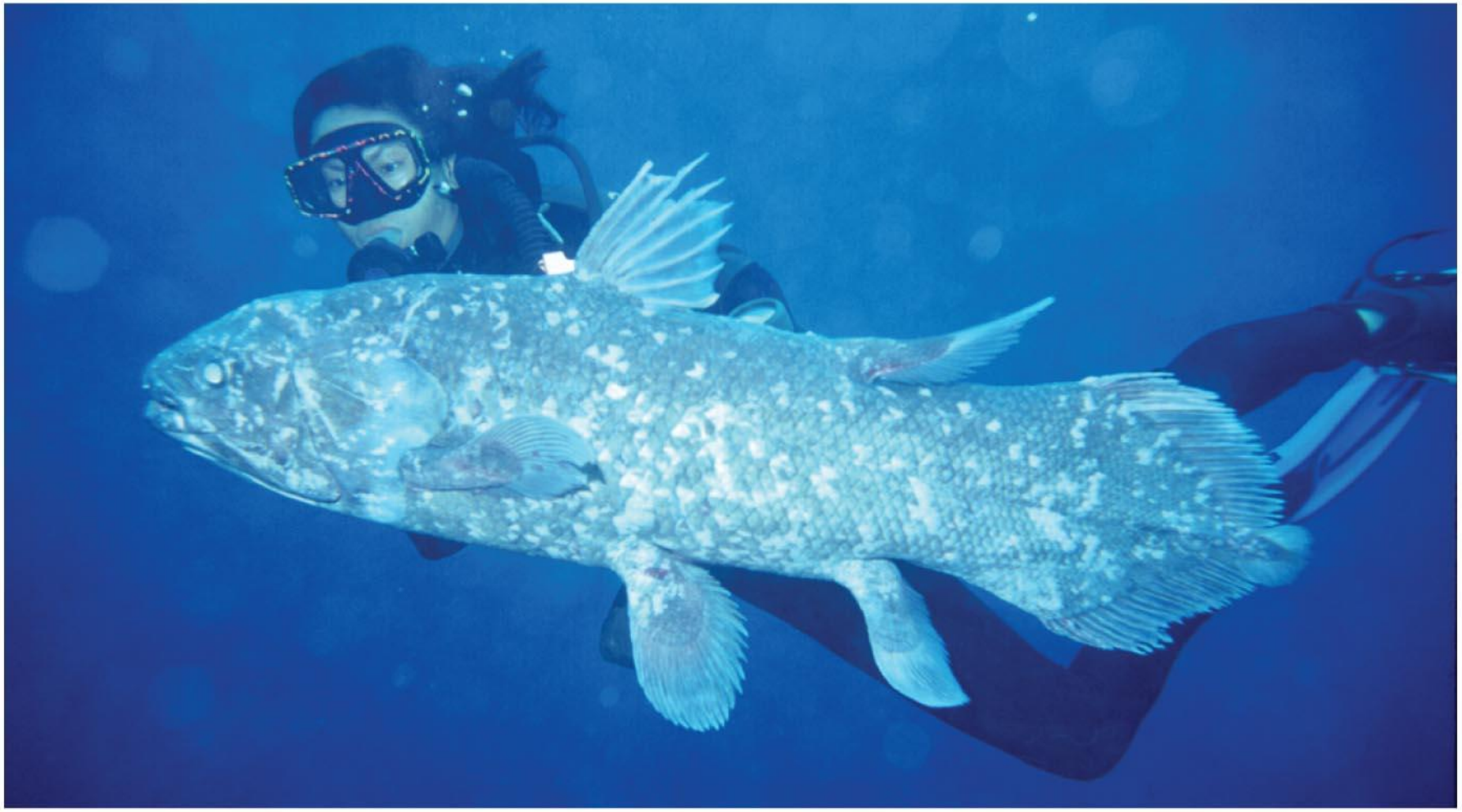
(b) Clownfish (*Amphiprion ocellaris*)

(c) Sea horse (*Hippocampus ramulosus*)

(d) Fine-spotted moray eel (*Gymnothorax dovii*)

Lobe-Fins

- The **lobe-fins** (Sarcopterygii) have muscular pelvic and pectoral fins
- Three lineages survive and include coelacanths, lungfishes, and tetrapods



Concept 34.5: Tetrapods are gnathostomes that have limbs

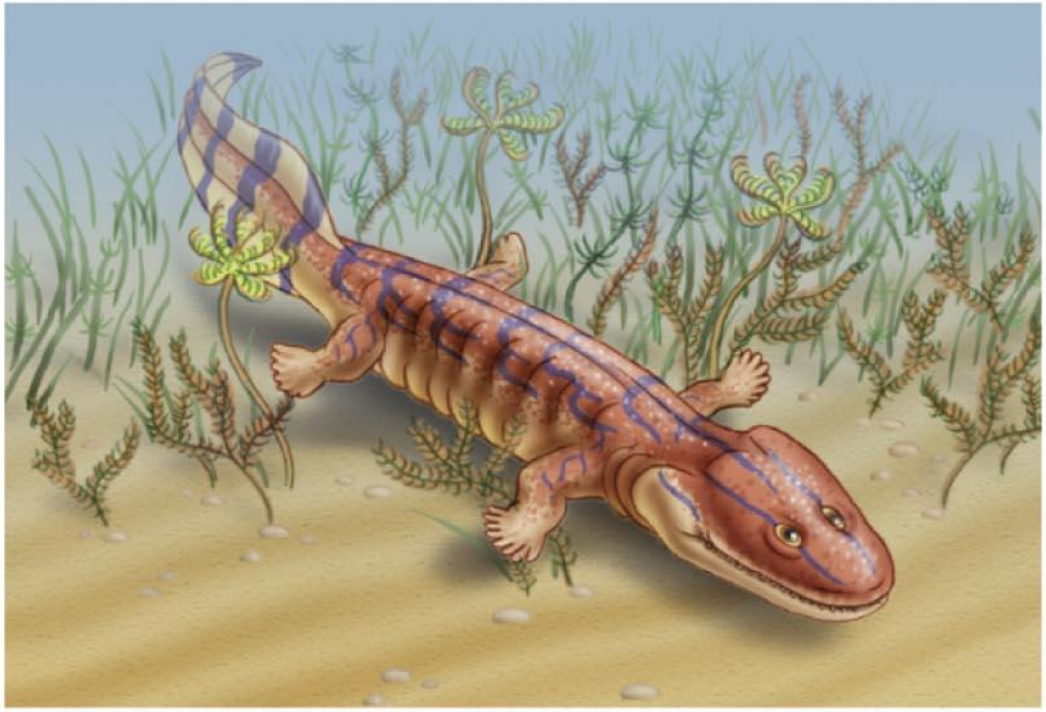
- One of the most significant events in vertebrate history was when the fins of some lobe-fins evolved into the limbs and feet of tetrapods

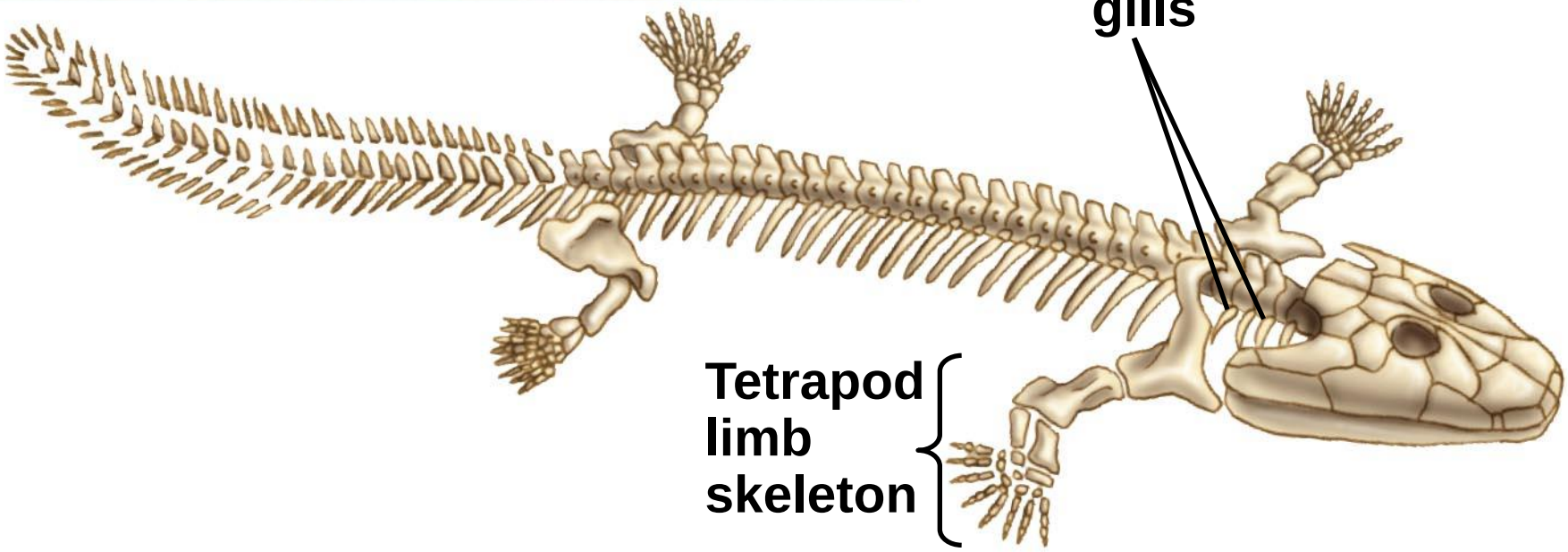
Derived Characters of Tetrapods

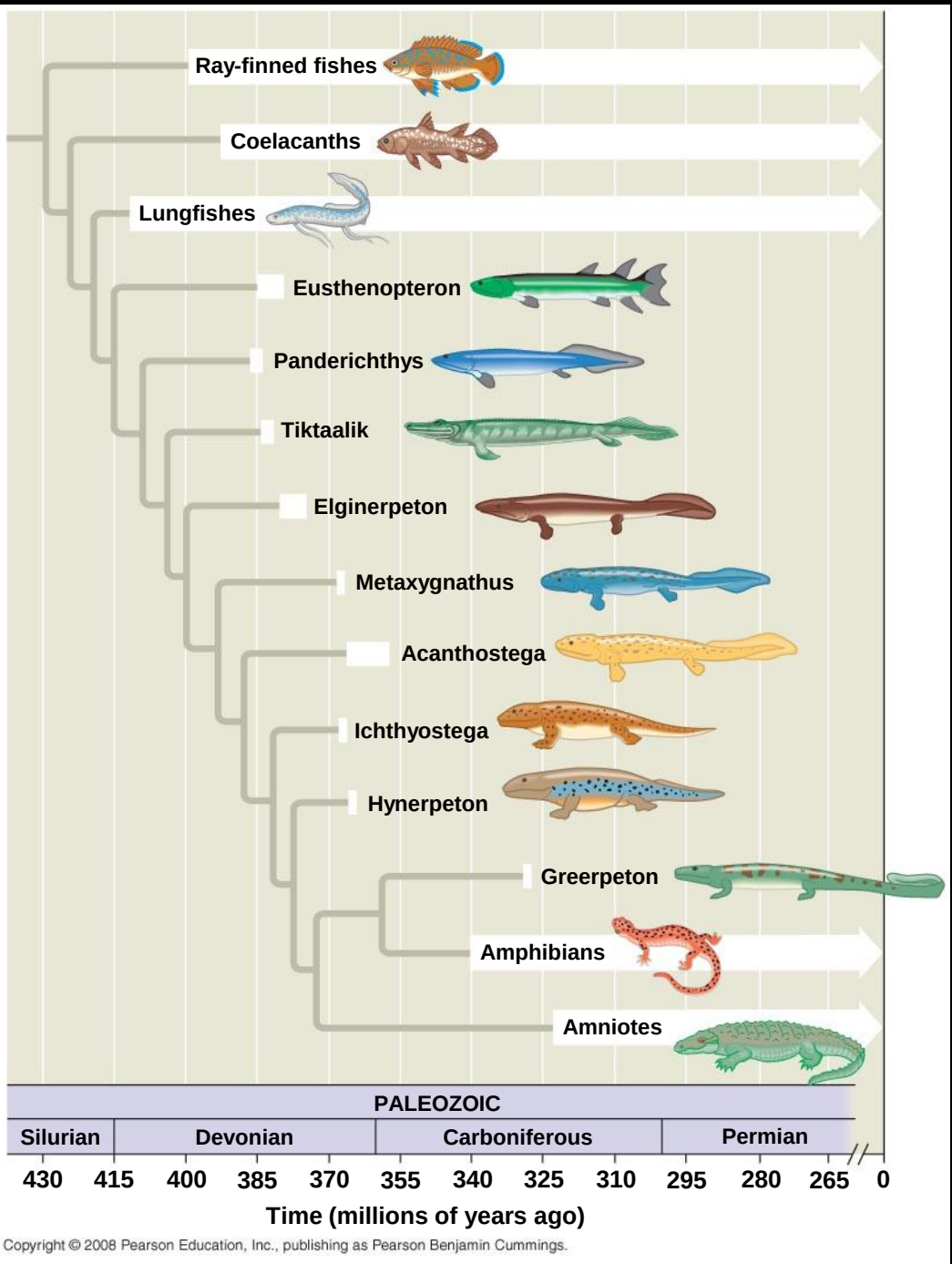
- **Tetrapods** have some specific adaptations:
  - Four limbs, and feet with digits
  - Ears for detecting airborne sounds

The Origin of Tetrapods

- In one lineage of lobe-fins, the fins became progressively more limb-like while the rest of the body retained adaptations for aquatic life
- For example, *Acanthostega* lived in Greenland 365 million years ago







Amphibians

- **Amphibians** (class Amphibia) are represented by about 6,150 species of organisms in three orders
- Order Urodela includes salamanders, which have tails

(a) Order Urodela

(b) Order Anura

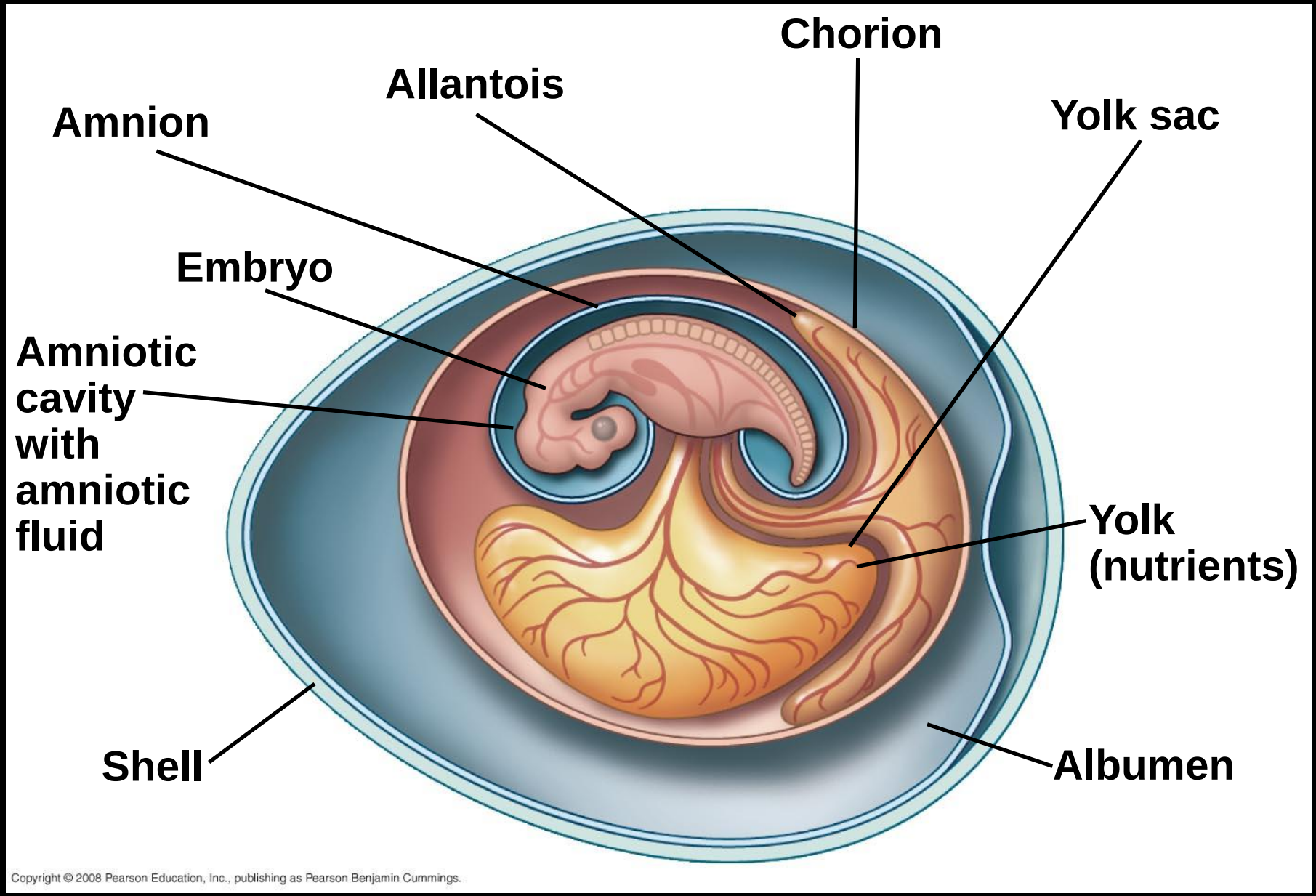
(c) Order Apoda

- *Amphibian* means “both ways of life,” referring to the metamorphosis of an aquatic larva into a terrestrial adult
- Most amphibians have moist skin that complements the lungs in gas exchange
- Fertilization is external in most species, and the eggs require a moist environment

Fig. 34-23

Derived Characters of Amniotes

- Amniotes are named for the major derived character of the clade, the **amniotic egg**, which contains membranes that protect the embryo
- The *extraembryonic membranes* are the amnion, chorion, yolk sac, and allantois



Early Amniotes

- Living amphibians and amniotes split from a common ancestor about 370 million years ago
- Early amniotes were more tolerant of dry conditions than early tetrapods

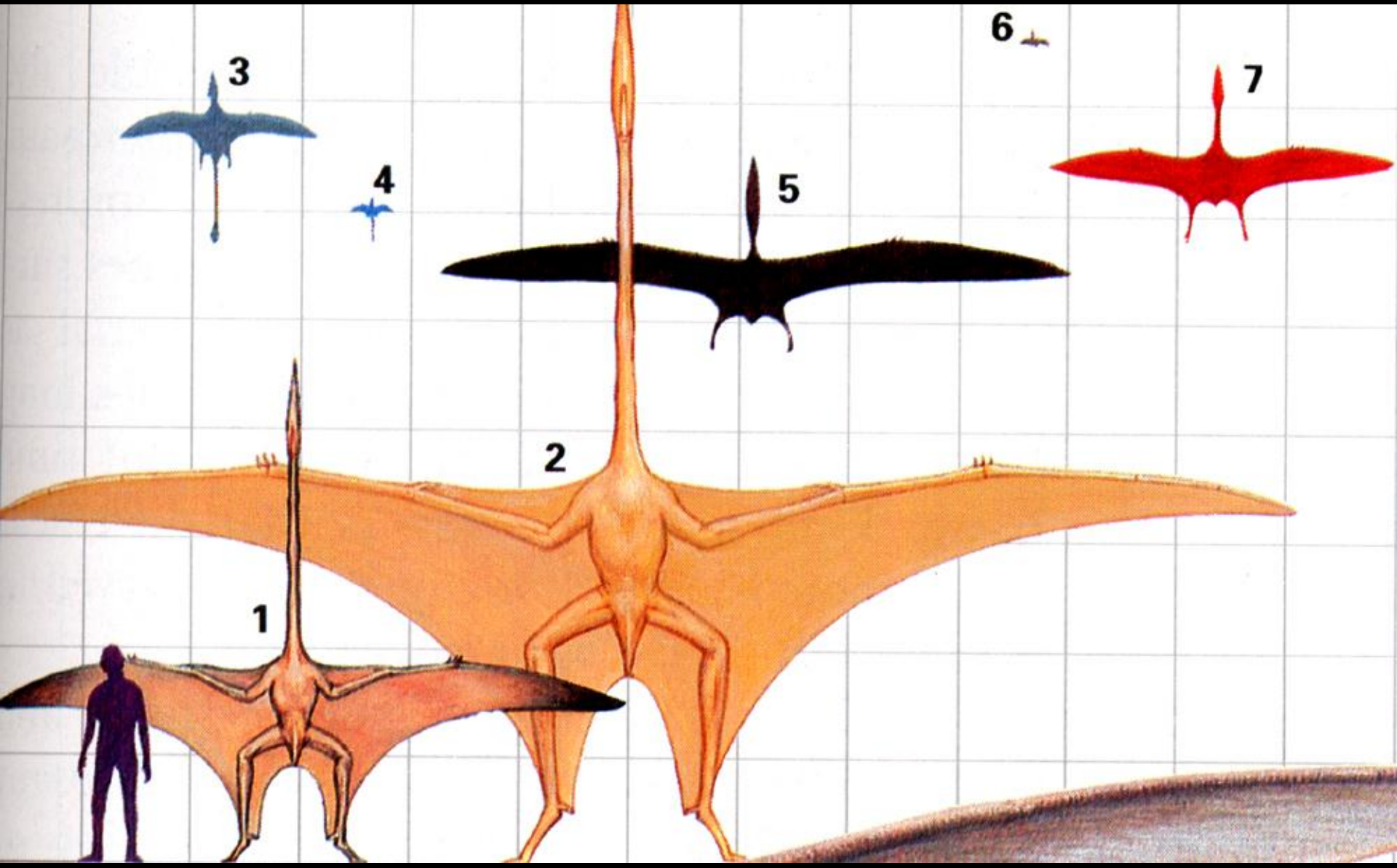
Reptiles

- The **reptile** clade includes the tuataras, lizards, snakes, turtles, crocodilians, birds, and the extinct dinosaurs
- Reptiles have scales that create a waterproof barrier
- They lay shelled eggs on land

- Most reptiles are **ectothermic**, absorbing external heat as the main source of body heat
- Birds are **endothermic**, capable of keeping the body warm through metabolism

The Origin and Evolutionary Radiation of Reptiles

- The oldest reptilian fossils date to about 310 million years ago
- The first major group to emerge were **parareptiles**, which were mostly large, stocky herbivores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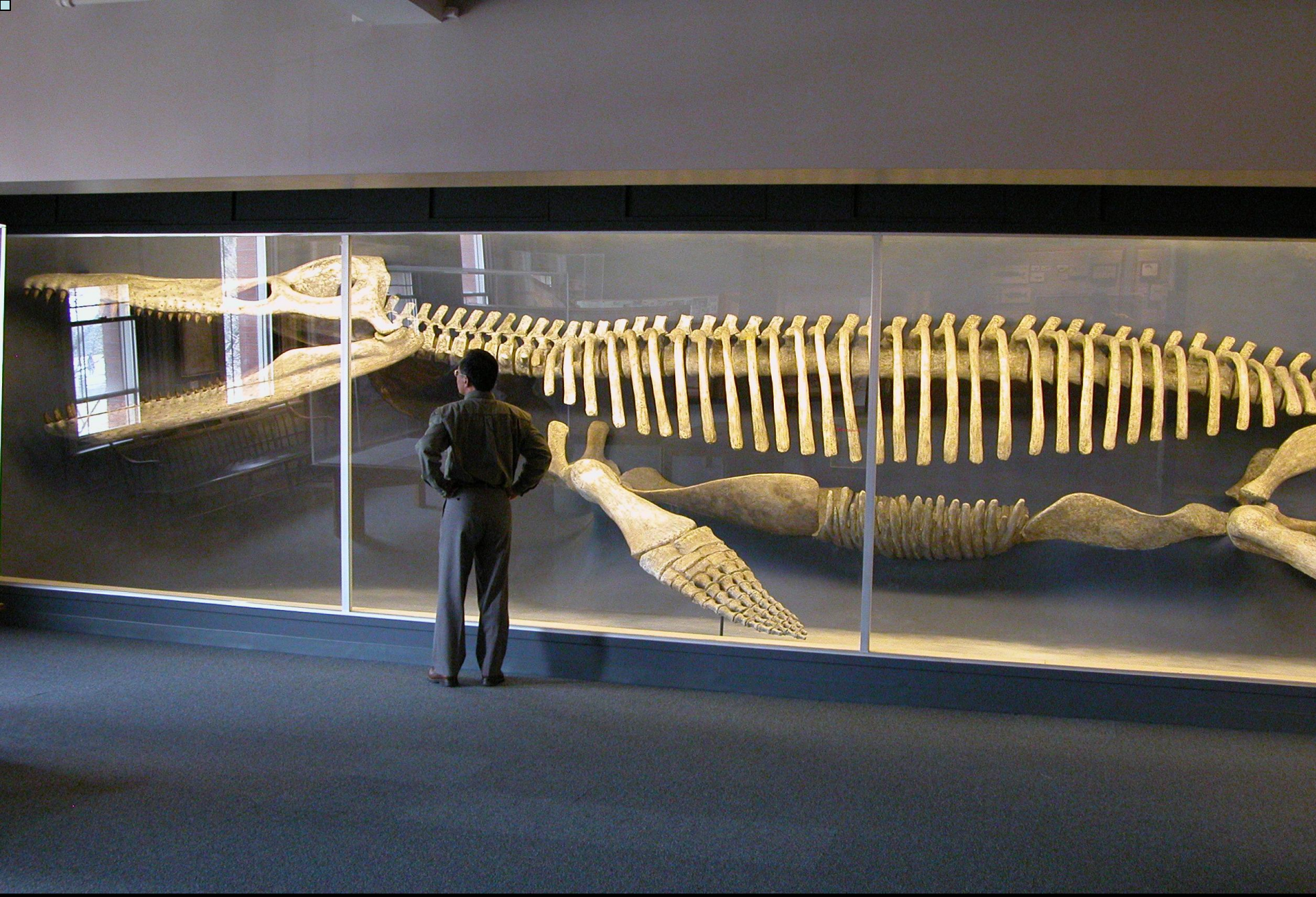
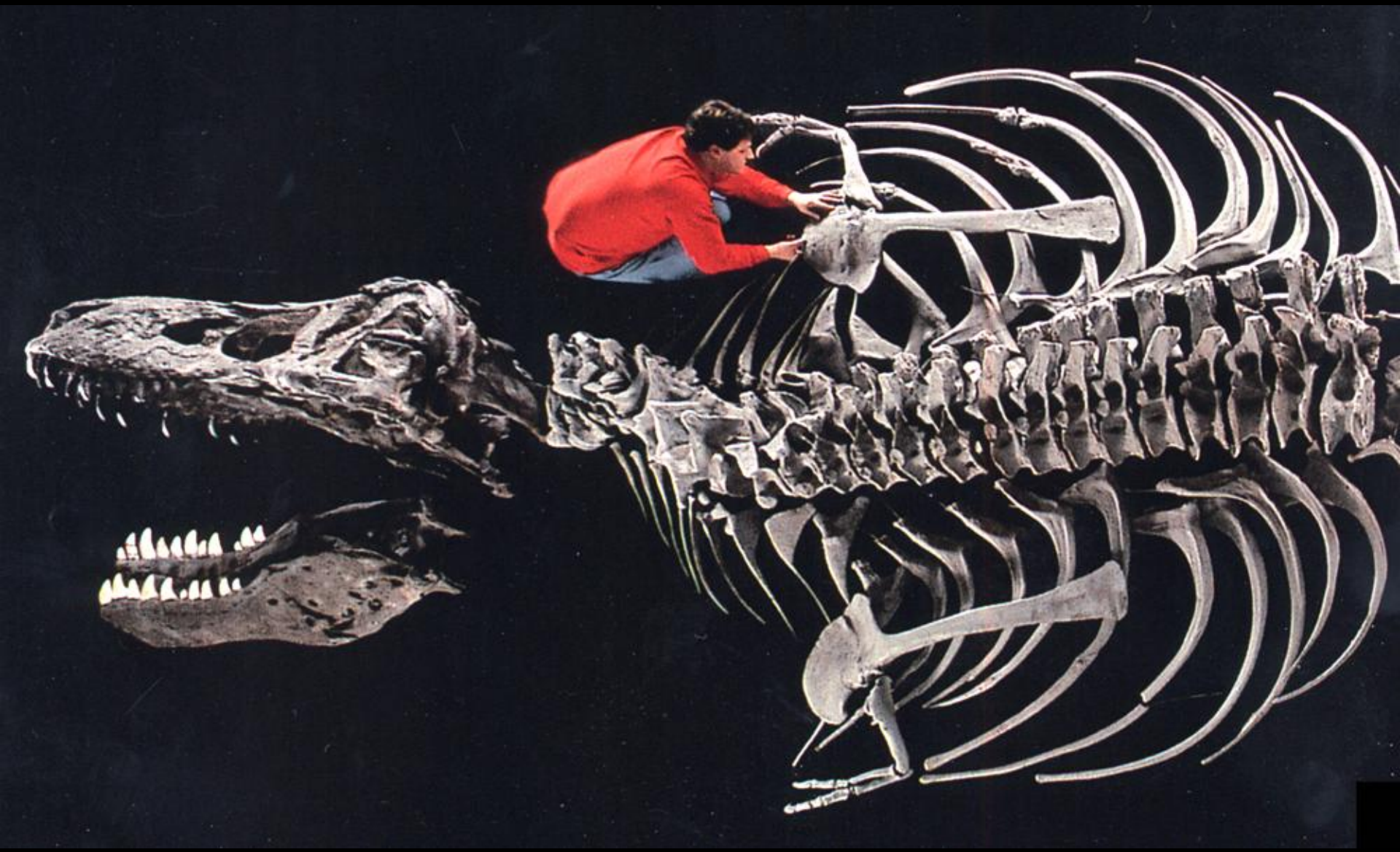
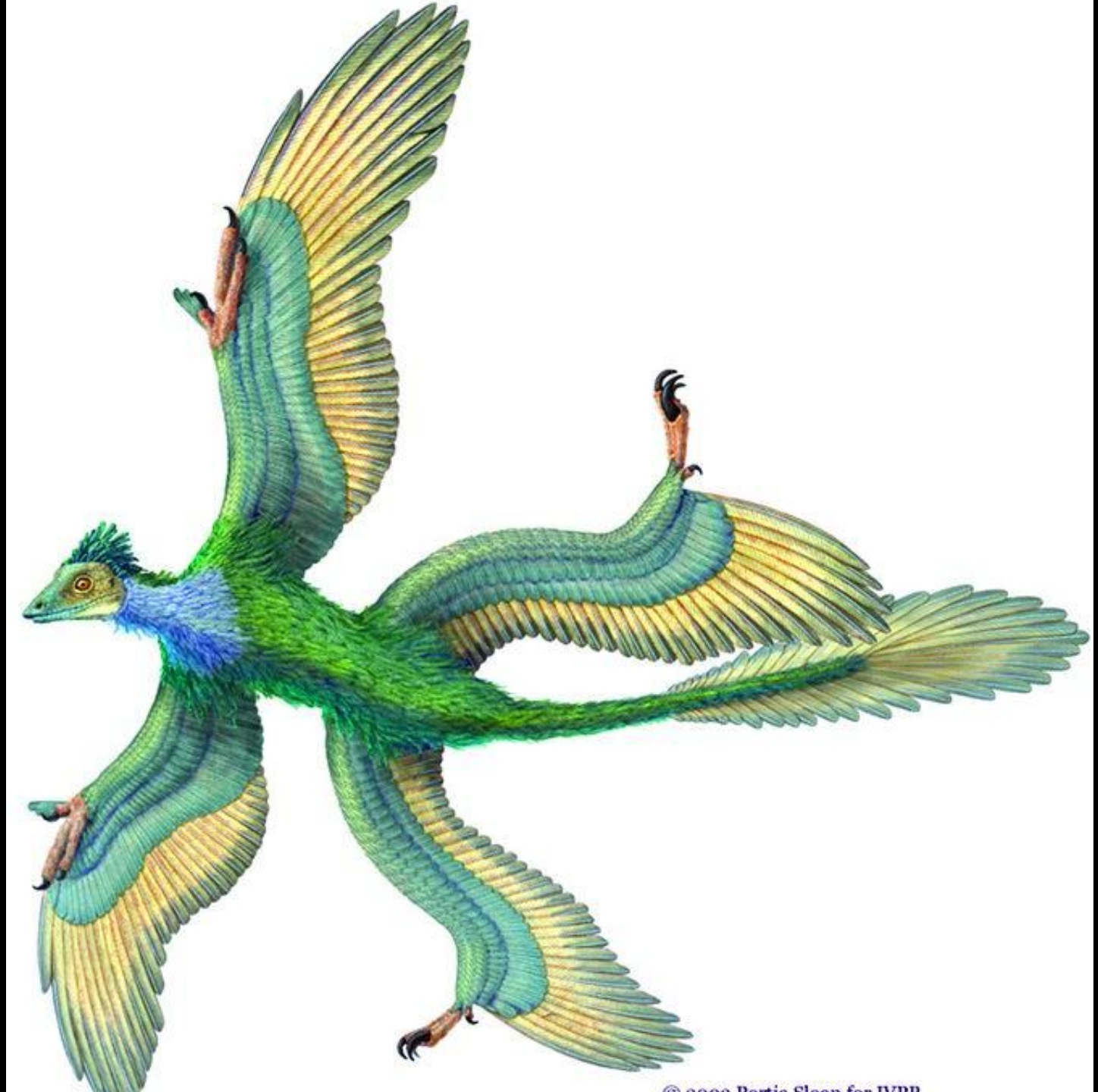




千禧中國鳥龍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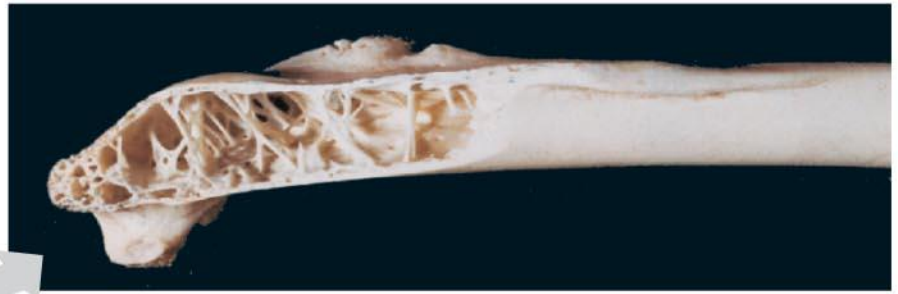
Derived Characters of Birds

- Many characters of birds are adaptations that facilitate flight
- The major adaptation is wings with keratin feathers
- Other adaptations include lack of a urinary bladder, females with only one ovary, small gonads, and loss of teeth



Finger 1

(b) Bone structure

Palm

Finger 2

Finger 3

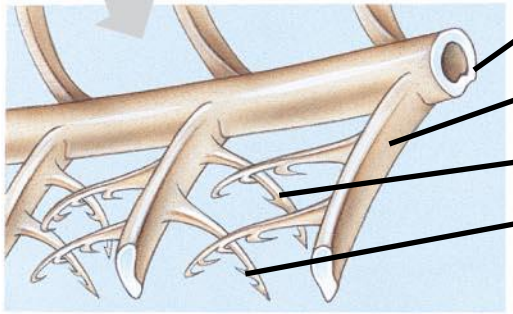
(a) Wing

Forearm

Wrist

Shaft

Vane



Shaft

Barb

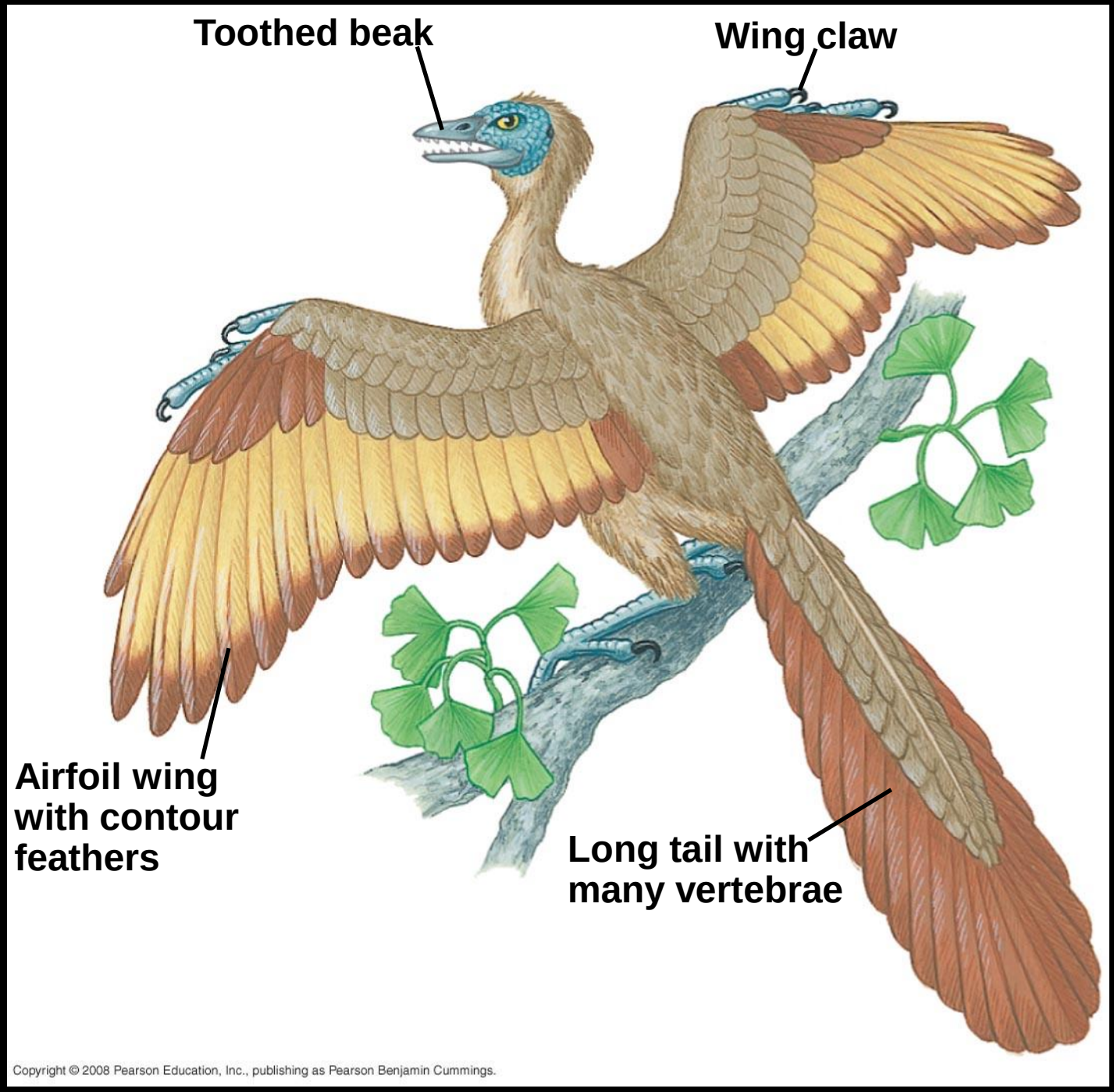
Barbule

Hook

(c) Feather structure

The Origin of Birds

- Birds probably descended from small theropods, a group of carnivorous dinosaurs
- By 150 million years ago, feathered theropods had evolved into birds
- *Archaeopteryx* remains the oldest bird known



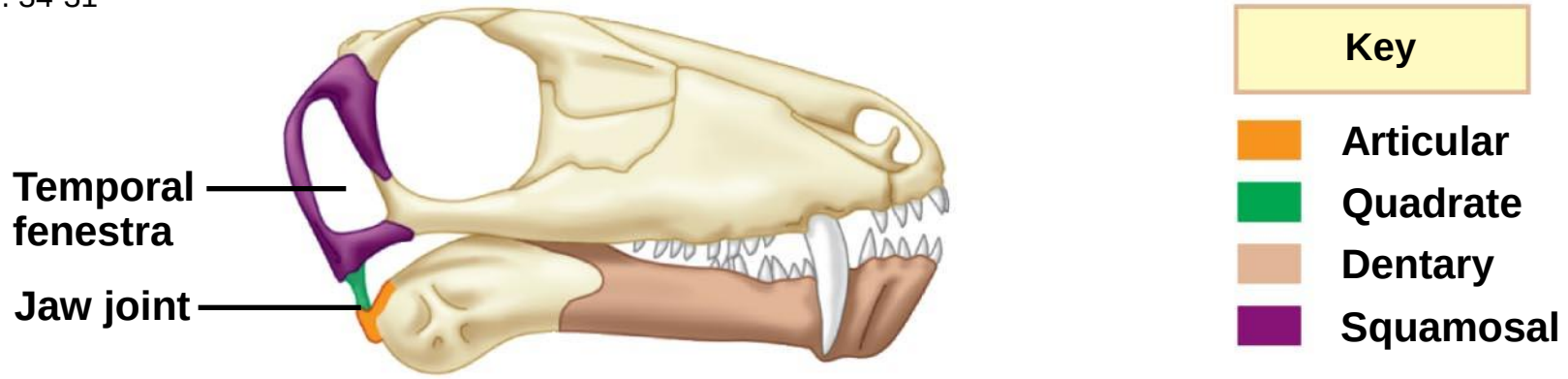
Concept 34.7: Mammals are amniotes that have hair and produce milk

- **Mammals**, class Mammalia, are represented by more than 5,300 species

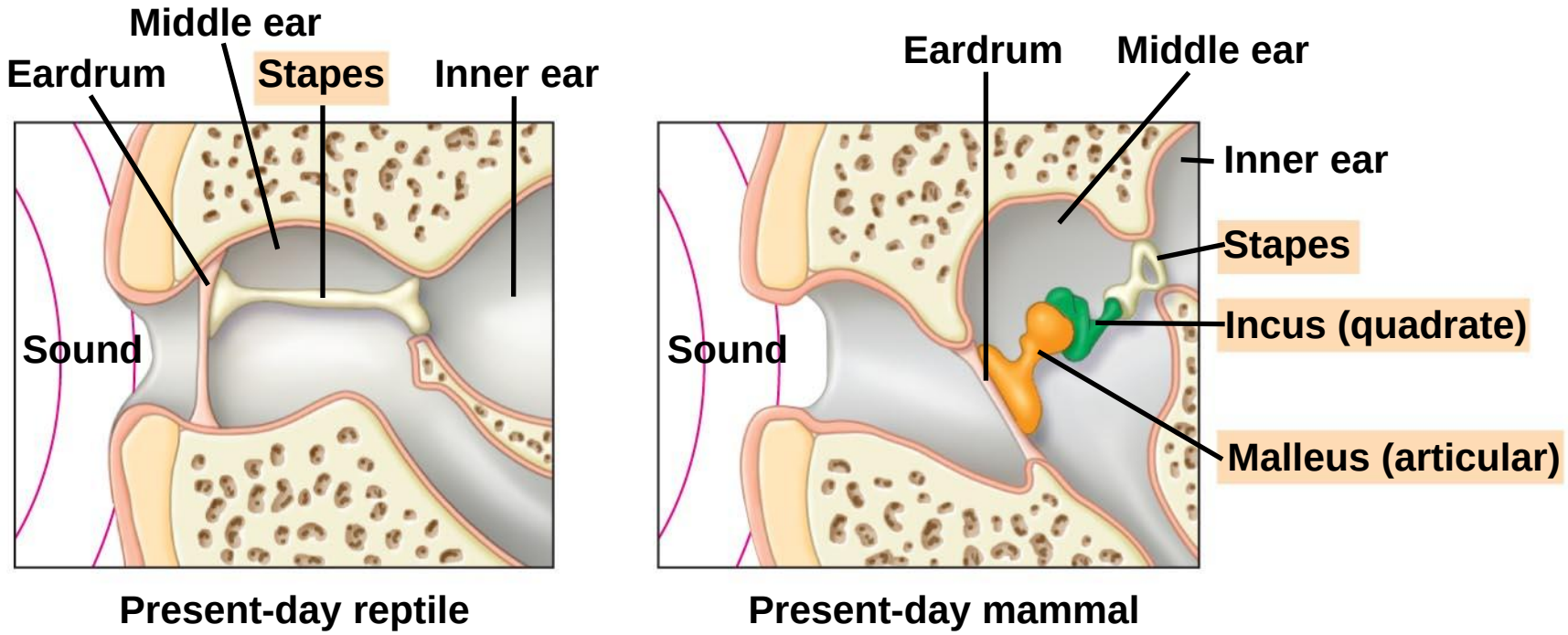
Derived Characters of Mammals

- Mammals have
  - Mammary glands, which produce milk
  - Hair
  - A larger brain than other vertebrates of equivalent size
  - Differentiated teeth

Fig. 34-31



(a) In *Biarmosuchus,* an early synapsid, the articular and quadrate bones formed the jaw joint.



(b) In mammals, the articular and quadrate bones are incorporated into the middle ear.

- By the early Cretaceous, the three living lineages of mammals emerged: monotremes, marsupials, and eutherians
- Mammals did not undergo a significant adaptive radiation until after the Cretaceous

Marsupials

- **Marsupials** include opossums, kangaroos, and koalas
- The embryo develops within a **placenta** in the mother's uterus
- A marsupial is born very early in its development
- It completes its embryonic development while nursing in a maternal pouch called a marsupium

(a) A young brushtail possum

Fig. 34-34

Marsupial mammals	Eutherian mammals
Plantigale	Deer mouse
Marsupial mole	Mole
Sugar glider	Flying squirrel

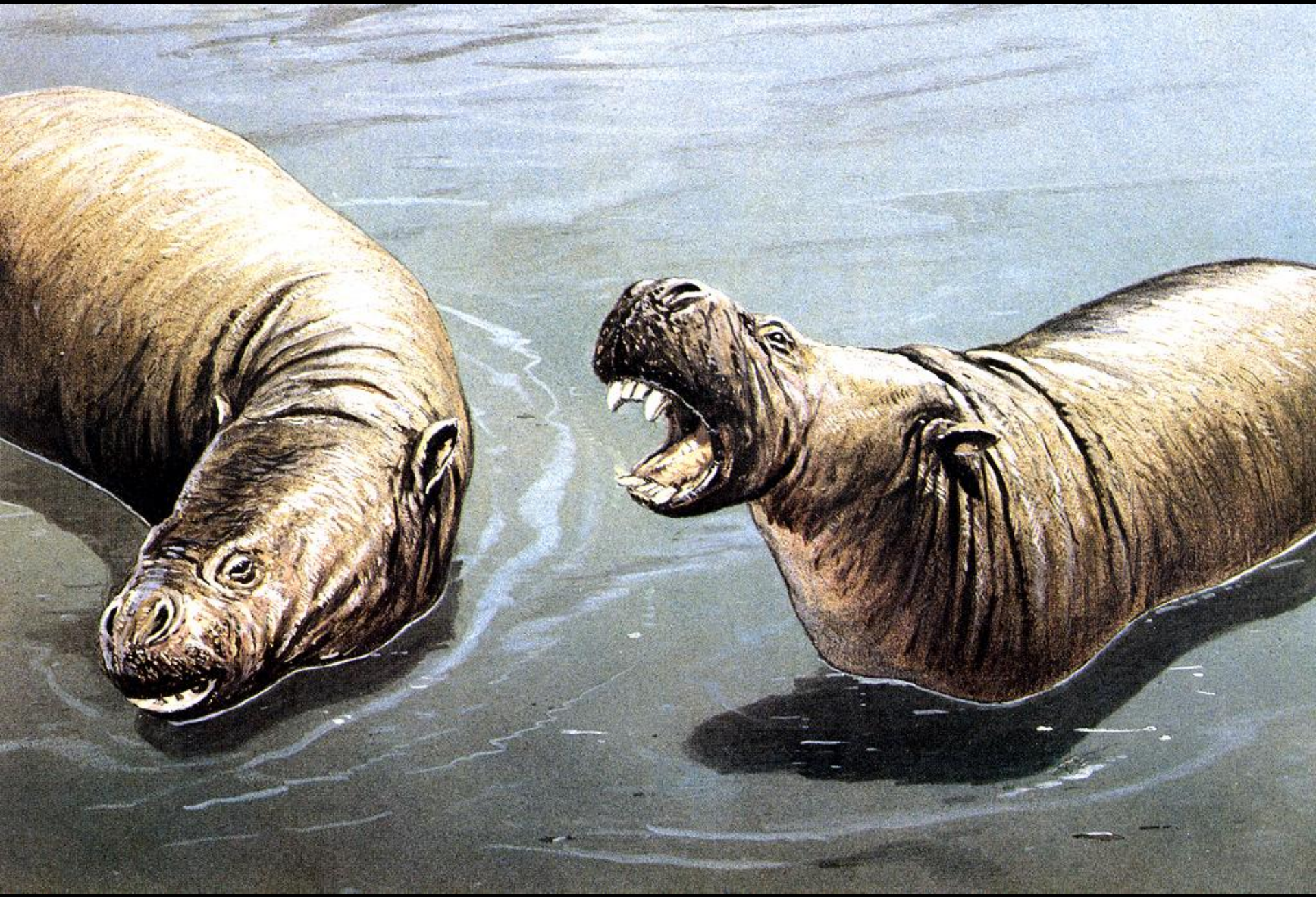
Marsupial mammals	Eutherian mammals
Wombat	Woodchuck
Tasmanian devil	Wolverine
Kangaroo	Patagonian cavy

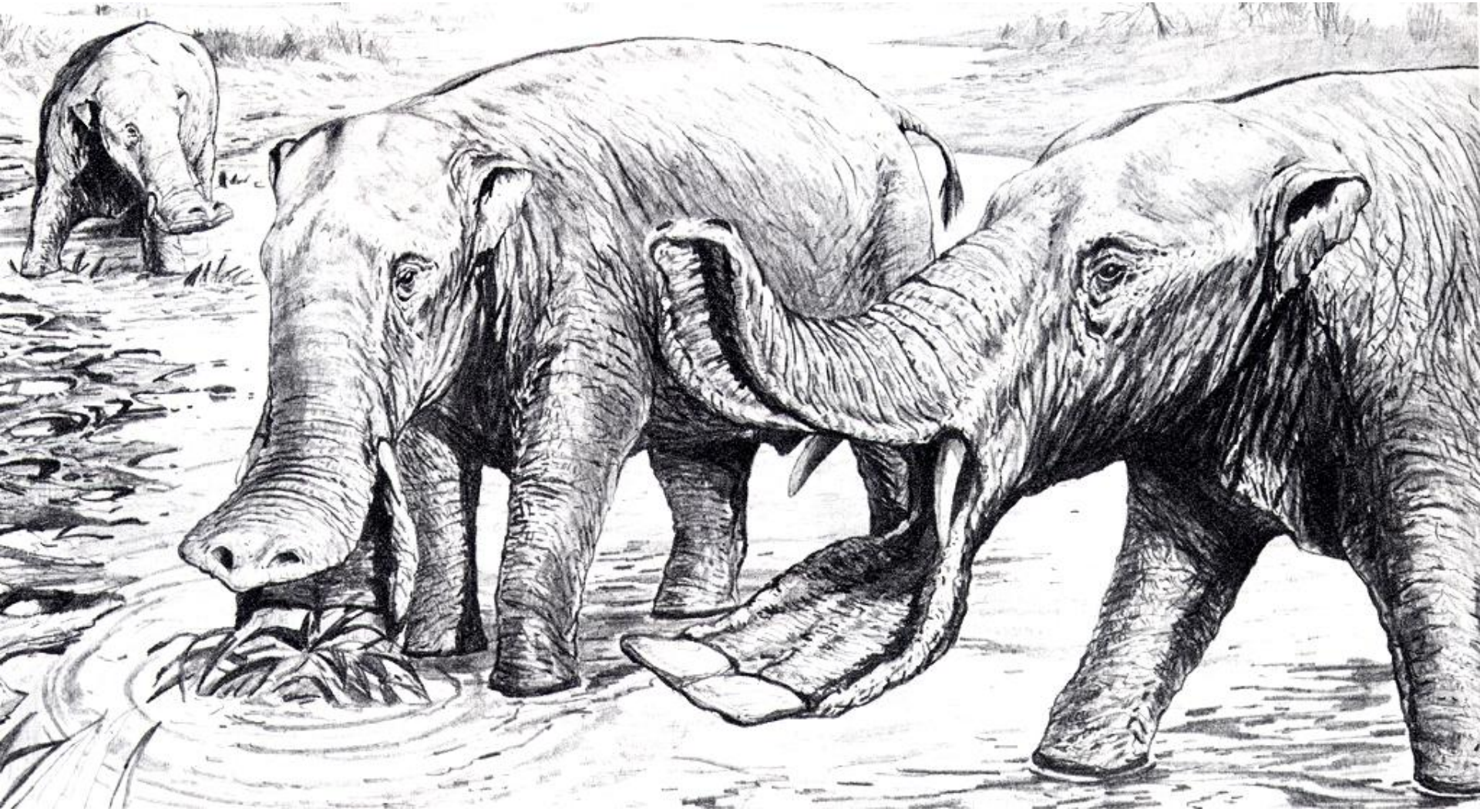
Eutherians (Placental Mammals)

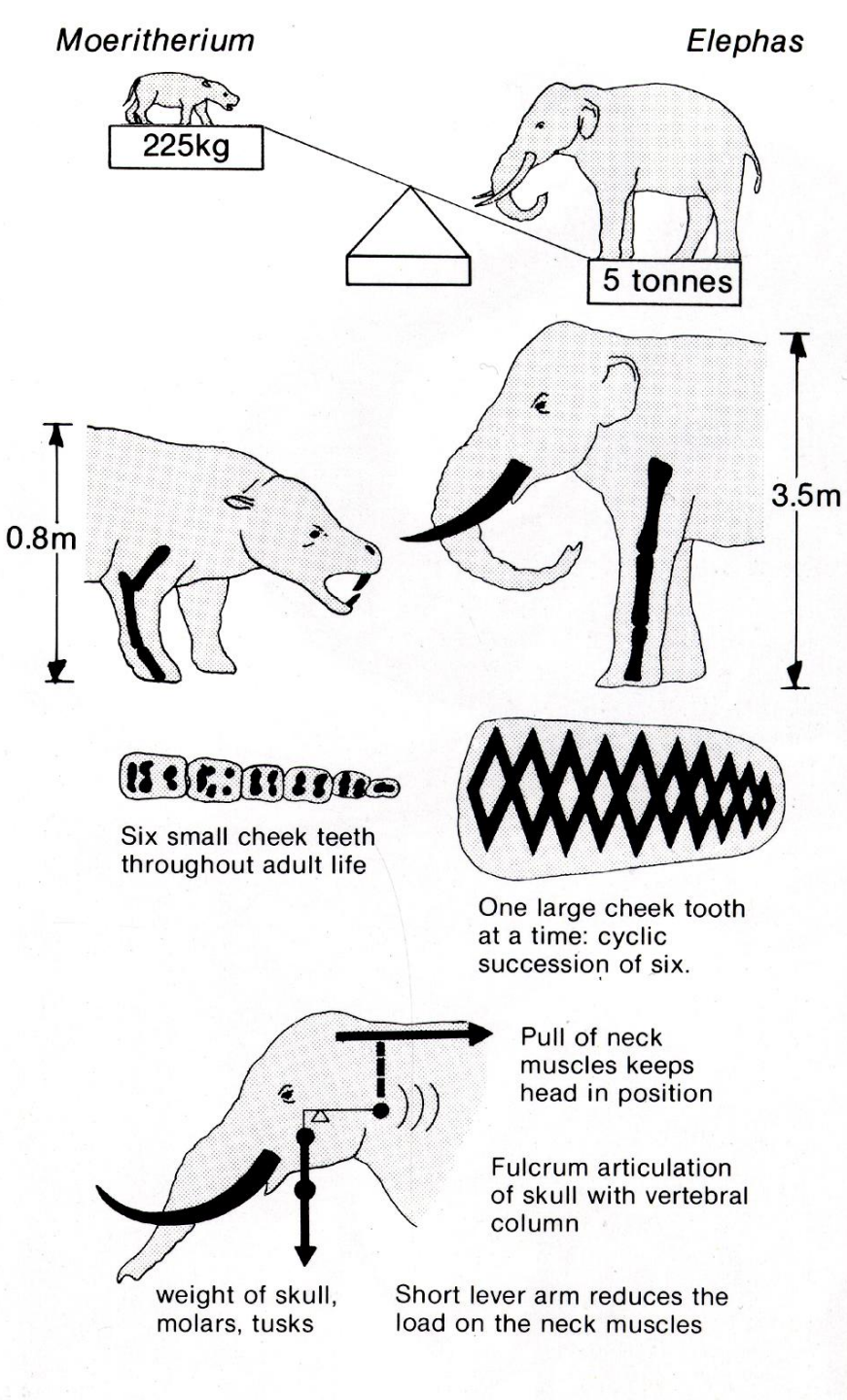
- Compared with marsupials, **eutherians** have a longer period of pregnancy
- Young eutherians complete their embryonic development within a uterus, joined to the mother by the placenta
- Molecular and morphological data give conflicting dates on the diversification of eutherians

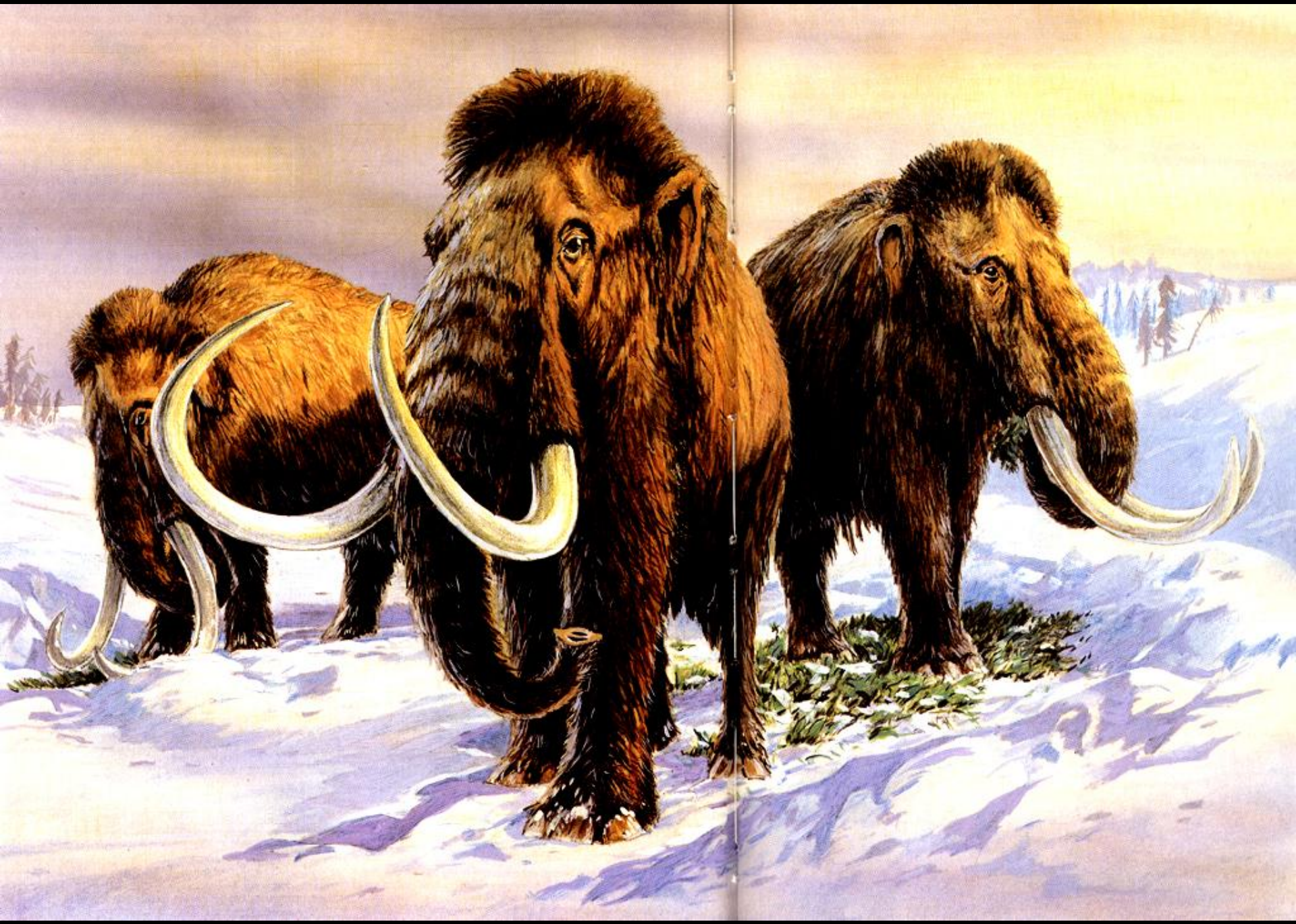
Orders and Examples	Main Characteristics
Monotremata Platypuses, echidnas  Echidna	Lay eggs; no nipples; young suck milk from fur of mother
Proboscidea Elephants  African elephant	Long, muscular trunk; thick, loose skin; upper incisors elongated as tusks
Sirenia Manatees, dugongs  Manatee	Aquatic; finlike forelimbs and no hind limbs; herbivorous
Xenarthra Sloths, anteaters, armadillos  Tamandua	Reduced teeth or no teeth; herbivorous (sloths) or carnivorous (anteaters, armadillos)
Lagomorpha Rabbits, hares, picas  Jackrabbit	Chisel-like incisors; hind legs longer than forelegs and adapted for running and jumping; herbivorous
Carnivora Dogs, wolves, bears, cats, weasels, otters, seals, walruses  Coyote	Sharp, pointed canine teeth and molars for shearing; carnivorous
Cetartiodactyla **Artiodactyls** Sheep, pigs, cattle, deer, giraffes  Bighorn sheep	Hooves with an even number of toes on each foot; herbivorous
Cetaceans Whales, dolphins, porpoises  Pacific white-sided porpoise	Aquatic; streamlined body; paddle-like forelimbs and no hind limbs; thick layer of insulating blubber; carnivorous

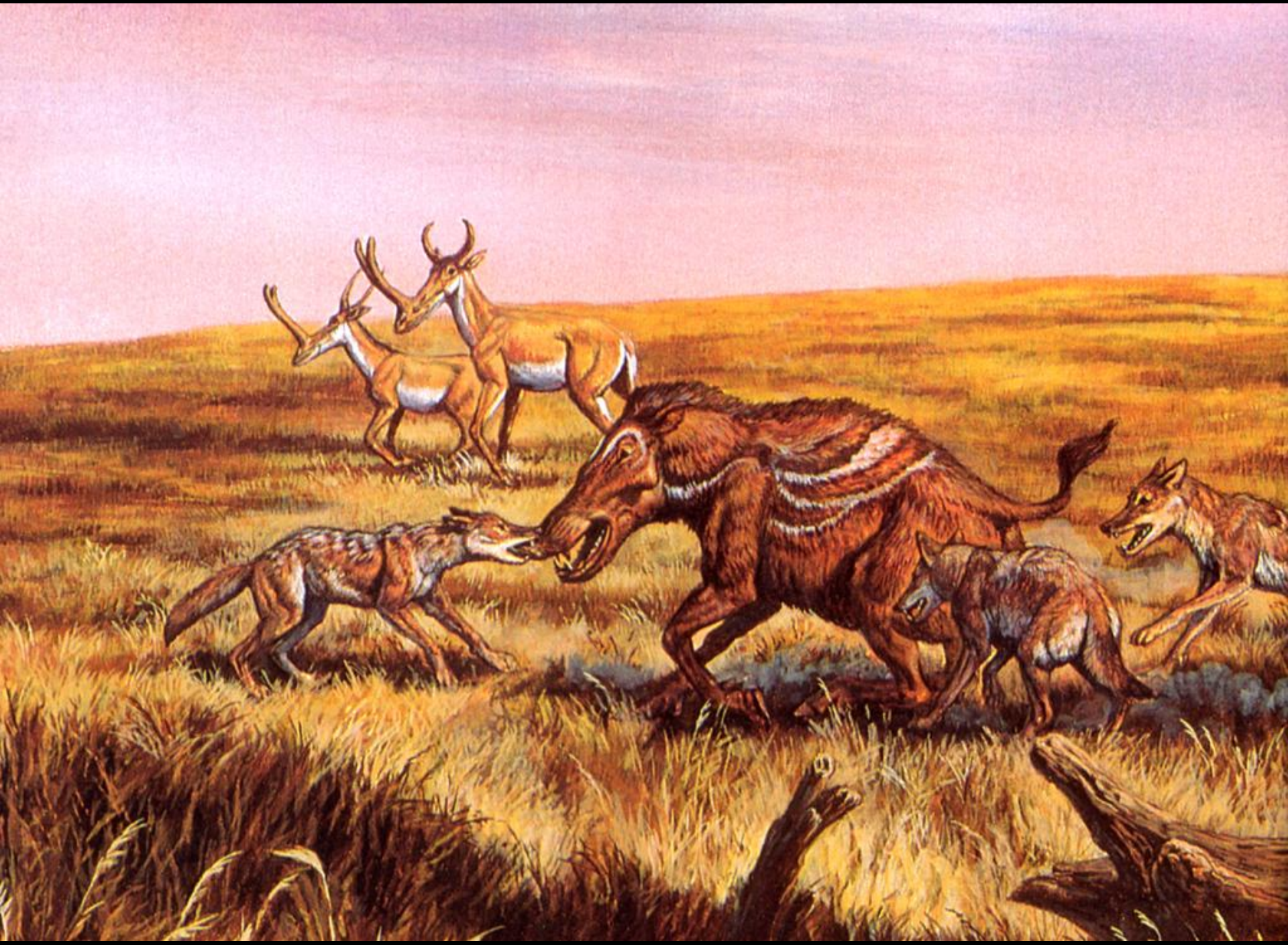
Orders and Examples	Main Characteristics
Marsupialia Kangaroos, opossums, koalas  Koala	Embryo completes development in pouch on mother
Tubulidentata Aardvarks  Aardvark	Teeth consisting of many thin tubes cemented together; eats ants and termites
Hyracoidea Hyraxes  Rock hyrax	Short legs; stumpy tail; herbivorous; complex, multichambered stomach
Rodentia Squirrels, beavers, rats, porcupines, mice  Red squirrel	Chisel-like, continuously growing incisors worn down by gnawing; herbivorous
Primates Lemurs, monkeys, chimpanzees, gorillas, humans  Golden lion tamarin	Opposable thumbs; forward-facing eyes; well-developed cerebral cortex; omnivorous
Perissodactyla Horses, zebras, tapirs, rhinoceroses  Indian rhinoceros	Hooves with an odd number of toes on each foot; herbivorous
Chiroptera Bats  Frog-eating bat	Adapted for flight; broad skinfold that extends from elongated fingers to body and legs; carnivorous or herbivorous
Eulipotyphla "Core insectivores": some moles, some shrews  Star-nosed mole	Diet consists mainly of insects and other small invertebrates

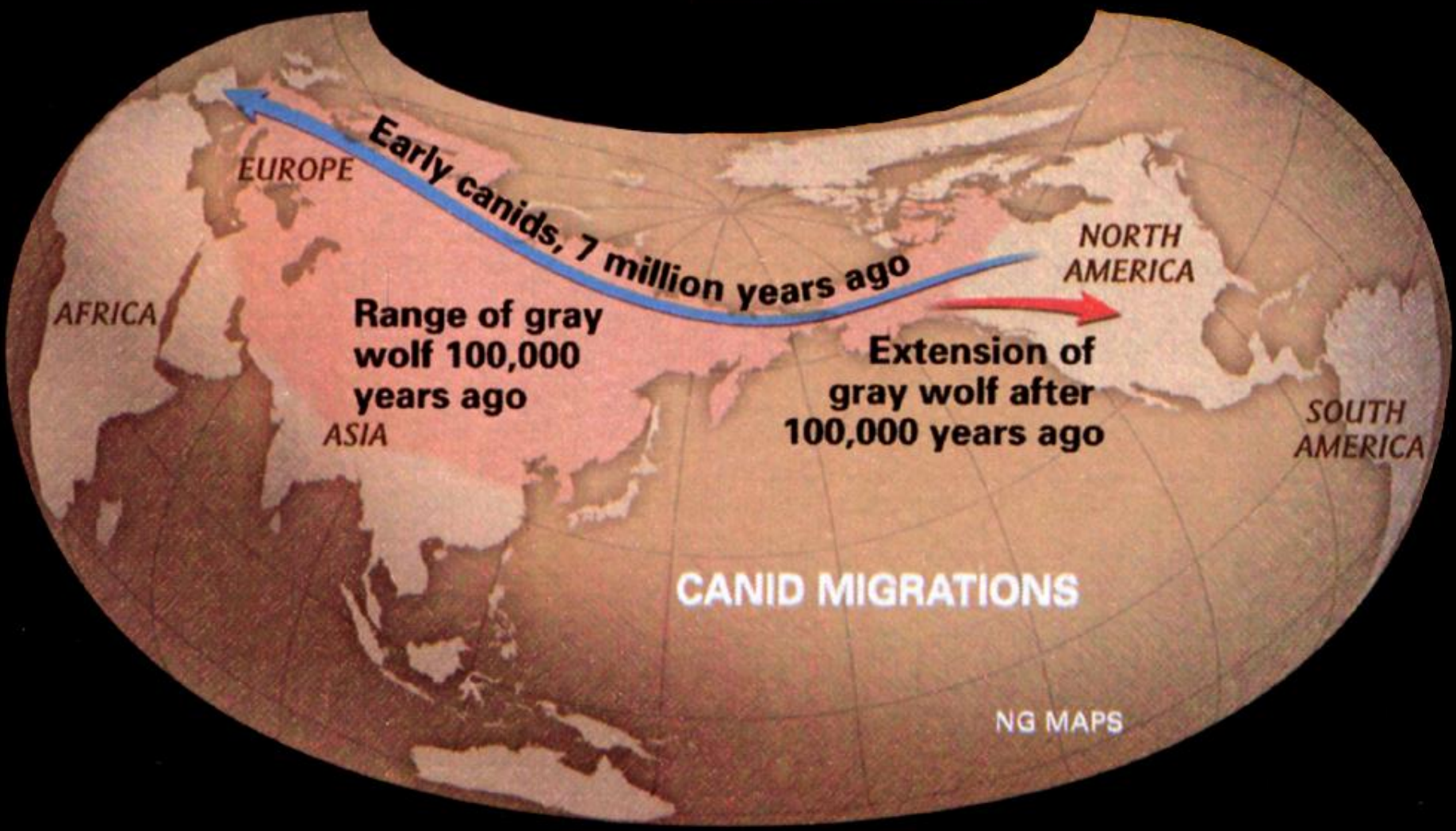





Moeritherium
Elephas
225kg
5 tonnes
0.8m
3.5m
Six small cheek teeth throughout adult life
One large cheek tooth at a time: cyclic succession of six.
Pull of neck muscles keeps head in position
Fulcrum articulation of skull with vertebral column
weight of skull, molars, tusks
Short lever arm reduces the load on the neck muscles






Early canids, 7 million years ago
EUROPE
AFRICA
ASIA
Range of gray wolf 100,000 years ago
NORTH AMERICA
Extension of gray wolf after 100,000 years ago
SOUTH AMERICA
CANID MIGRATIONS
NG MAPS

貓的演化

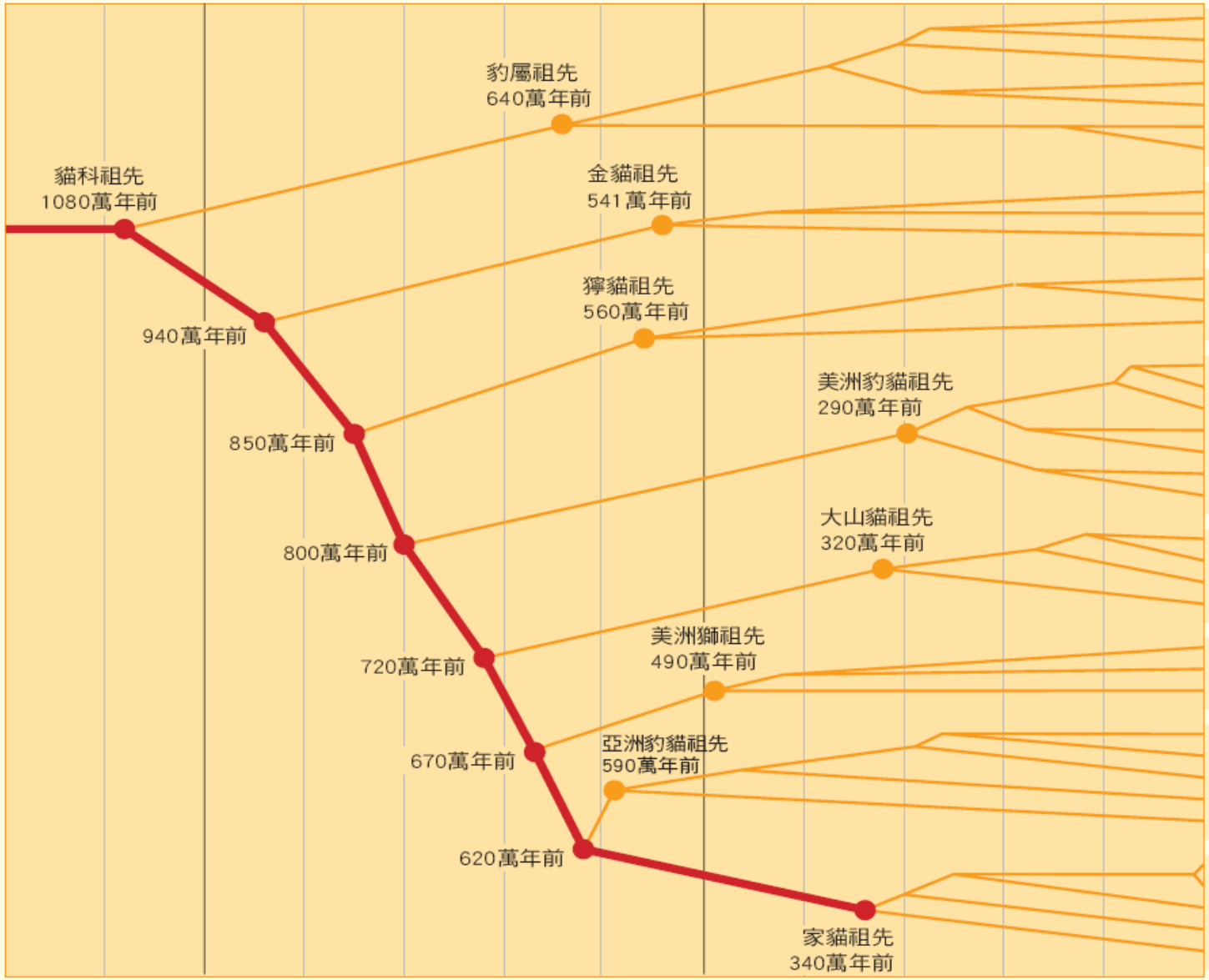
全球野生貓科動物完成基因定序，科學家不僅描繪出貓科的系譜樹，也揭露了牠們過去歲月裡幾次重要的遷徙。

撰文／歐布萊恩（Stephen J. O'Brien）、強生（Warren E. Johnson）
翻譯／鍾慧元

貓科動物既優雅又如謎般難解，被牠們逗弄得心癢難搔的，不只是與貓咪共享沙發的我們，還有那些試圖解開牠們大型表親起源與演化之謎

貓科家族的系譜樹

科學家比較了總共37種貓科動物的基因序列，以判斷系譜樹上的分支。
化石提供的資料，可指出主要分支發生的時間。



37個物種（及其學名）

獅 *Panthera leo*
花豹 *Panthera pardus*
美洲豹 *Panthera onca*
虎 *Panthera tigris*
雪豹 *Panthera uncia*
雲豹 *Neofelis nebulosa*
婆羅洲雲豹 *Neofelis diardi*

亞洲金貓 *Pardofelis temmincki*
婆羅洲金貓 *Pardofelis badia*
紋貓 *Pardofelis marmorata*

獴貓 *Caracal caracal*
非洲金貓 *Caracal aurata*
藪貓 *Caracal serval*

美洲漁貓 *Leopardus geoffroyi*
智利小豹貓 *Leopardus guigna*
美洲虎貓 *Leopardus tigrinus*
南美山貓 *Leopardus jacobita*
南美草原貓 *Leopardus colocolo*
美洲小豹貓 *Leopardus wiedii*
美洲豹貓 *Leopardus pardalis*

伊比利大山貓 *Lynx pardina*
歐亞大山貓 *Lynx lynx*
加拿大大山貓 *Lynx canadensis*
美國大山貓 *Lynx rufus*

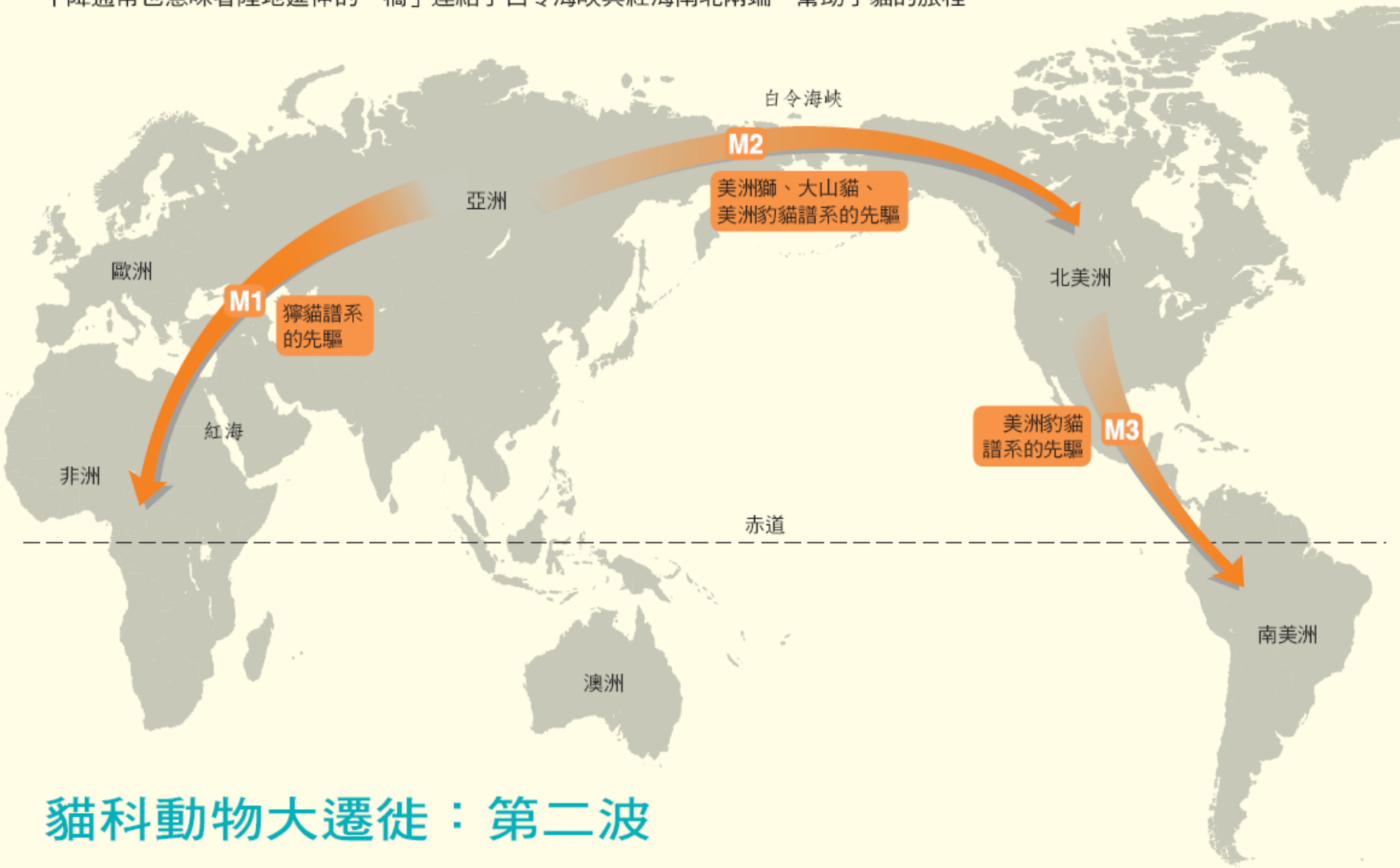
美洲獅 *Puma concolor*
懶貓 *Puma yaguarond*
獵豹 *Acinonyx jubatus*

亞洲豹貓 *Prionailurus bengalensis*
漁貓 *Prionailurus viverrina*
扁頭貓 *Prionailurus planiceps*
鏽斑貓 *Prionailurus rubiginosus*
鬃貓 *Otocolobus manul*

家貓 *Felis catus*
野貓 *Felis silvestris*
沙貓 *Felis margarita*
黑足貓 *Felis nigripes*
叢林貓 *Felis chaus*

貓科動物大遷徙：第一波

所有現代貓類的祖先是一種外表如豹的掠食者，大約在900萬年前，這種動物的後代開始從亞洲家鄉往非洲M1及北美洲M2遷徙（很晚之後也遷徙到南美洲M3）。在這個期間，海平面下降通常也意味著陸地延伸的「橋」連結了白令海峽與紅海南北兩端，幫助了貓的旅程。

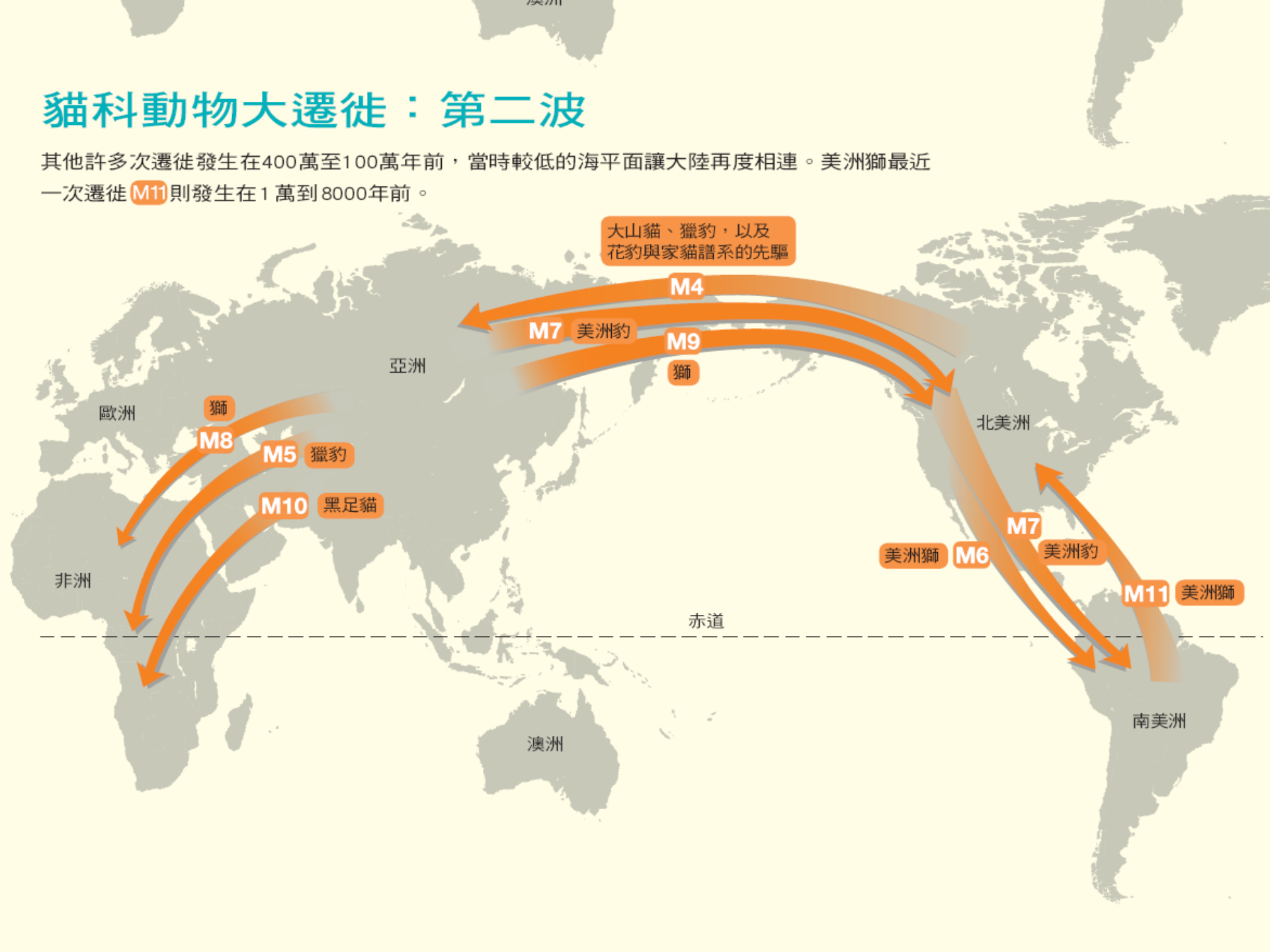


貓科動物大遷徙：第二波

其他許多次遷徙發生在400萬至100萬年前，當時較低的海平面讓大陸再度相連。美洲獅最近

貓科動物大遷徙：第二波

其他許多次遷徙發生在400萬至100萬年前，當時較低的海平面讓大陸再度相連。美洲獅最近一次遷徙M11則發生在1萬到8000年前。



這種是4800萬年前的巴基斯坦，鯨魚祖先（左、右前方各一）正在大啖海洋大餐，而後方的陸行鯨正在攻擊一隻小型陸棲哺乳類。

他們說，海洋很冷
但是海洋中有
最熱血的生物
最野性的，最熱切的。
——勞倫斯，〈鯨魚別哭！〉

【演　化】

鯨魚如何征服海洋？

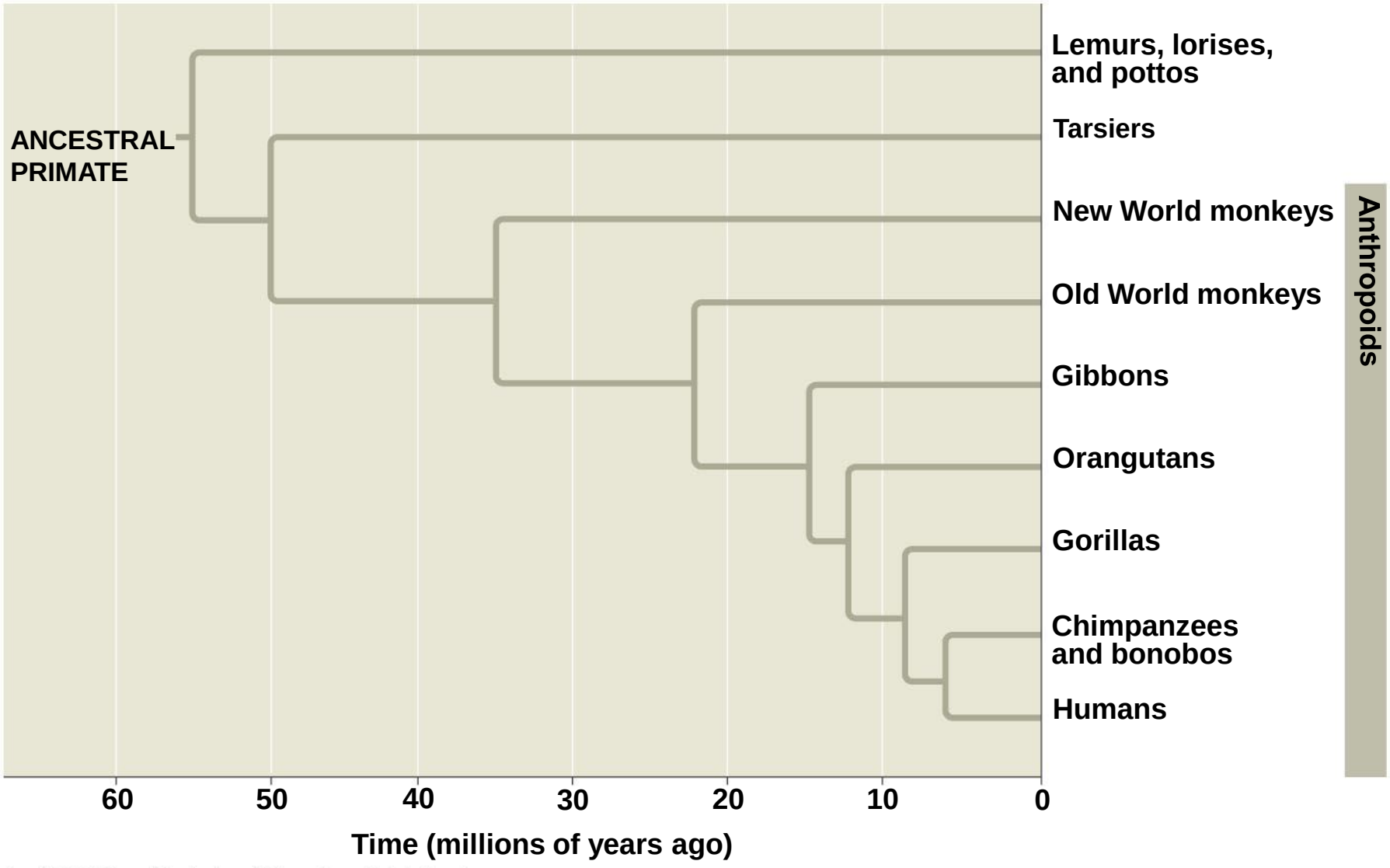
撰文／王凱特（Kate Wong）
翻譯／王道還

鯨豚是生活在大海中的哺乳動物，然而，
哺乳類的祖先都是陸棲動物。
是什麼樣的契機，什麼樣的生物適應，使鯨豚能夠
順利轉戰水域，征服海洋？
由於最近發現的新化石與DNA分析結果，
這段演化史上最驚人的形態變化過程逐漸明朗。

鯨豚演化小辭典

- 鯨目（Cetacea）是哺乳動物的一個目，包括現生的鯨魚、海豚、鼠海豚及牠們滅絕的祖先：古鯨。現生物種可大別為兩個亞目。齒鯨亞目包括抹香鯨、領航鯨、白鯨，以及所有海豚、鼠海豚。鬚鯨亞目包括藍鯨、長須鯨。“whale”這個字通常指所有鯨豚類動物。
- 中爪獸（Mesonychids）是一群原始的有蹄哺乳類，體型與狼差不多。過去許多人相信鯨豚是從中爪獸演化出來的。
- 偶蹄目（Artiodactyla）是哺乳動物的一個目，蹄的趾頭為偶數，包括駱駝、牛羊等反芻動物、河馬。現在大多數研究人員都同意，鯨豚也是偶蹄類。
- 始新世（Eocene）距今 5500~3400 萬年前。鯨豚在這期間從陸棲動物演變成海棲動物。
- 漸新世（Oligocene）距今 3400~2400 萬年前。齒鯨與鬚鯨在這期間從古鯨祖先演化出來。

Fig. 34-37



- The first monkeys evolved in the Old World (Africa and Asia)
- In the New World (South America), monkeys first appeared roughly 25 million years ago
- New World and Old World monkeys underwent separate adaptive radiations during their many millions of years of separation

(a) New World monkey

(b) Old World monkey