

A man with a grey beard and glasses, wearing a blue beanie and a red puffy jacket, is holding a large, dark, fossilized skull fragment. He is standing in a snowy, mountainous landscape under a blue sky. The background shows snow-covered hills and a rocky foreground.

## DRIVING QUESTIONS

1. How does the fossil record reveal information about evolutionary changes?
2. What features make *Tiktaalik* a transitional fossil, and what role do these types of fossil play in the fossil record?
3. What can anatomy and DNA reveal about evolution?





# A Fish with Fingers?

A transitional fossil fills a  
gap in our knowledge of  
evolution

**F**OR 5 YEARS, BIOLOGISTS NEIL SHUBIN AND TED DAESCHLER spent their summers trekking through one of the most desolate regions on Earth. They were fossil hunting on remote Ellesmere Island, in the Canadian Arctic, about 600 miles from the north pole. Even in summer, Ellesmere is a forbidding place: a windswept, frozen desert where sparse vegetation grows no more than a few inches tall, where sleet and snow fall in the middle of July, and where the sun never sets. Only a handful of wild animals survive here, but those that do make for dangerous working conditions: hungry polar bears and charging herds of muskoxen are known hazards of working in the Arctic, says Daeschler, who carried a shotgun for protection.

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Fossil hunting in the vast wilderness of Ellesmere Island in the Canadian Arctic.

When not looking over their shoulders, the researchers drilled, chiseled, and hammered their way through rocks looking for fossils. Not just any rocks and fossils, but ones dating from 375 million years ago, when animals were taking their first tentative steps on land. For three summers, they scoured the site of what was once an active streambed but found little of interest. Then, in 2004, the team made a tantalizing discovery: the snout of a curious-looking creature protruding from a slab of pink rock. Further excavation revealed the well-preserved remains of several flat-headed animals between 4 and 9 feet long. In some ways, the animals resembled giant fish—they had fins and scales. But they also had traits that resembled those of land-dwelling amphibians—notably, a neck, wrists, and fingerlike bones. The researchers named the new species *Tiktaalik roseae*; *tiktaalik* (pronounced tic-TAH-lick) is a native word meaning “large freshwater fish.” This ancient hybrid animal no longer exists, but it represents a critical phase in the evolution

of four-legged, land-dwelling **vertebrates**—including humans.

*Tiktaalik* “splits the difference between something we think of as a fish and something we think of as a limbed animal,” says Daeschler, a curator of vertebrate zoology at the Academy of Natural Sciences in Philadelphia. “In that sense, it is a wonderful transitional fossil between two major groups of vertebrates.”

Today, of course, four-legged animals roam far and wide over land. But 400 million years ago it was a different story. Life was mostly aquatic then, restricted to oceans and freshwater streams. How life made the jump from water to land is a question that has long intrigued evolutionary biologists. In fact, scientists have been searching for evidence of this milestone ever since Charles Darwin first proposed that all life on the planet is related by a tree of common descent. According to Shubin, a professor of biology at the University of Chicago and the Field Museum of Natural History, *Tiktaalik* is the most compelling example yet of an animal that lived at the cusp

#### VERTEBRATE

An animal with a bony or cartilaginous backbone.



of this important transition. Not only does it fill a gap in our knowledge, the discovery also provides persuasive evidence in support of Darwin's theory.

## Reading the Fossil Record

The theory of evolution—what Darwin called **descent with modification**—draws two main conclusions about life on Earth: that all living things are related, and that the different species we see today have emerged over time as a result of natural selection operating over millions of years. Many lines of evidence support this theory (remember that in science a “theory” is an idea supported by a tremendous amount of evidence and which has never been disproved; see Chapter 1). One of the most compelling lines of evidence for evolution comes from **fossils**, the preserved remains or impressions of once-living organisms. Fossils are like snapshots of past life, capturing what life was like at particular moments in time.

Fossils are formed in a number of ways: an animal or plant may be frozen in ice, trapped in amber (hardened tree sap), or buried in a thick layer of mud. The entombed organism is thereby protected from being eaten by scavengers or rapidly decomposed by bacteria. Over time, if conditions are right—for example, if the mud encasing the specimen remains undisturbed long enough for hardening to occur—the organism's shape is preserved. Not all organisms are equally likely to form fossils, however: animals with bones or shells are more likely to be preserved than animals without such hard parts (think earthworms or jellyfish) that decay quickly. And conditions permitting fossilization are rare: the organism has to be in just the right place at just the right time (INFOGRAPHIC 15.1).

Because not all organisms are preserved, the **fossil record** is not a complete record of past life. Nevertheless, the existing fossil record is remarkably rich and offers a revealing window into the past. **Paleontologists**, scientists who study ancient life, have uncovered hundreds of thousands of fossils throughout the world, from many evolutionary time periods. When fossils are arranged in order of age, they provide a tangible history of life on Earth. The fossil record also allows biologists to test certain tenets of Darwin's theory.

For example, if all organisms have descended from a single common ancestor that lived billions of years ago, as the theory of evolution concludes they did, then we would expect the fossil record to show an ordered succession of evolutionary stages as organisms evolved and diversified. And, indeed, that is exactly what we see: prokaryotes appear before eukaryotes, single-celled organisms before multicellular ones, water-dwelling organisms before land-dwelling ones, fish before amphibians, reptiles before birds, and so on.

Moreover, we would expect to see changes over time within a family of organisms, and we do. One exceptionally well studied example is horses. Comparisons of modern-day horse bones with fossils of horse ancestors

### DESCENT WITH MODIFICATION

Darwin's term for evolution, combining the ideas that all living things are related and that organisms have changed over time.

### FOSSILS

The preserved remains or impressions of once-living organisms.

### FOSSIL RECORD

An assemblage of fossils arranged in order of age, providing evidence of changes in species over time.

### PALEONTOLOGIST

A scientist who studies ancient life by examining the fossil record.

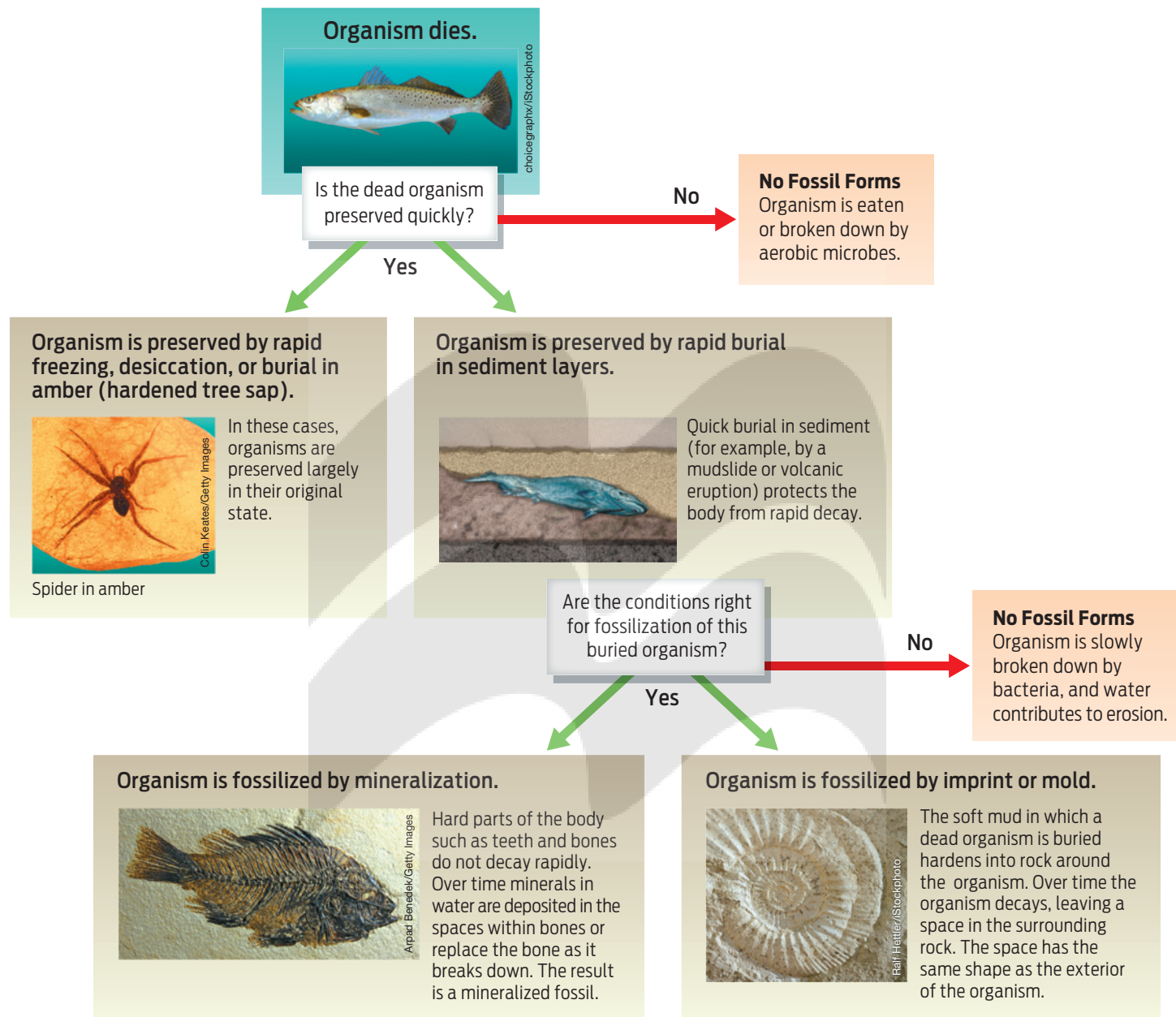


Ted Daeschler/Academy of Natural Sciences/VIREO

A *Tiktaalik roseae* fossil.

## INFOGRAPHIC 15.1 Fossils Form Only in Certain Circumstances

➔ Not every organism that dies forms a fossil. Organisms are more likely to fossilize if they have bony skeletons or hard shells. In addition, the organism must be preserved quickly and kept undisturbed while mineralization or mud hardening occurs. Therefore, the fossil record is not a complete record of past life, but it has supplied an impressive body of evidence for evolution.



### ? Why are flies in amber more common than fossilized flies?

reveal how, in the course of evolution, horses have lost most of their toes. The fossils show a series of changes in bone structure over time, with the most recent fossils being the most similar to modern organisms, and the more ancient fossils being the most different.

There are several branches and lineages of horse ancestors, including many that died out, but the fossils all clearly share a family resemblance (INFOGRAPHIC 15.2).

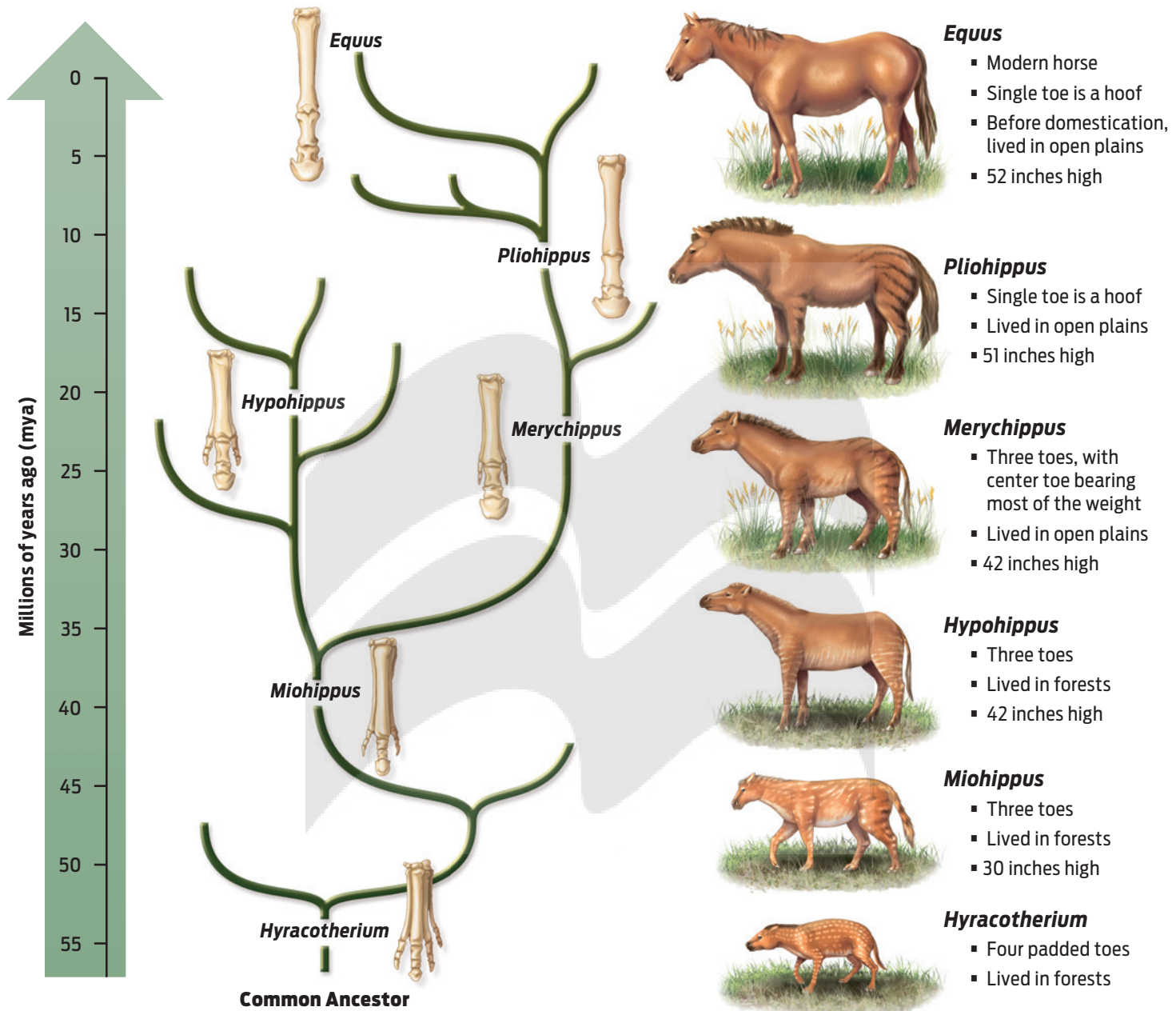
Descent with modification also predicts that the fossil record should contain evidence



## INFOGRAPHIC 15.2 Fossils Reveal Changes in Species over Time



The fossil record of horses supports the theory of descent with modification. Forelimb fossils are similar to one another, but show changes over time from the earliest horse ancestors to modern-day horses as species diverged from a common ancestor. In the fossil record we can observe over time a reduction in toe number, as the central toe became dominant, allowing horses to move more rapidly in new prairielike environments.



What changes can be observed between three-toed *Miohippus* and three-toed *Merychippus*?

of intermediate organisms—those with a mixture of “old” and “new” traits. Darwin acknowledged in *The Origin of Species* that the fossil record of his day did not provide many examples of such intermediate organisms—a state of affairs he described as “probably the gravest

and most obvious of all the many objections which may be urged against my views.” Yet Darwin knew that if his hypothesis were correct, then intermediate fossils would eventually be found. And indeed many have been. Scientists have discovered animals with mixtures

of reptile and bird characteristics and animals with mixtures of reptile and mammal characteristics. But the transition between fish and amphibians has so far remained more obscure.

## The Fossil Hunt

Shubin and Daeschler began their hunt for fossils in the Canadian Arctic in 1999 after stumbling upon a map in an old geology textbook. The map showed that the region contained large swaths of exposed rock dating back 375–380 million years—just the period of time the researchers were interested in.

Why was this period so important to Shubin and Daeschler? They knew that there are no land-dwelling vertebrates in the fossil record before 385 million years ago. By 365 million years ago, organisms easily recognizable as amphibians are well documented in the fossil record. The scientists hypothesized that if they looked at rocks sandwiched in between these two time periods—those around 375 million years old—they might find one of Darwin’s elusive “intermediates.” Moreover,

### RADIOMETRIC DATING

The use of radioactive isotopes as a measure for determining the age of a rock or fossil.



Ellesmere Island, nearly as large as Great Britain, contains Canada’s most northern point.

Ellesmere Island is one of only three places on Earth where rocks of this time period are exposed. To Shubin and Daeschler’s knowledge, no other paleontologists had explored the area, which meant it was a potential fossil gold mine.

Knowing exactly where to look for fossils was tricky, since Ellesmere Island covers 75,000 square miles. To locate the most promising dig site, the scientists first studied aerial photographs. Once on the ground, the scientists and their team split up and spent the first two seasons just walking the rocky exposures, prospecting for bits and pieces of fossils that had eroded out from the rock. When they found something interesting on the surface, they would start to dig.

It was while walking these rocky exposures in 2002 that Daeschler and his team found the first piece of what would turn out to be a *Tiktaalik* fossil—“basically part of the snout,” he says. At first, they didn’t think much of the find, but collected it anyway along with other fossil pieces. Back in Philadelphia, researchers cleaned the fossil, removing the remaining rock. Even then, Daeschler says, it wasn’t clear what the snout belonged to. Not until a visiting graduate student remarked on the resemblance of the skull to one from the earliest known amphibians did the researchers realize what they had found. If ever there was a “lightbulb” moment, he says, this was it. But, alas, they had only one small piece of the creature.

The team returned to Ellesmere in 2004 for another round of hunting and digging. It didn’t take long for their patience to be rewarded: “Literally inches,” Daeschler says, from where they’d been excavating before, they hit pay dirt.

The fossils they found looked like the elusive intermediate creature the team had been hunting for. But how could they be sure it was the right age? Logically, fossils are at least as old as the rocks that encase them, so if you know the age of the rocks, then you know the age of the fossils, too. Some types of rocks can be dated directly by **radiometric dating**, in which the proportion of certain radioactive isotopes in rock



crystals serves as a geologic clock (isotopes and radiometric dating are described further in Chapter 16). Fossils found in or near these layers can be dated quite precisely. If fossils are found in rock layers that cannot be directly dated by radiometric dating, they can be dated indirectly by their position with respect to rocks or fossils of known age that

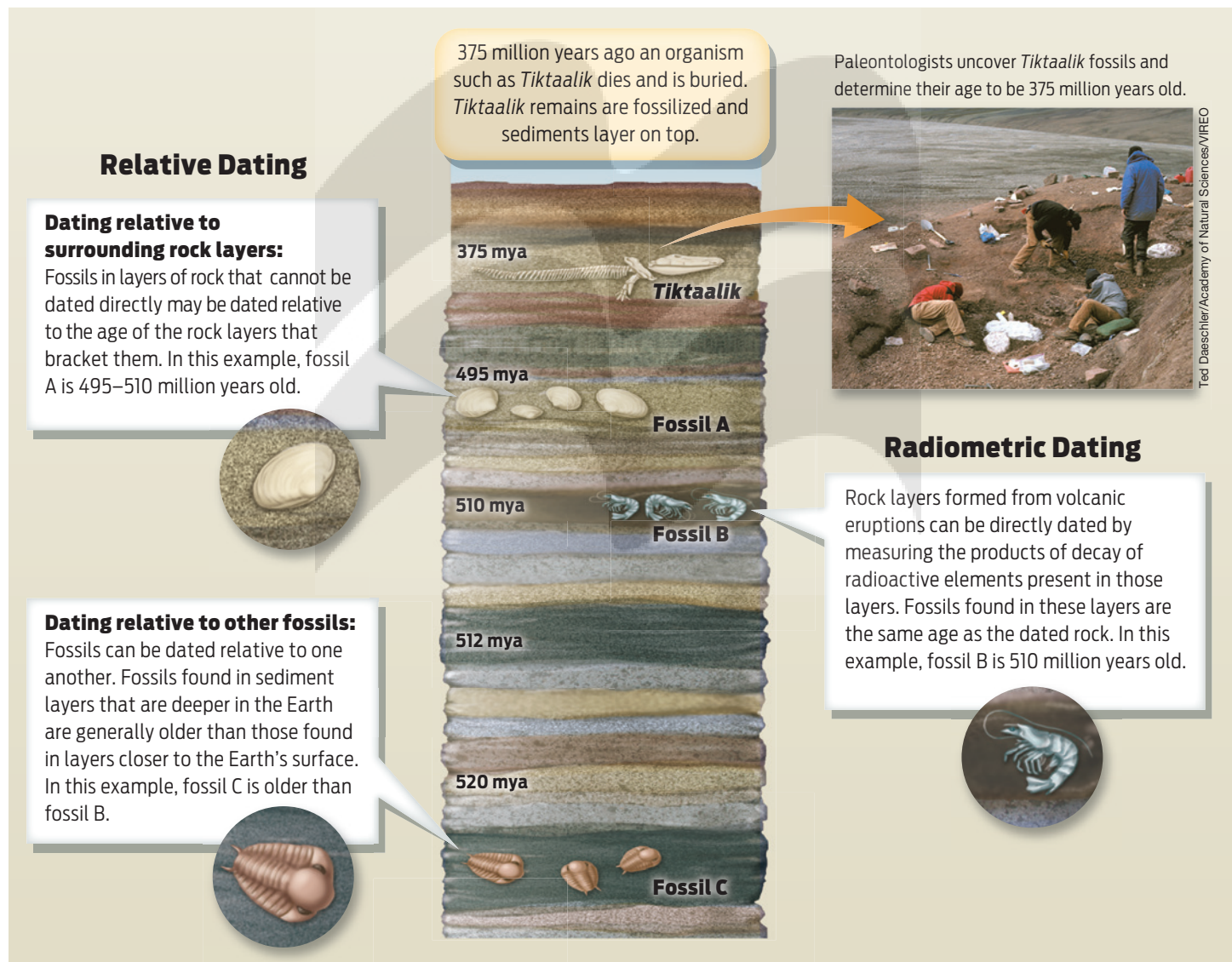
are either deeper or shallower, a technique called **relative dating**. Generally speaking, the deeper the fossils, the older they are. Using a combination of both methods, scientists have determined that the rocks where *Tiktaalik* was found are 375 million years old, which means *Tiktaalik* is that old as well (**INFOGRAPHIC 15.3**).

### RELATIVE DATING

Determining the age of a fossil from its position relative to layers of rock or fossils of known age.

## INFOGRAPHIC 15.3 How Fossils Are Dated

➔ When an organism dies and is preserved, its remains may in time become fossilized and buried under layers of sediment, which accumulate on top of even older layers of sediment. When a fossilized organism is uncovered, its age can be determined by two main forms of dating: radiometric and relative.



? What is the approximate age of a fossil found in the blue-gray layer immediately below fossil B?



## Setting the Stage for Life on Land

The geologic time period that Shubin and Daeschler are interested in is known as the Devonian—roughly 400–350 million years ago. Great transformations were occurring during the Devonian: jawed fishes, sharks, land plants, and insects all diversified in this period. Because sea levels were high worldwide, and much of the land lay under water, the Devonian Period has been called the Age of Fishes.

Back then, what is now the Canadian Arctic had a warm, wet climate and a landscape veined by shallow, meandering streams. Early in the Devonian Period there was little plant growth, and the world would have looked fairly brown and empty. By the middle of the Devonian, says Daeschler, if you were standing on the bank of a stream you would have seen some of the first land plants, the first forests, as well as the first **invertebrates**—spiderlike creatures and millipedes, for example—crawling on land. Still, there would have been no land-dwelling vertebrates at this time: nothing with bony limbs, nothing with a backbone or skull.

By the late Devonian, things were changing quickly. By then, says Daeschler, “you had a green floodplain, a green world.” It was this green world—a rich and productive ecosystem, with energy-rich leaf litter flowing into shallow streams—that set the stage for the move of vertebrates onto land.

The physical challenges of living on land are very different from those in water. Water provides buoyancy to aquatic animals, supporting their bodies and helping to keep them afloat. By contrast, animals that walk

on land have to cope with gravity. Air doesn’t support land animals, so their bodies need a sturdier structure. Animals on land can also dry out, which is dangerous for them because cells need water to function. And, of course, taking in oxygen is different on land and in water.

Of the many features that distinguish land animals from fish, biologists have singled out one as a key evolutionary milestone: limbs. Fish do not have limbs, in the sense of jointed, bony appendages with fingers and toes. Instead, they have webbed fins. In most fishes, the fin bones are thin and fan out away from each other. These so-called ray-finned fishes include the modern-day perch, trout, and bass. By contrast, amphibians, birds, most reptiles, and mammals all have two pairs of limbs, defining them as **tetrapods** (from the Greek for “four-footed”).

While having limbs is a key feature distinguishing tetrapods from fish, one small group of fish—the lobe-finned fish—seems to blur this distinction. First appearing in the fossil record about 400 million years ago,

lobe-finned fish have fleshy fins supported by a stalk of bones that resemble primitive limb bones.

Lobe-finned fish are thought to have evolved in shallow streams, where rich plant material lured small fish and other creatures close to the water’s edge. The lobe-finned fish likely used their sturdy fins to touch the bottom of the streambed while maneuvering to catch prey. As Daeschler explains, it was the unique ecological opportunity afforded by shallow streams that enabled ancient fish to start evolving features, like lobed fins, that were adaptive in shallow water. Through natural selection, these traits would have become more common in the fish population. But

“It looks like a fish in that it has scales and fins, but when you look inside the skeleton you see how special it really is.”

—Neil Shubin

### INVERTEBRATE

An animal without a backbone.

### TETRAPOD

A vertebrate animal with four true limbs, that is, jointed, bony appendages with digits. Mammals, amphibians, birds, and reptiles are tetrapods.

A Comparison of Different Fins

*Tiktaalik*'s forelimbs were technically fins. However, they more closely resembled lobe fins than ray fins.

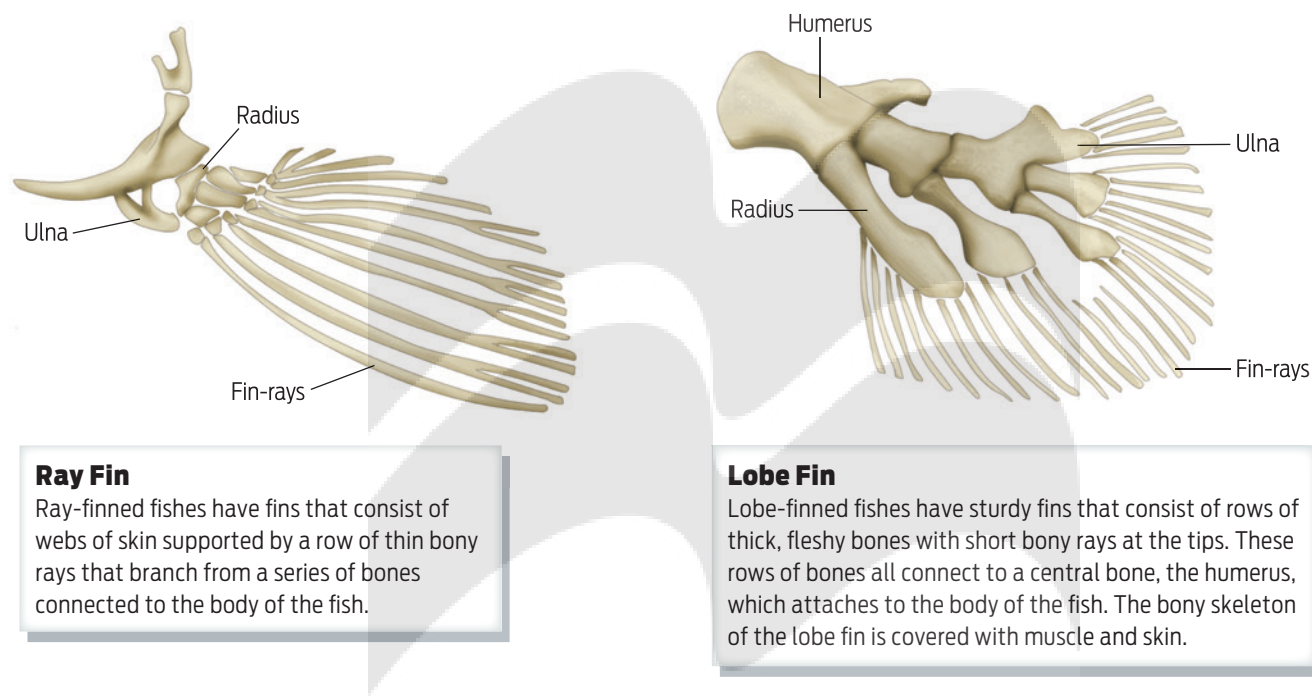


Kallop Monoyios; Neil Shubin Lab

Tiktaalik Forelimb

*Tiktaalik* forelimbs had thick, weight-bearing bones covered in muscle and skin. The bones included a series of flexible wrist bones and digits ending in a small number of bony rays.

A physical model of *Tiktaalik*'s forelimb fin, made from replicas of fossil bones fused with flexible wire.



Ray Fin

Ray-finned fishes have fins that consist of webs of skin supported by a row of thin bony rays that branch from a series of bones connected to the body of the fish.

Lobe Fin

Lobe-finned fishes have sturdy fins that consist of rows of thick, fleshy bones with short bony rays at the tips. These rows of bones all connect to a central bone, the humerus, which attaches to the body of the fish. The bony skeleton of the lobe fin is covered with muscle and skin.

lobe-finned fish were still very far from being true tetrapods. *Tiktaalik* is a step closer: “It looks like a fish in that it has scales and fins,” Shubin told reporters in 2006 after the discovery, “but when you look inside the skeleton you see how special it really is.”

The Fish That Did Push-Ups

Shubin and Daeschler were lucky: the fossils they found were so well preserved that they were able to study *Tiktaalik*'s skeletal anatomy in detail, even seeing how the bones

interacted and where muscles attached. From these fossil bones, they determined that *Tiktaalik* was a predatory fish with sharp teeth, scales, and fins. In addition to these fishy attributes, it had a flat skull reminiscent of a crocodile head, as well as a flexible neck. To Shubin and Daeschler, the neck was one of the most surprising finds. Having a flexible neck meant that, unlike a fish, *Tiktaalik* could swivel its head independently of its body. This feature may have enabled it to catch a glimpse of predators sneaking up on it from behind, or to snap its jaws sideways like a crocodile. *Tiktaalik* also had the full-fledged



ribs of a modern land animal, sturdy enough to support the animal's trunk out of water even against the force of gravity.

But it is *Tiktaalik*'s fins that have justly made it famous. While possessing many features of a lobe-finned fish, including a sturdy stalk of limblike bones, *Tiktaalik* appears also to have had a jointed elbow, wrist, and fingerlike bones. From the fossil pieces, Shubin and Daeschler were able to create a model of how the bones would have moved relative to one another, and they have visualized these movements on screen. The model shows that the bones and joints were strong enough to support the body and worked like those of the earliest known tetrapods—the early amphibians. “This animal was able to hold its fin below its body, bend the fin out toward what we think of as a wrist, and bend the elbow,” explains Daeschler. In other words, it was a fish that could do a push-up.

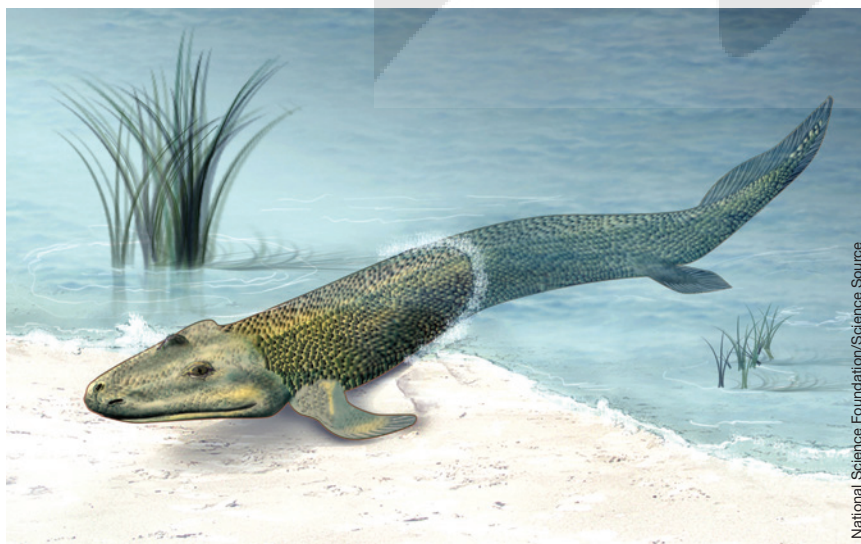
With this hybrid anatomy, *Tiktaalik* was not galloping on land, of course. It probably lived most of the time in water, but Shubin and Daeschler suspect that *Tiktaalik* may have used its supportive fins to pull itself out of the water for brief periods. “This is a fish that can live in the shallows and even make short excursions onto land,” Shubin said. The ability to crawl onto land would certainly

have been a useful trait in the Devonian, when open water was a brutal fish-eat-fish world, whereas land was a predator-free paradise, full of nourishing bugs.

Like other fish living at the time, *Tiktaalik* is thought to have had both lungs and gills, which explains how it could breathe out of water for these short excursions. People sometimes assume that lungs were a late evolutionary adaptation, and that they came from modified gills, which modern-day fish use to breathe in water. But in fact, lungs—air-filled organs used for respiration—evolved very early in evolutionary history, more than 375 million years ago. They existed in ancient fish. We know this because fish fossils containing lung cavities and calcified bones surrounding them have been discovered in former mudbanks. Most modern fish have retained their gills but lost their lungs over time (the lungs have evolved into a balloonlike structure called a swim bladder, which helps fish float). Some modern fish known as lungfish, however, have retained this ancestral trait. Lungfish are lobe-finned fish closely related to the lobe-finned fish from which *Tiktaalik* is believed to have descended.

There was, of course, no forethought involved in the process of limb evolution or the emergence of other suitable land traits. Fish did not develop limbs for the purpose of walking on land. Rather, limbs first evolved in shallow water, where they proved adaptive and were thus retained in the descendants of the organisms who first developed them. Then, when there was an opportunity to take advantage of a tantalizing new habitat—land—the amphibious creatures already had the skeletal “toolkit.”

For all its amphibian-like adaptations, *Tiktaalik* is still considered a fish because its limbs lack the true jointed fingers and toes that characterize tetrapod limbs (in other words, they're still fins). But it's by far the most tetrapod-like of all the ancient fishes discovered to date. Scientists have jokingly referred to it as a “fishapod” (INFOGRAPHIC 15.4).



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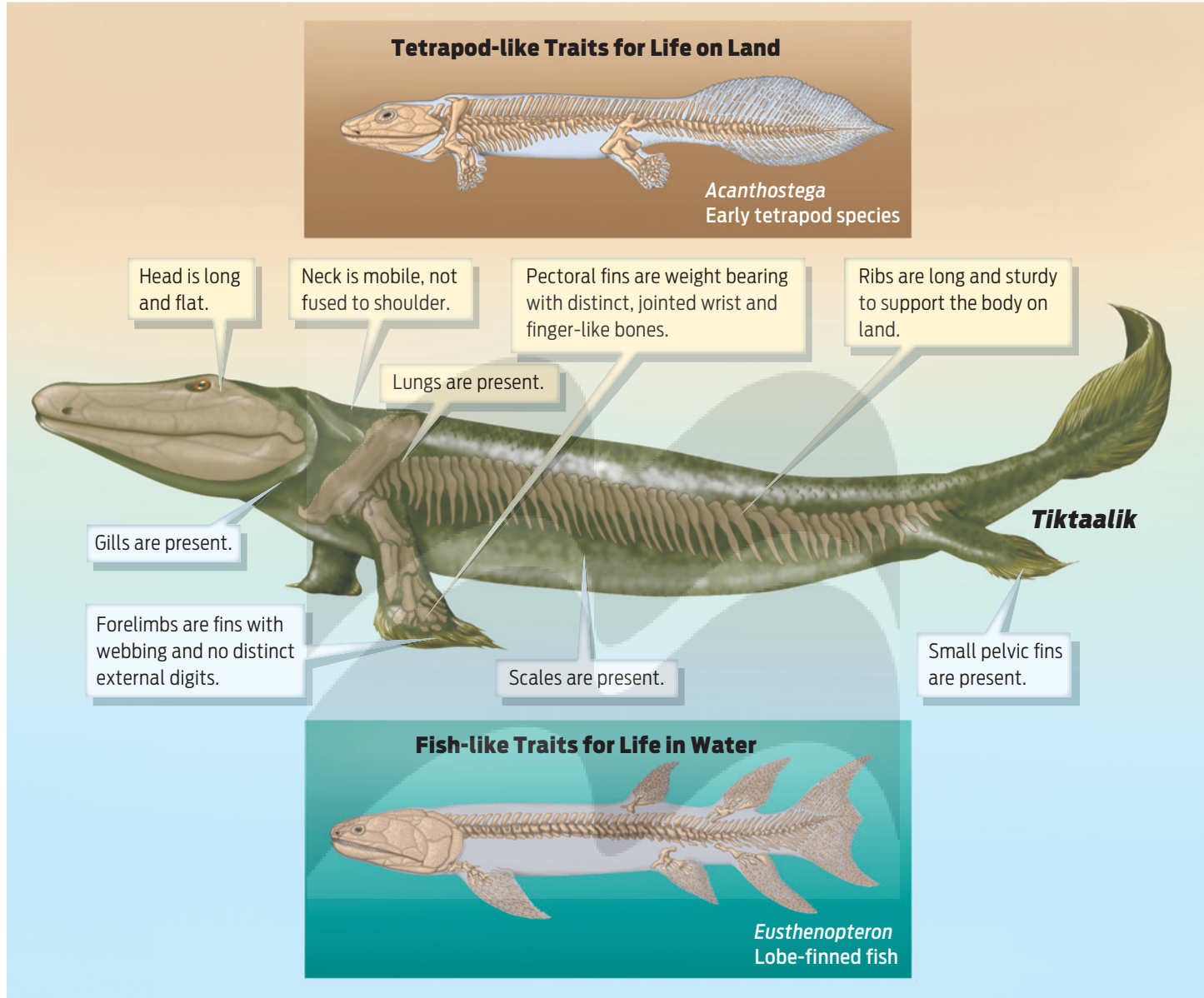
***Tiktaalik* likely used its sturdy forelimb fins to pull itself out of the water for short excursions on land.**

# INFOGRAPHIC 15.4 *Tiktaalik*, an Intermediate Fossilized Organism

15

EVIDENCE FOR EVOLUTION

➔ *Tiktaalik* possesses adaptations of both fish and tetrapods. The fish-like traits would have been useful when in water, while the tetrapod-like traits would have been useful when *Tiktaalik* ventured onto land. For all its amphibian-like characteristics, *Tiktaalik* is still technically a fish because its limbs lack true jointed fingers and toes, a defining feature of tetrapods.



? Why would weight-bearing forelimbs be an advantage for *Tiktaalik*?

And that's what makes *Tiktaalik* such an important find: it occupies a midpoint between fish and tetrapods. "It very much fits in that gray area between things we typically call fish and things we typically call limbed animals," says Daeschler. Such intermediate,

or transitional, fossils document important steps in the evolution of life on Earth. They help biologists understand how groups of organisms evolved, through natural selection, from one form into another. And they confirm that Darwin's theory of descent with

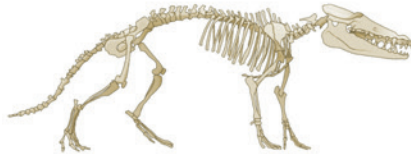


## Another Evolutionary Transition: Land-dwelling mammals to ocean-dwelling whales

Ancestors of whales were terrestrial mammals. A very early whale, *Pakicetus*, was also terrestrial. Transitional fossils illustrate adaptations for an increasingly aquatic existence, including specializations of the ear and neck and almost complete loss of the hindlimbs.

### *Pakicetus* (52 million years ago)

- 1.8 meters long
- Spent time on land and in water
- Had hindlimbs



### *Rodhocetus* (46 million years ago)

- 3 meters long
- Spent time on land and in water
- Had hindlimbs



### *Dorudon* (40 million years ago)

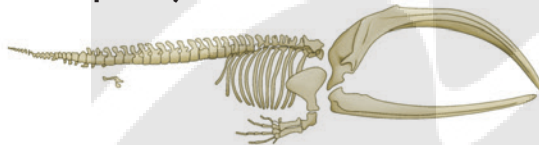
- 6 meters long
- Lived only in water
- Had reduced hindlimbs



### Bowhead Whale

#### *Balaena mysticetus* (modern species)

- 15–18 meters long
- Lives only in water
- Has vestigial hindlimbs



modification—which predicts such intermediate forms—is correct.

Another famous transitional fossil is *Pakicetus*, an early whale. Unlike tetrapods, which evolved first in water and then spread to land, some land-dwelling creatures eventually made their way back to the sea, adapting to an aquatic life once more. That group includes cetaceans—whales, porpoises, and dolphins. The ancestor of cetaceans was a wolf-size land-dwelling mammal that lived 50 million years ago. Although this animal, *Pakicetus*, had the body of a land animal, including four legs and paws, its head had the long skull shape reminiscent of a whale's. Fossils dating from the period since the time that *Pakicetus* lived show how whales

became increasingly adapted to an aquatic existence.

## A Fin Is a Paw Is an Arm Is a Wing

In *The Origin of Species*, Darwin asked, “What can be more curious than that the hand of a man, formed for grasping, that of a mole for digging, the leg of the horse, the paddle of the porpoise, and the wing of the bat, should all be constructed on the same pattern, and should include similar bones, in the same relative positions?” To Darwin, this uncanny similarity was evidence that all these organisms were related—that they share a common ancestor in the ancient past.

The fact that all tetrapods share the same forelimb bones, arranged in the same order, is an example of **homology**—a similarity due to common ancestry. Before Darwin, comparative anatomists had identified many such similarities in anatomy; what they lacked was a satisfactory explanation for why such similarity should exist. Darwin provided that explanation: homologous structures are ones that are similar because they are inherited from

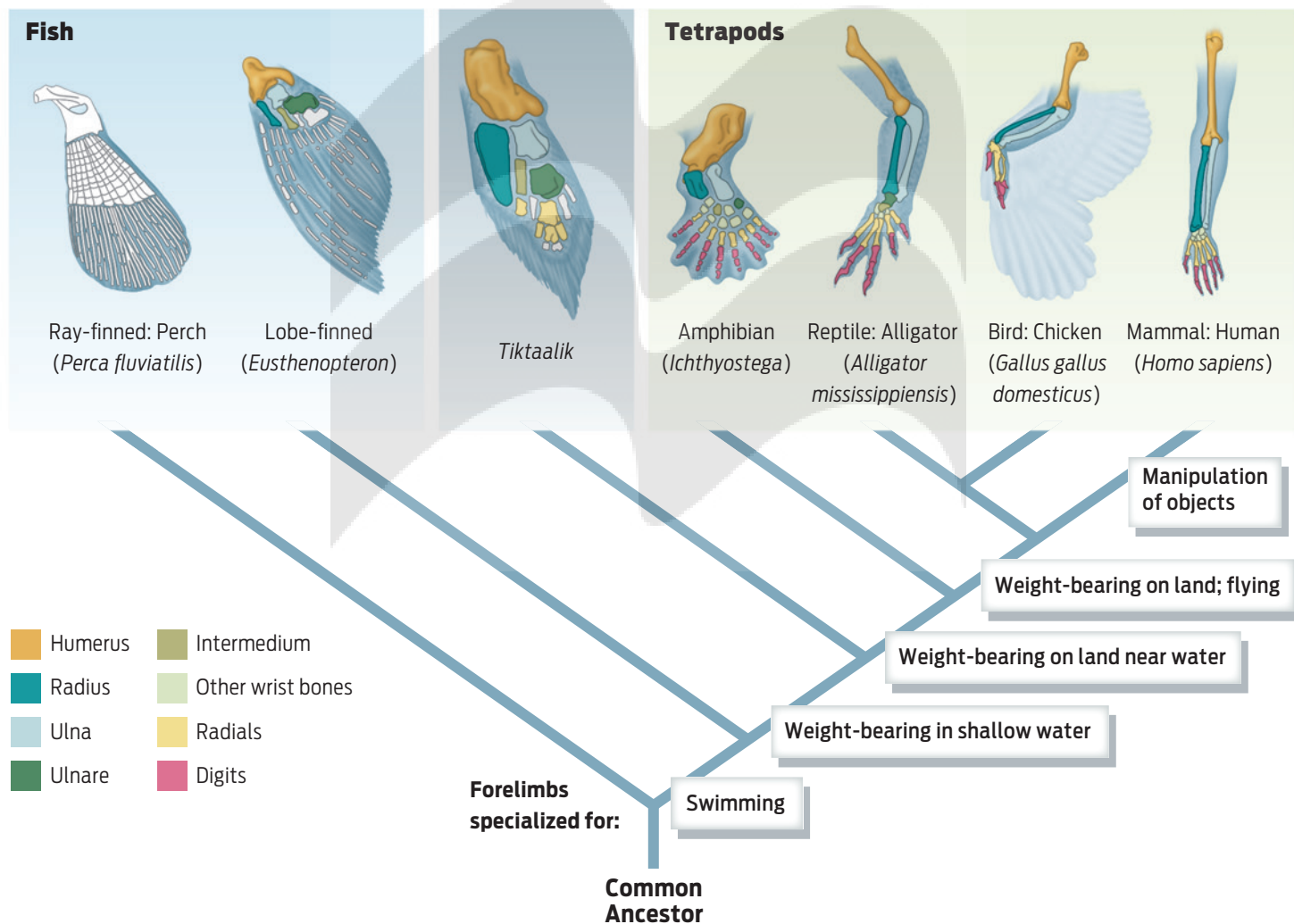
the same ancestor—in this case, an amphibious creature like *Tiktaalik*. Why is this significant? Think of it this way: every time you bend your wrist back and forth—to swipe a paint brush or hold a cell phone to your ear, for example—you are using structures that first evolved 375 million years ago in fish. As Shubin points out, “This is not just some archaic, weird branch of evolution; this is *our* branch of evolution” (INFOGRAPHIC 15.5).

**HOMOLOGY**

Anatomical, genetic, or developmental similarity among organisms due to common ancestry.

## INFOGRAPHIC 15.5 Forelimb Homology in Fish and Tetrapods

➔ The number, order, and underlying structure of the forelimb bones are similar in all the groups illustrated below. The differences in the relative width, length, and strength of each bone contribute to the specialized function of each forelimb. This anatomical shape and function reflect evolutionary adaptations to different environments.



? Which bone is closest to the body in all the weight-bearing forelimbs?



**VESTIGIAL  
STRUCTURE**

A structure inherited from an ancestor that no longer serves a clear function in the organism that possesses it.

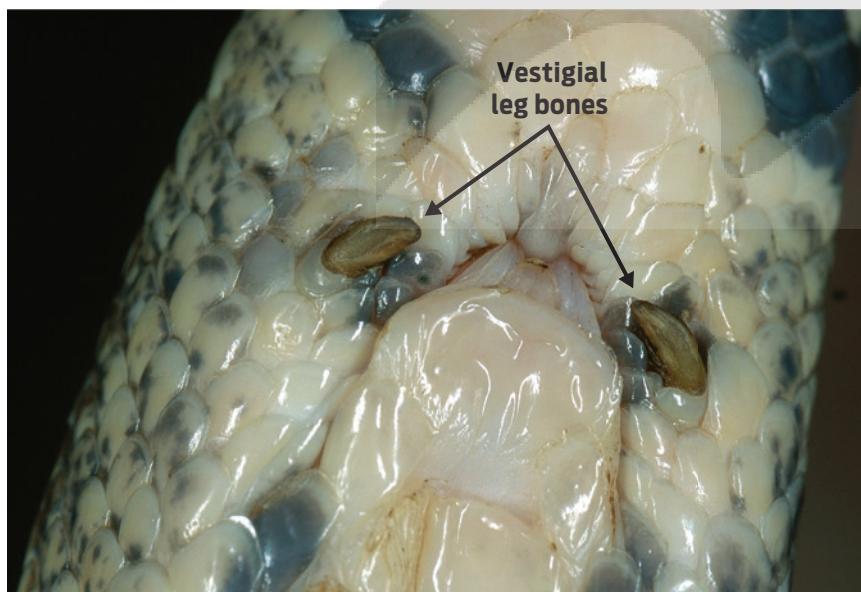
If they have the same bones, why then do a human arm and a bird wing look so different? Remember that during the process of cell division, mutations are continually being introduced into the DNA of genes, and that when these mutations occur in sperm or egg cells, they are inherited. Such mutations can produce subtle changes in the proteins encoded by those genes—proteins involved in constructing the bones that make up an arm or a wing, for example. Changes in bone proteins can result in slightly altered bones, for instance making them longer or thinner. When these modified bones are helpful to an organism’s survival and reproduction, the advantageous traits are passed on to the next generation, and populations emerge that have these adaptations. This “descent with modification” (Darwin’s phrase again) results in diverse organisms sharing common—homologous—structures and putting them to different uses.

We can see homology not only in adult anatomy, but in early development as well. Take a look at early embryos of vertebrate animals as diverse as humans, fish, and

chickens and you’ll see that they all look remarkably similar. Why should the embryonic stage of a human resemble the embryonic stage of a fish when the adults of each species look so different? Similar embryological structures are further evidence that all vertebrates have a common ancestor (**INFOGRAPHIC 15.6**).

Development helps us solve other evolutionary conundrums as well, such as why reptiles like snakes don’t have limbs like other tetrapods. In fact, snake embryos *do* possess the beginnings of limbs, but these limb buds remain rudimentary and do not develop into full-fledged limbs (although you can still see stubby hindlimbs in some species of snake today). Such **vestigial structures**, which serve no apparent function in a modern organism, are strong evidence for evolution: these now apparently useless features are inherited from an ancestor in whom they *did* serve a function. Other examples of vestigial structures include the human tailbone and the phenomenon of “goose pimples” (technically called erector pili), which in fur-covered animals help to puff fur up to better maintain heat.

Zooming in even further, to the molecular level, we find still more examples of homology—and thus more evidence of common ancestry. Scientists have known since the 1950s that DNA is the molecule of heredity, and that it is shared by all living organisms on Earth. Every molecule of DNA—whether from fish, maple tree, bacterium, or human—is made of the same four nucleotides (A, C, T, and G), and all organisms use the information encoded by those nucleotides to make proteins in the same basic way, using the universal genetic code (see Chapter 8). Why should all living things use the same system of decoding genetic information? The best explanation is that this system was the one used by the ancient ancestor of all living organisms, passed on to all of its descendants, and preserved throughout billions of years of evolution.



Some snakes have remnants of pelvis and leg bones left over from their four-legged ancestors.

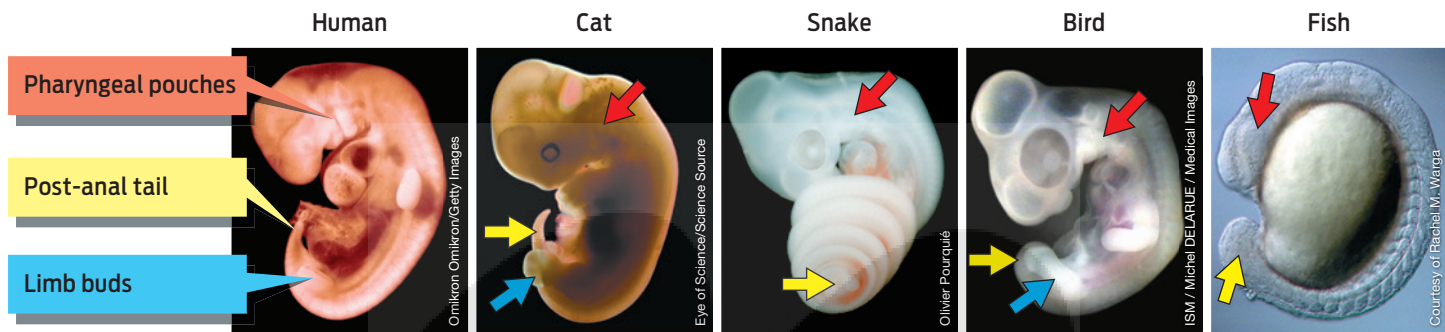
Simon D. Pollard/Science Source

## INFOGRAPHIC 15.6 Vertebrate Animals Share a Similar Pattern of Early Development

➔ We can identify homologous structures by tracing their embryological development. Some of our middle ear bones, for example, are homologous with the jaw bones of reptiles and bones supporting gills in fish. We know this because all of these structures develop from the pharyngeal pouches that appear in all vertebrate embryos early in development. Similarly, all vertebrates have a post-anal tail (the extension of the spinal cord past the anus) during development. These developmental homologies are strong evidence that all vertebrate animals are related by common ancestry. Genetic changes over time have introduced modifications in later stages that give rise to distinct species with vast physical differences.

### Early Embryos

Early-stage embryos of related organisms share common structures.



### Adult Organisms

Later in development, these structures take on species-specific shape and function.



? Of the organisms shown, which have a post-anal tail as adults?

## DNA and Descent

While all living organisms share DNA and the genetic code, no two species share the exact same sequence of DNA nucleotides. That's because (as described in Chapter 10) errors in DNA replication and other mutations are continually introducing variation into DNA sequences (and the proteins they encode). Over time, neutral and advantageous

mutations will tend to be preserved, while harmful mutations will tend to be selected against and eliminated. In addition, much of our DNA consists of long stretches of non-coding sequences with no known function. Because mutations in these regions have no effect on an organism, they accumulate over time. As mutations are passed on to descendants, the number of sequence differences between the ancestor and its descendants



grows—slowly in the case of sequences coding for critical proteins whose structures are well adapted to their functions, and more rapidly in the case of noncoding DNA, which is not involved in making proteins. Closely related species will therefore have more similar DNA sequences than species that are more distantly related.

For example, when scientists looked at one specific region of DNA—the cystic fibrosis transmembrane regulator (or *CFTR*) region—they discovered that human DNA in this region is 99% identical to chimpanzee DNA. The fact that the DNA of these two species is nearly identical reflects the fact that humans and chimps share a common ancestor that lived relatively recently—just 5–7 million years ago. By contrast, human DNA is 85% identical to the DNA of a mouse at this same region, which makes sense given that humans and mice share a common ancestor that lived between 60 and 100 million years ago. Less sequence identity would be seen between a human and a toad, whose common ancestor—a lobed-finned fish—lived roughly 375 million years ago. The more distantly related two species are, the more sequence differences in DNA sequences, and the less homology, you will see. DNA serves as a kind of molecular clock: each additional sequence difference is like a tick of the clock, showing the amount of time that has elapsed since the two species shared a common ancestor (**INFOGRAPHIC 15.7**).

When combined with evidence from the fossil record, anatomy, development (and biogeography, a fourth line of evidence, discussed in Chapter 16), molecular data become a powerful tool for understanding evolution. As we'll see in

Chapter 16, DNA evidence is often a more reliable clue to common ancestry than is physical appearance, and can serve as a check on conclusions derived from the fossil record or anatomy. As well, DNA is deepening our knowledge of how limbs are constructed at the molecular level. Scientists working in Shubin's lab have shown that the same genes orchestrate limb development in animals as diverse as chickens, mice, and humans. In 2016, they discovered that these same genes also coordinate fin development in fish—though

with a different end result (fins rather than limbs). Learning how these genes work and how changes in their DNA sequences can produce large-scale changes in body plan or limb structure is a hot area of biology right now, informally known as “evo-devo” (short for “evolutionary developmental biology”).

*Tiktaalik* “splits the difference between something we think of as a fish and something we think of as a limbed animal.”

—Ted Daeschler

## Filling in the Gaps

Asked what he thinks is most interesting about the discovery of *Tiktaalik*, Daeschler homes in on what he says is a popular misconception about the fossil record—that it's “spotty” and “chaotic.” But that's simply not true, he says. Despite the fact that it does not record *all* past life, the fossil record is still “very good”—so good, in fact, that you can use it to make and test predictions. You can, for example, look at the fossil record of fish and tetrapods and—suspecting on the basis of anatomy that the two groups are related—hypothesize that an intermediate-looking animal must have existed at some point. Then you can go look for it. Daeschler refers to this process as “filling in the gaps,” and it's exactly what he and Shubin did with *Tiktaalik*. They knew, from the existing fossil

# INFOGRAPHIC 15.7 Related Organisms Share DNA Sequences

15

EVIDENCE FOR EVOLUTION

➔ Related organisms share DNA sequences inherited from a common ancestor. Over time, the sequence in each species acquires independent mutations. The more time that has passed, the greater the number of sequence differences that will be present. Thus, the percentage of nucleotides that differ between two species gives an indication of the evolutionary distance between them.

## Sequence homology between species

Species A	GGTATCGAGGTTCTACATTGCAACTTCTAC
Close relative	GGAAACGAGGTTCTACATTGCCACTTCTAC
Distant relative	GGAAACGAGGTTTCACATAGCCACTTCTAC

3 differences in 30 nucleotides  
 $3/30 = 10\%$ ; or 90% similarity

5 differences in 30 nucleotides  
 $5/30 = 17\%$ ; or 83% similarity

## Similarity to human DNA sequences for the CFTR region



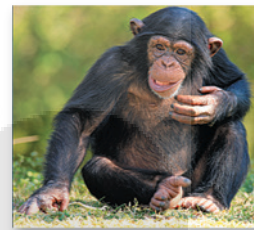
Steven Hunt/Getty Images

Pufferfish  
65% similarity



Tier und Naturfotografie / Superstock

Mouse  
85% similarity



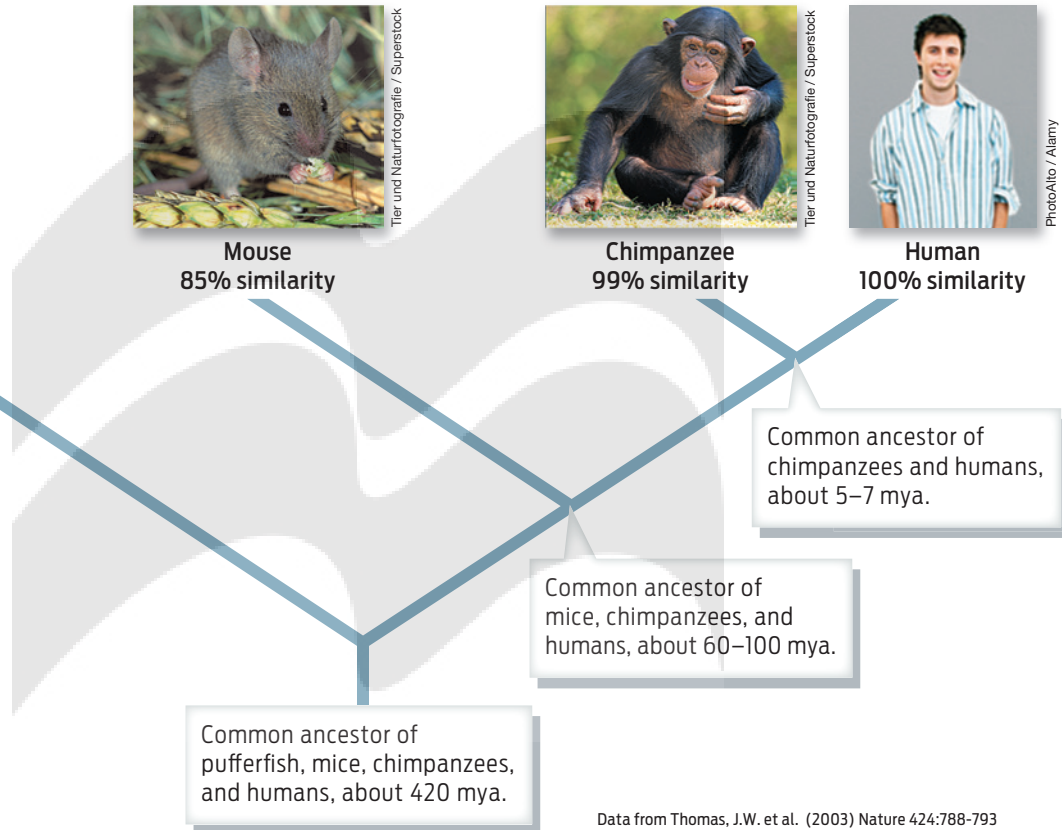
Tier und Naturfotografie / Superstock

Chimpanzee  
99% similarity



PhotoAlto / Alamy

Human  
100% similarity



Data from Thomas, J.W. et al. (2003) Nature 424:788-793

? What is the percent similarity between the close relative and the distant relative shown in the top panel?

record, when such a creature was likely to have existed, so then it was just a question of where to look for it.

For Shubin and Daeschler, *Tiktaalik* is exciting because it shows that our understanding

of evolution is correct: “It confirms that we have a very good understanding of the framework of the history of life,” says Daeschler. “We predicted something like *Tiktaalik*, and sure enough, with a little time and effort, we found it.” ■



# CHAPTER 15 SUMMARY

- The theory of evolution—what Darwin called “descent with modification”—draws two main conclusions about life: that all living things are related, sharing a common ancestor in the distant past; and that the species we see today are the result of natural selection operating over millions of years.
- The theory of evolution is supported by a wealth of evidence, including fossil, anatomical, and DNA evidence.
- Fossils are the preserved remains or impressions of once-living organisms that provide a record of past life on Earth. Not all organisms are equally likely to form fossils.
- Fossils can be dated directly or indirectly: on the basis of the age of the rocks they are found in, or on their position relative to rocks or fossils of known ages.
- When fossils are dated and placed in sequence, they show how life on Earth has changed over time.
- As predicted by descent with modification, the fossil record shows the same overall pattern for all lines of descent: younger fossils are more similar to modern organisms than are older fossils.
- Descent with modification also predicts the existence of intermediate organisms, such as *Tiktaalik*, that possess mixtures of “old” and “new” traits. *Tiktaalik* has features of both fish and tetrapods (four-limbed vertebrates).
- An organism’s anatomy reflects adaptation to its ecological environment. Changed ecological circumstances provide opportunities for new adaptations to evolve by natural selection.
- Homology—the anatomical, developmental, or genetic similarities shared among groups of related organisms—is strong evidence that those groups descend from a common ancestor.
- Homology can be seen in the common bone structure of the forelimbs of tetrapods, the similar embryonic development of all vertebrate animals, and the universal genetic code.
- Many genes, including those controlling limb development, are shared among distantly related species, an example of molecular homology owing to common ancestry.
- DNA can be used as a molecular clock: more-closely related species show greater DNA sequence homology than do more-distantly related species.

## MORE TO EXPLORE

- *Tiktaalik roseae* home page: <http://tiktaalik.uchicago.edu>
- PBS, *Your Inner Fish* (2014): <http://www.pbs.org/your-inner-fish/home/>
- Shubin, N. (2008) *Your Inner Fish: A Journey into the 3.5-Billion-Year History of the Human Body*. New York: Random House.
- Nakamura, T., et al. (2016). Digits and fin rays share common developmental histories. *Nature* 537:225–228.
- Daeschler, E. B., et al. (2006) A Devonian tetrapod-like fish and the evolution of the tetrapod body plan. *Nature* 440:757–763.
- PBS, NOVA (2009) *What Darwin Never Knew*, based on Carroll, S. (2006) *Endless Forms Most Beautiful: The New Science of Evo Devo*. New York: Norton.

# CHAPTER 15 Test Your Knowledge

**DRIVING QUESTION 1** How does the fossil record reveal information about evolutionary changes?

By answering the questions below and studying Infographics 15.1, 15.2, and 15.3, you should be able to generate an answer for the broader Driving Question above.

## KNOW IT

- 1 Which of the following is most likely to leave a fossil that represents most of the organism?
  - a. a jellyfish
  - b. a worm
  - c. a wolf
  - d. an octopus (an organism that lacks a skeleton)
  - e. All of the above are equally likely to leave a fossil.
- 2 Generally speaking, if you are looking at layers of rock, at what level would you expect to find the newest—that is, the youngest—fossils?
- 3 You are examining a column of soil that contains vertebrate fossils from deeper to shallower layers. Would you expect a fossil with four limbs with digits to occur higher or lower in the soil column relative to a “standard” fish? Explain your answer.
- 4 What can the fossil shown below tell us about the structure and lifestyle of the organism that left it? Describe your observations.



Mantonature/istockphoto

## USE IT

- 5 You have molecular evidence that leads you to hypothesize that a particular group of soft-bodied sea cucumbers evolved at a certain time. You have found a fossil bed with many hard-shelled mollusks dating from the critical time, but no fossil evidence to support your hypothesis about the sea cucumbers. Does this cause you to reject your hypothesis? Why or why not?
- 6 A specific type of oyster is found in North American fossil beds dated from 100 million years ago. If similar oyster fossils are found in European rock, in layers along with a novel type of barnacle fossil, what can be concluded about the age of the barnacles? Explain your answer.

## BRING IT HOME

*apply* YOUR KNOWLEDGE

- 7 Do an Internet search to find out about fossils discovered in your home state. Determine what kinds of organisms they represent, how old they are, and where in your state you would need to go in order to have a chance of finding fossils in the field.

**DRIVING QUESTION 2** What features make *Tiktaalik* a transitional fossil, and what role do these types of fossils play in the fossil record?

By answering the questions below and studying Infographics 15.4 and 15.5, you should be able to generate an answer for the broader Driving Question above.

## KNOW IT

- 8 Which of the following features of *Tiktaalik* is not shared with other bony fishes?
  - a. scales
  - b. teeth
  - c. a mobile neck
  - d. fins
  - e. none of the above



- 9 *Tiktaalik* fossils have both fishlike and tetrapod-like characteristics. Which characteristics are related to supporting the body out of the water?

### USE IT

- 10 *Tiktaalik* fossils are described as “intermediate” or “transitional” fossils. What does this mean? Why are transitional organisms significant in the history of life?
- 11 *Tiktaalik* has been called a “fishapod”—part fish, part tetrapod. Speculate on the fossil appearance of its first true tetrapod descendant—what features would distinguish it from *Tiktaalik*? How old would you expect those fossils to be relative to *Tiktaalik*?
- 12 If some fish evolved modifications that allowed them to be successful on land, why didn’t fish just disappear? In other words, why are there still plenty of fish in the sea if the land presented so many favorable opportunities?

### DRIVING QUESTION 3 What can anatomy and DNA reveal about evolution?

By answering the questions below and studying Infographics 15.5, 15.6, and 15.7, you should be able to generate an answer for the broader Driving Question above.

### KNOW IT

- 13 Compare and contrast the structure and function of an eagle wing with the structure and function of a human arm.

- 14 Vertebrate embryos have structures called pharyngeal pouches. What do these structures develop into in an adult human? In an adult bony fish?

- 15 You have three sequences of a given gene from three different organisms. How could you determine how closely the three organisms are related?

### USE IT

- 16 What is the evolutionary explanation for the fact that both human hands and otter paws have five digits?
- 17 Could you use the presence of a tail to distinguish a human embryo from a chicken embryo? Why or why not?
- 18 If, in humans, the DNA sequence TTTCTAGGAATA encodes the amino acid sequence phenylalanine–leucine–glycine–isoleucine, what amino acid sequence will that same DNA sequence specify in bacteria?
- 19 Gene *X* is present in yeast and in sea urchins. Both produce protein *X*, but the yeast protein is slightly different from the sea urchin protein. What explains this difference? How might you use this information to judge whether humans are closer evolutionarily to yeast or to sea urchins?

apply YOUR KNOWLEDGE

INTERPRETING DATA

20 The gene responsible for hairlessness in Mexican hairless dogs is called *comeodesmosin (CDSN)*. This gene is present in other organisms. Look at the sequence of a portion of the *CDSN* gene from pairs of different species, given below. For each pair, determine the number of differences. From the variations in this sequence, which organism appears to be most closely related to humans? Which organism appears to be least closely related to humans?

Species	Sequence
<i>Homo sapiens</i> (human)	ACTCCGGCCCCTACATCCCCAGCTCCCA
<i>Canis lupus familiaris</i> (dog)	ATTCTGGCTCCTACATTTCCAGCTCCCA
<i>Homo sapiens</i> (human)	ACTCCGGCCCCTACATCCCCAGCTCCCA
<i>Pan troglodytes</i> (chimpanzee)	ACTCCGGCCCCTACATCCCCAGCTCCCA
<i>Homo sapiens</i> (human)	ACTCCGGCCCCTACATCCCCAGCTCCCA
<i>Sus scrofa</i> (pig)	AGTCTGGCTCCTACATCTCCAGCTCCCA
<i>Homo sapiens</i> (human)	ACTCCGGCCCCTACATCCCCAGCTCCCA
<i>Macaca mulatta</i> (rhesus monkey)	ACTCTGGCCCCTACATCCCCAGCTCCCA

apply YOUR KNOWLEDGE

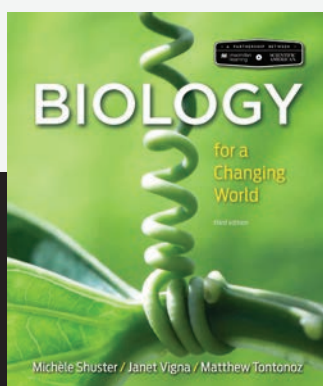
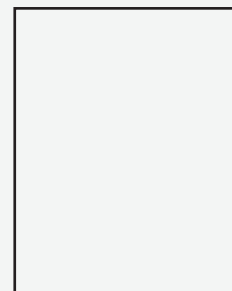
MINI CASE

21 Fossils allow us to understand the evolution of many lineages of plants and animals. They therefore represent a valuable scientific resource. What if *Tiktaalik* (or an equally important transitional fossil) had been found by amateur fossil hunters and sold to a private collector? Do you think there should be any regulation of fossil hunting to prevent the loss of valuable scientific information from the public domain?



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