

**Technology and the Textbook: Adding Interactivity to Improve Understanding**

> **Emiko Paul**, Creative Director, Roberts & Co. Publishers

**Alison Perkins**, School of Journalism/Montana PBS

## Carl Zimmer



Award winning science journalist and author of 12 books about biology including the *Tangled Bank* and *Evolution: the Triumph of an Idea*.

# Doug Emlen



Professor at the University of Montana, conducts research on the evolution of animal development.



### **What makes for a good reading experience?**

- **Comfortable in your hands.**
- **Easy to find what you are looking for.**
- **Way to make notes and a place to store them.**
- **Great visuals.**
- **Not too expensive.**











## **Advantages of e-textbook**

- **Lightweight.**
- **Tons of storage.**
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- **Interactivity!**
	- **Slideshows**
	- **F** Search functions
	- **Videos**
	- **Assessment**

# Purpose of Interactivity

- » Focus on key concepts that students struggle to understand or are difficult to explain with text and static images.
- » Provide instantaneous feedback to the student about his or her understanding.



















The Tree of Life: How Biologists Use Phylogeny to Reconstruct the Deep Past **Chapter 4: Introduction** 



Tiktaalik lived 375 million years ago. It was an ancient relative of living tetrapods, which include amphibians, reptiles, and mammals. It possessed some traits of living tetrapods, such as a wrist and neck, while lacking others, such as true digits.

#### **Learning Objectives:**

- · Identify the different components of phylogenies and the functions of each.
- Analyze the relationships of characters in a phylogeny.
- Describe the significant steps in the evolution of tetrapods.
- Explain how the bones of the middle ear can be used to trace the evolution of mammals.
- Describe the role of feathers in dinosaur evolution.
- Analyze the evidence related to the current state of understanding of human evolution.

Neil Shubin spends the school year at the University of Chicago, where he teaches paleontology and anatomy. But his summers have frequently taken him north of the Arctic Circle, to a barren patch of land called Ellesmere

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four species. Humans and frogs share a common ancestry represented by **branches** and the node P. Goldfish and trout likewise descend from a common ancestor A. And A and P, in turn descend from a common ancestral species G. A, P, and G are known as *internal* nodes because they are located within the phylogeny representing ancestral populations or species that have long since disappeared. We can organize the species in this tree according to their relationships. We refer to an organism and all its descendants as a clade. As we see in the figure, smaller clades are nested in larger ones. Humans and frogs belong to a clade known as tetrapods, which is nested within a clade that includes G and all its descendants (known as Osteichthyes).

When a phylogeny only shows the relationship between species, as in the case of Figure 4.5B, we refer to it as a cladogram. The branches do not precisely measure the period of time it took between speciation events. But they do offer some information about the timing of events. The divergence from G occurred before the ancestor of humans and frogs diverged. Later in this chapter, we'll show how we can display more information about the passage of time when we represent phylogenies. Figure 4.6

There are many ways to visualize a phylogenetic tree. This flexibility can be a great strength because evolutionary biologists can select the representation that's most relevant to the question they're investigating. But it can also give rise to confusion. Depending on the paper you read, you may encounter phylogenetic trees with branches that form right angles, curves, or diagonal lines, for example. There's no difference in the evolutionary relationship these trees are intended to represent. In this book, we will use right-angled branches, where time moves from left to right (Figure 4.7 -).

We can also rotate branches around their nodes, much like swinging the arms of a mobile that hangs from a ceiling. Figure 4.8  $\blacksquare$  shows a cladogram of six vertebrate species. If we swing around some of the branches, we end up with Figure 4.8B. Both cladograms represent exactly the same phylogenetic relationships. This equivalence is very important to appreciate when we examine evolutionary trees.

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#### Chapter 1: Introduction



Blue whales and viruses demonstrate the staggeringly different forms that life can take. They're so different, in fact, that it can be hard to imagine that a single explanation could account for them both—not to mention all of the other living things that share the planet with them. And yet such an explanation does exist: viruses and whales—and all other living things—are the products of evolution.  $(Figure 1.1)$ 

In 1973, the Russian-born biologist Theodosius Dobzhansky wrote one o eloquent accounts for evolution's place in the study of life. He entitled his "Nothing in Biology Makes Sense Except in the Light of Evolution" (Dobzhansky 1973). "Seen in the light of evolution, biology is, perhaps, intellectually the most satisfying and inspiring science," he wrote. "Without that light it becomes a pile of sundry facts some of them interesting or curious but making no meaningful picture as a whole."

#### [Read Theodosius Dobzhansky's original article] a

By understanding evolution, Dobzhansky explained, we can understand why the natural world is the way it is. We can understand the similarities among different species, as well as the differences. We can understand why some species are present in some parts of the world and not others. We can understand the adaptations of living things, as well as their weaknesses.

This understanding is important simply for what it tells us about life. But it's also important in practical ways. Evolution provides scientific tools we can use to address some of the challenges we face as a society. The viruses and bacteria that cause diseases are continually evolving, rendering many drugs ineffective. Insect populations that feed on crops can evolve resistance to pesticides, and weed populations evolve resistance to herbicides. We are altering the environment on a planetary scale, by introducing invasive species to new habitats, spreading pollution, and altering the climate. All these changes are driving animals and plants in new evolutionary trajectories. Globally we are witnessing a wave of extinctions the likes of which the Earth may not have seen for tens of millions of years. By



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As recently as 1966, shelk Abd el Aziz bin Baz asked the king of Saudi Arabia to suppress a heresy that was spreading in his land. Wrote the shelk:

"The Holy Koran, the Prophet's teachings, the majority of Islamic scientists, and the actual facts all prove that the sun is running in its orbit . . . and that the earth is fixed and stable, spread out by God for his mankind. . . . Anyone who professed otherwise would uffer a charge of falsehood toward God, the Koran, and the Prophet."

The good shelk evidently holds the Copernican theory to be a "mere theory," not a "fact." In this he is technically correct. A theory can be verified by a mass of facts, but it becomes a proven theory, not a fact. The sheik was perhaps unaware that the Space Age had begun before he asked the king to suppress the Copernican heresy. The sphericity of the earth has been seen by astronauts, and even by many earth-bound people on their television screens. Perhaps the shelk could retort that those who venture beyond the confines of God's earth suffer hallucinations, and that the earth is really flat.

Parts of the Copernican world model, such as the contention that the earth rotates around the sun, and not vice versa, have not been verified by direct observations even to the extent the sphericity of the earth has been. Yet scientists accept the model as an accurate representation of reality. Why? Because it makes sense of a multitude of facts which are otherwise meaningless or extravagant. To nonspecialists most of these facts are unfamiliar. Why then do we accept the "mere theory" that the earth is a sphere revolving around a spherical sun? Are we simply submitting to authority? Not guite: we know that those who took the time to study the evidence found it convincing.

The good shelk is probably ignorant of the evidence, Even more likely, he is so hopelessly biased that no amount of evidence would impress him. Anyway, it would be sheer waste of time to attempt to convince him. The Koran and the Bible do not contradict Copernicus, nor does Copernicus contradict them. It is ludicrous to mistake the Bible and the Koran for primers of natural science. They treat of matters even more important: the meaning of man and his relations to God. They are written in poetic symbols that were understandable to people of the age when they were written, as well as to peoples of all other ages. The king of Arabia did not comply with the sheik's demand. He knew that some people fear. enlightenment, because enlightenment thrastens their vested interests. Education is not to be used to promote obscurantism.

The earth is not the geometric center of the universe, although it may be its spiritual center. It is a mere speck of dust in the cosmic spaces. Contrary to Bishop Ussher's calculations, the world did not appear in approximately its present state in 4004 BC. The estimates of the age of the universe given by modern cosmologists are still only rough approximations, which are revised (usually upward) as the methods of estimation are refined. Some cosmologists take the universe to be about 10 billion years old; others suppose that it may have existed, and will continue to exist, eternally. The origin of life on earth is dated tentatively between 3 and 5 billion years ago; manlike beings appeared relatively quite recently, between 2 and 4 million years ago. The estimates of the age of the earth, of the duration of the geologic and paleontologic eras, and of the antiquity of man's ancestors are now based mainly on radiometric evidence the proportions of isotopes of certain chamical elements in rocks suitable for such studies.

Shiek bin Baz and his like refuse to accept the radiometric evidence, because it is a "mere theory." What is the alternative? One can suppose that the Creator saw fit to play deceitful tricks on geologists and biologists. He carefully arranged to have various rocks provided with isotope ratios just right to mislead us into thinking that certain rocks are 2 billion years old, others 2 million, which in fact they are only some 6,000 years old. This kind of pseudo-explanation is not very new. One of the early antievolutionists, P. H. Gosse, published a book entitled Omphalos ("the Navel"). The gist of this amazing book is that Adam, though he had no mother, was created with a navel, and that fossils were placed by the Creator where we find them now - a deliberate act on His part. to give the appearance of great antiquity and geologic upheaveals. It is easy to see the fatal flaw in all such notions. They are blasphemies, accusing God of absurd deceitfulness. This is as revolting as it is uncalled for.

#### Diversity of Living Beings

The diversity and the unity of life are equally striking and meaningful aspects of the living world. Between 1.5 and 2 million species of animals and plants have been described and studied: the number yet to be described is probably as great. The diversity of sizes, structures, and ways of life is staggering but fascinating. Here are just a few examples.

The foot-and-mouth disease virus is a sphere 8-12 mm in diameter. The blue whale reaches 30 m in length and 135 t in weight. The simplest viruses are parasites in cells of other organisms, reduced to barest essentials minute amounts of DNA or RNA, which subvert the biochemical machinery of the host cells to replicate their genetic information, rather than that of the host.

It is a matter of opinion, or of definition, whether viruses are considered living organisms or peculiar chemical substances. The fact that such differences of opinion can exist is in itself highly significant. It means that the borderline between living and inanimate matter is obliterated. At the opposite end of the simplicity complexity spectrum you have vertebrate animals, including man. The human brain has some 12 billion neurons: the synapses between the neurons are perhaps a thousand times numerous

Some organisms live in a great variety of environments. Man is at the top of the scale in this respect. He is not only a truly cosmopolitan species but, owing to his technologic achievements, can survive for at least a limited time on the surface of the moon and in cosmic spaces. By contrast, some organisms are amazingly specialized. Perhaps the narrowest ecologic niche of all is that of a species of the fungus family Laboulbeniaceae, which grows exclusively on the rear portion of the elytra of the beetle Aphenops crone), which is found only in some limestone caves in southern France. Larvae of the fly Psilopa petrolei develop in seepages of crude oil in California cillieids; as far as is known they occur nowhere else. This is the only insect able to live and feed in oil, and its adult can walk on the surface of the oil only as long as no body part other than the tarsi are in contact with the oil. Larvae of the fly Drosophila carciniphila develop only in the nephric grooves. beneath the flaps of the third maxiliped of the land crab

#### 3.1 The Ancient Earth



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Darwin drew sharp criticisms from some quarters for these geological claims. The most famous of his critics was the eminent physicist William Thomson (Lord Kelvin). Kelvin argued that the world could not be as old as many geologists proposed. His argument was based not on formations of rocks, but on their temperature.

Let's assume that the Earth began as a ball of molten rock, Kelvin said. The crust would rapidly cool and harden, and then the interior heat would flow through it to escape into space. Since a hot rock cools at a steady rate, Kelvin reasoned that you could use the current temperature of rocks to estimate how long they had been cooling. Rocks on the planet's surface would not give a reliable estimate, because they were heated by the Sun every day and cooled every night. The rocks deep underground in mine shafts, on the other hand, stayed at the same warm temperature year round. Based on those mine rocks, Kelvin calculated that the Earth could be Copy **Highlight (Yellow) Highlight (Blue) Add Note** 

Kelvin, it would later turn out, was wrong. To calculate the Earth's heat flow, he had assumed that the planet was a rigid sphere. In the twentieth century, geophysicists would discover that the planet's interior is dynamic. Hot rock rises through the mantle, cools, and then sinks back down again. This movement drives the motion of tectonic plates across the surface of the Earth. It also makes the upper layers of the Earth warmer than in Kelvin's model (*England et al. 2007*).

In the early 1900s, physicists finally found a way to measure the absolute age of rocks. They discovered that radioactive atoms decay into other elements at a precise rate. As we explain in Box 3.1, scientists can measure this decay in rocks and use these measurements as a radioactive clock. Such measurements allow scientists to date the age of geological formations and establish narrow estimates for the ages of fossils. They also allow scientists to conclude with strong confidence that the Earth began to form from the solar system's primordial dust cloud 4.568 billion

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A: Here is a phylogeny of vertebrates, with six species representing some of the major lineages. It's important not to interpret the sequence of species as a linear ancestordescendant relationship. B: To emphasize this point, we can rearrange the tree so that humans no longer appear to be the endpoint of evolution. Yet both trees represent the same underlying relationships. Frogs did not evolve from humans. Nor did humans evolve from frogs.

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Platypuses are mammals that lay eggs. That does not mean they are "primitive," however.

Incorporating fossils into phylogenies makes it possible to discover things that we would not know if we studied only extant taxa (i.e., those still in existence). Consider the phylogeny of five living species in Figure 4.13A . We can say that the common ancestor of A, B, and C lived after the common ancestor of all five species, but we can't say when either common ancestor lived. To constrain the range of time in which these branches diverged, we can determine how fossil taxa are related to extant ones.

Let's say you dig up a fossil and carry out a phylogenetic analysis that shows it is related to A, B, and C as shown in Figure 4.13B  $\blacksquare$ . Isotopic dating reveals that it is approximately 55 million years old. By combining this data, we can conclude that Y, the common ancestor of A, B, C, and F, lived before 55 million years ago. After all, a descendant can't live before its own direct ancestor. Likewise, X, the common ancestor of all five extant taxa and the fossil taxa, must have lived even earlier than that.

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Platypus

Figure 4.13 **Branching events** in a phylogeny



Figure 4.14 **Coelacanths** 





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Figure 4.18 Tetrapod phylogeny



Box Figure 4.2.1 March of progress misconception





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Figure 4.17 **limbs** 

Figure 4.18 **Tetrapod** phylogeny



Box Figure 4.2.1 March of progress misconception



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Lobe fins and





Figure 3.2 Found form after organcum die. In some cases, then bodies are covered by sectionist and then gramally turned to minerals, (Adapted from Posthero 2007.)

Lageratistic (plural Lagerstätten): A sion with an abundant supply of ensually well preserved laugh from the same period of time, place including self-times.

Rorgess Shale: A Laprodution in Canada that preserved forain hom the Cambrian period

has secured Front depends prosecuting such stresses are called Lagressiance, school and the security of German by almost every instance, the forening, has secured Fourth depends protecting must every instance, the foodined anguage and the model of the model and the model and the model and the model in General Models producing the second stress. the second results before an German be appears, or have. Microbers and other stand means required and allows appear to the standard the property control and the standard means of the bodiers investment and the property of were overge and arount, before posts against they were trapped in fine sedances pers treatif not destroy their beams. Inclusive to some hold times fourth and retaining which preserved even that most some they preserve an incredible amount of dear which preserved even because it aggregates in the Instead of poleomials as dear say important to scenarity requirements in the history of pulcoundage was a control of the most important Lagentation in the mountain shapes was a One of the most important logorousing in 1969 high in the mountain slopes of hours covered by Charles Decards Watter and have more yielded more than 65,000 variables On the first Bargers shale have more yielded more than 65,000 variables of the first Bargers shale have the state with contract and

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Around 905 million may again a route formed as sediments accumulated must an determined throughout the control of the set o and on studies underwater mail was located adjacent to a steep escarptment, and pay over margins of a reef. The red was located below these animals rists that it and pay poster margins of a reef. The next manage, but<br>ling these animals into the above being objectly the und large would collapse, but<br>and upmer discusses strings, and after the decay being odically the used large www.steel trent decomposition, and after the traciality of There, are<br>not contained in the turbal waters settled down and around the bodies of<br>the clearly of sediment in the turbal waters of all 1995). This arrocess clearly of sedment in the timest (Briggs et al. 1995). This process appears to be animals, preserving them intact (Briggs et al. 1995). This process is preserved animate preserving prairielly humbug a thick sequence of focul rich rock occurred repeatedly gradually humbug a thick sequence of focul rich rock

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Tigari S.S. A. A Soul che ia ma-Cardulian Nocki-kis railed the Norgean This has been prefered to act witness and then relation more available afects for the pile pears, the A restanting than of Casinovia. Looked for a likely cregory block through the D.A Hermanatties of Helicopens to pay of the food there is in the

publicated oglest studies in the Burgess Shale with studies on endersos and ecology to: understand the evolution of animal diversity.

#### Bringing Fossils to Life

ruleontologists have made trettersdous advances in recent decades in using fossils to understand the loss of extinct civatures, from their modes of reproduction to their. behavior (Bower 1990). Pears 3.4 offers and a few examples of these connectivities. fromly of whilt marine reptiles preserved with their offigenig have revealed that they give buth to live young. Fordly preserve evidence of predictors vating prey, butmarks on ancient relatives of humans demoustrate that our ancestors were regularly eaten by carnivertes. When animals widt, on soft ground, they sometimes leave tracks. behand, and sometimes those cashies become perserved. Support dimensions-hougsucked plant cating glasts-have left behind long trackways that provide clues to their magnitude at well as the structure of the beech in which they traveled. We can even infer the enistence of parental care from fossily. Fossil mosts containing the

#### 3.2 A Vast Museum



One of the most important Lagerstätten in the history of paleontology was discovered by Charles Doolittle Walcott in 1909 high in the mountain slopes of British Columbia. Quarries of this Burgess Shale have now yielded more than 65,000 specimens of mostly soft-bodied animals representing at least 93 species.



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reconstruction of Hallucigenia. based on the fossil shown in (E).

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each other in order to mate with females, which gather together in harems. Males rear up on their flippers and throw their tremendous bodies against each other, regularly gashing each other with their teeth (Figure 11.12  $\equiv$ ). The losers slink away, to lurk at the edges of the colony. Hoelzel found that 90 percent of the seals that fathered pups were the heads of harems. The other 10 percent of the seals that fathered pups were lurkers who managed to sneak in and mate with a female while the dominant male was distracted by a fight with another male.

Sexual selection may explain why male elephant seals are several times larger than female elephant seals (sexual dimorphism). Bigger males tend to win fights with smaller ones, and so bigger males tend to hold onto harems. The big males thus have more offspring. Female elephant seals, on the other hand, don't fight with each other, and so extremely large females don't have a reproductive advantage over smaller ones. In other words, sexual selection for body size is much stronger in male elephant seals than in females. (Figure 11.13 $\equiv$ )

## Extreme variance in reproductive success.

## Figure 11.13 **B**



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## **Figure 3.7 Fossil melanosomes**

A: Fossils of a 150-million-year-old dinosaur called Anchiornis huxleyi preserve feathers. B: The feathers retain cellular structures called melanosomes that help produce color. C: The melanosomes produced a complex pattern of colors on Anchiornis. The size, shape, and organization of the melanosomes allows paleontologists to reconstruct their original color.

Even medical technologies can be used to study fossils. CT scans were invented to give doctors detailed, three-dimensional views of the insides of patients' bodies. In 2009, David Evans, of the Royal Ontario Museum in Toronto, and Lawrence Witmer and Ryan Ridgely, of Ohio University, used a CT scanner to probe the skulls of a particularly bizarre group of dinosaurs known as hadrosaurs. The plant-eating dinosaurs grow extravagantly long crests on their heads in a diversity of species-specific shapes (Figure 3.8  $\blacksquare$ ).



## Figure 3.8 Hadrosaur nasal cavities

A: A group of dinosaur species called hadrosaurs had bizarre crests and nasal cavities. B: By taking CT scans of hadrosaur skulls, scientists can reconstruct the structure of the cavities in different species. C: Researchers have made computer models of these cavities, such as the one shown here, to test hypotheses about their function. These studies suggest that hadrosaurs used their nasal cavities and hollow crests to make species-specific sounds.

Paleontologists have speculated that the crests served as some kind of signal -possibly to competing rivals or to potential mates. (We'll discuss such sexual displays in more detail in Chapter 11.) The hollow crests are connected to the nasal opening of hadrosaurs, which led Hopson  $(1975)$ and Weishampel  $(1981)$  to propose that the dinosaurs moved air through

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To test this hypothesis, Evans and his colleagues took CT scans of hadrosaur skulls, getting detailed images of the interior spaces. The paleontologists looked at the braincase and observed that the region for interpreting smells was small. That finding suggested that the crests were not an adaptation that enhanced sensitivity to odors.

Evans and his colleagues also looked at the ear regions of the hadrosaur skulls. The shape of an animal's ear bones determines which frequencies it is most sensitive to. Evans and his colleagues found that its ears were tuned to the frequencies that would have been produced by the crests. These results are compelling evidence that the dinosaurs used the crests to make species-specific sounds (Evans et al. 2009; Figure 3.8 =).

## Audio clip of Parasaurolophus sound

Listen to audio **B** 

Video clip of Corythosaurus nasal passages

Watch the video **B** 

# **Traces of Vanished Life**

A fossil is not the only trace that an organism can leave behind. Some rocks themselves are made from the remains of dead organisms. About 300 million years ago, for example, giant swamps spread across many of the continents. When plants died there, they did not immediately decay. Instead, they fell into the swamps and were rapidly buried in sediment. Bacteria then began to break them down. Eventually, the swamps were drowned by rising oceans and then buried under vast amounts of marine

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## 3.2 A Vast Museum



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### 4.1 Tree Thinking



It's easy to look at a tree like the one in Figure 4.8A and see it not as a branching process, but as a continuum. We might erroneously conclude that humans evolved from a distant goldfish ancestor, through a frog intermediate, and so on until we reached our final form. In fact, the goldfish have a more distant common ancestor with us than cats, but they are not ancestral to us. After our lineage and the goldfish lineage split from each other, the goldfish lineage underwent its own evolutionary changes that produced the goldfish we know today. As we'll see below, we can compare species at different positions in a phylogeny to infer what their common ancestors were like.

Evolutionary biologists can also choose how much phylogenetic information they want to represent in a tree. Figure 4.9A  $\blacksquare$  shows a large tree with seven tips. If we remove species A, C, and D, we can represent the remaining species in the tree shown in Figure 4.9B simply by straightening the remaining branches. These two trees are compatible, because they represent parts of the same underlying phylogeny. This flexibility allows scientists to compare different clades without having to represent all of the species they contain.



## Fig. 4.9 Clades

Within a clade, we can choose how many species we want to include in a phylogeny. A: If we leave out species A, C, and D from the full tree on the left, we get the smaller tree on the right. These trees are in agreement about the underlying phylogeny. B: We can collapse an entire set of species into one tip, if they all belong to the same clade. (Adapted from Baum and Smith, in press.)

## **Key Concept:**

• Phylogenies represent the branching pattern of evolution over time.

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# **Section Review**

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# **Section Review**









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**Assessment: 4.1 Tree Thinking** 



Which of the following phylogenies does not indicate the same relationship among whales and other groups?



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a.







**Results** 

**Assessment: 4.1 Tree Thinking** 



**Percent of Points Earned** 50% **Question 1** 5/5 Points Which term is not associated with tree-like depictions of evolutionary histories known as phylogenies? Question 2 4/5 Points Which of the following statements are depicted by this phylogeny? (from Gregory 2008) Question 3 If you were looking at a phylogeny of living bird species, where 1/5 Points could you find the name of a species of non-theropod dinosaur? Question 4 0/5 Points Which of the following phylogenies does not indicate the same relationship among whales and other groups?

> Email **Answers**





- The oldest fossils of vertebrates with four legs (tetrapods) date back about 370 million years.
- The oldest known fossils of animals that looked similar to living mammals are 200 million years old.
- The oldest fossils of our own species are about 200,000 years old.
- Paleontologists can test their predictions about fossils against new evidence as it is discovered.

## **Chapter 3 Concept Map**

Concept Map - Scientific Theory O

## **Additional Reading**

- Conway Morris, S. 1998. The Crucible of Creation: The Burgess Shale and the Rise of Animal Life. Oxford: Oxford University Press.
- · Gould, S. J. 1990. Wonderful Life: The Burgess Shale and the Nature of History. New York: W. W. Norton.
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- Prothero, D. R. 2007, Evolution: What the Fossils Say and Why It Matters. New York: Columbia University Press.
- · Schopf, W. 1999. Cradle of Life: The Discovery of Earth's Earliest Fossils. Princeton, NJ: Princeton University Press.
- Xian-Guang, H., R. J. Aldridge, J. Bergström, D. J. Siveter, D. J. Seveter, et al. 2007. The Cambrian Fossils of Chengjian, China: The Flowering of Early Animal Life. Malden, MA: Blackwell.

# **Chapter Review**





Examine Connor (2007) from the Primary Literature section. Summarize the results. Do you agree with the author(s)' conclusions? Why or why not? (click "View PDF" to read the paper.





Phil. Trans. R. Soc. B (2007) 362, 587-602. doi:10.1098/rstb.2006.1997 Published online 12 February 2007

# Dolphin social intelligence: complex alliance relationships in bottlenose dolphins and a consideration of selective environments for extreme brain size evolution in mammals

### Richard C. Connor\*

Biology Department, University of Massachusetts at Dartmouth, North Dartmouth, MA 02747, USA

Bottlenose dolphins in Shark Bay, Australia, live in a large, unbounded society with a fission-fusion grouping pattern. Potential cognitive demands include the need to develop social strategies involving the recognition of a large number of individuals and their relationships with others. Patterns of alliance affiliation among males may be more complex than are currently known for any non-human, with individuals participating in 2-3 levels of shifting alliances. Males mediate alliance relationships with gentle contact behaviours such as petting, but synchrony also plays an important role in affiliative interactions. In general, selection for social intelligence in the context of shifting alliances will depend on the extent to which there are strategic options and risk. Extreme brain size evolution may have occurred more than once in the toothed whales, reaching peaks in the dolphin family and the sperm whale. All three 'peaks' of large brain size evolution in mammals (odontocetes, humans and elephants) shared a common selective environment; extreme mutual dependence based on external threats from predators or conspecific groups. In this context, social competition, and consequently selection for greater cognitive abilities and large brain size, was intense.

Keywords: dolphins; brain size; alliances; social complexity

The open sea is an environment where technical knowledge can bring little benefit and thus complex societies-and high intelligence-are contraindicated (dolphins and whales provide, maybe, a remarkable and unexplained exception).

(Humphrey 1976)

#### 1. INTRODUCTION

In his famous essay on 'The social function of intellect', Humphrey linked social complexity to environments where improvements in 'technical knowledge' paid large dividends. Dolphins were left as an unexplained puzzle. Many would agree now that Humphrey's essay deserves praise for getting it right as to what we use our big brains for (social competition) but not necessarily why the environment humans lived in was one where social success paid big dividends (although technical knowledge may have played two very important roles in human brain evolution, as I describe below).

The most complex social relationships described so far in cetaceans are found in bottlenose dolphins (Tursiops aduncus, family Delphinidae) that live in Shark Bay, Australia. Males affiliate in nested alliances that vary in stability, size and relatedness. Synchrony may play an important role in mediating alliance relationships, suggesting an interesting convergence with humans based on imitative abilities, motion

One contribution of 19 to a Dicumion Meeting Issue 'Social intelligence: from brain to culture'.

perception or relationship uncertainty. A consideration of the ecology of alliance formation reveals that the interaction between ecology, alliance relationships and degree of social competition is a complex arena in dolphins just as it is in primates.

The evolution of a large brain probably played a keyrole in the impressive delphinid radiation. One of the reasons the delphinids have large brains is that they can afford them. A high quality diet supports a high metabolic rate that renders large brains less costly. The small-brained dolphins also consume a high quality diet, but it remains unclear whether they have a high metabolic rate. I offer a novel cost-saving hypothesis for delphinid brain evolution, based on the evolution of a high energy budget for group-feeding on schooling fish.

Increasingly, it seems that the social competition hypothesis may be the best explanation for all three 'peaks' in mammalian brain size: humans (and apes), elephants and odontocetes (primarily delphinids and sperm whales). It seems a good time, therefore, to revisit the question of environment to see if we can find common selective pressures that favoured extreme brain size evolution in these groups. This presents an interesting challenge, as one would be hard pressed to find three more different types of mammals in appearance and lifestyle.

In §17, I argue that extreme brain size evolution in elephants, toothed whales and humans was driven by a shared feature of their environment: a threat from conspecifics and/or predators leading to an extreme degree of mutual dependence. The relative importance

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 $\checkmark$ 

 $\checkmark$ 



## Select if included in your answer

Kelvin claimed that it would only take at most 20 million years for rocks found below the surface of the Earth to cool to their present temperature.

More recent evidence showed that plate tectonics deliver more heat to the upper layers of the Earth, demonstrating the prediction based on cooling time vastly underestimated the Earth's age.

Kelvin said 20 million years for rocks to cool.

Plate tectonics bring hot rocks to the surface, making estimates of time based on cooling different.







**Entries for Section 3.2 A Vast Museum** 



Quiz

Quiz



Figure 3.4 Bringing fossils to life





## Figure 3.9 Okenone

Okenone is a carotenoid pigment found exclusively in purple sulfur bacteria. A series of chemical reactions can turn it into okenane.

## Figure 3.10 Carbon isotopes extracted from the enamel of fossil teeth



Using carbon isotopes extracted from the enamel of fossil teeth, Julia Lee-Thorp and Matt Sponheimer of the University of Cape Town have compared the diets of early hominin fossils to those of browsing mammals that fed on shrubs and grazing mammals that ate grass sampled from the same geological time periods. Across three successive periods (3 million years ago, 2.4-2.6 million years ago, and 1.7 million years ago), hominin enamel showed chemical signatures of a mixed diet that included a surprising amount of grasses (i.e., isotope values offset from that of pure browsers and more in the direction of grazers). Such studies provide valuable glimpses into the behavior of our early ancestors. (Modified from Lee-Thorp et ai. 2003.)

### Highlights



Fossils preserve evidence of predators eating prey; bite marks on ancient relatives of humans demonstrate that our ancestors were regularly eaten by carnivores

### **Notes**



Check this article for more info on how Trex ran

### **Answered Assessment Questions**



How did the fossils of the Burgess Shale form?



How did John Hutchinson and Mariano Garcia determine that Tyrannosaurus rex could not run very fast?



**Entries for Section 3.2 A Vast Museum** 



Quiz

Quiz

Figure 3.4 Bringing fossils to life

# Figure 3.8 Hadrosaur nasal cavities



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## Highlights



Fossils preserve evidence of predators eating prey; bite marks on ancient relatives of humans demonstrate that our ancestors were regularly eaten by camivores

### **Notes**



Check this article for more info on how Trex ran

### **Answered Assessment Questions**



How did the fossils of the Burgess Shale form?



How did John Hutchinson and Mariano Garcia determine that Tyrannosaurus rex could not run very fast?






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#### Evolution: Making Sense of Life - Study Guide Entries

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Chapter 4, Section 2

Highlight: taxonomic unit such as "mammals" is considered legitimate only if it represents a clade: that is, the group is made up of an organism and all its descendants. Such a group of species is called monophyletic. You can think of it as a piece of a larger tree that can be removed with a single cut. If you need to cut the tree in two places to get all the species in a group, then it is

Chapter 3 Bookmark: Biomarker

Chapter 3 Bookmark: Chordates

Chapter 3, Section 1 Highlight: most

Chapter 3, Section 1 Note: Type notes here...

Chapter 3, Section 2

Highlight: In 2002, John Hutchinson and Mariano Garcia, then at the University of California at Berkeley, developed a biomechanical model of running animals, estimating how much force leg muscles of a given size could generate (Hutchinson and Garcia 2002).

Chapter 3, Section 5

Highlight: In 2010, an international team of scientists described the oldest known fossils of a multicellular organism (Albani et al. 2010). The fossils, dating back 2.1 billion years, were found in Gabon in West Africa. They are scalloped disks, measuring up to 12 centimeters across. It's not clear whether the fossils were formed by early eukaryotes, some type of bacteria, or archaea (Figure 3.14). The oldest recognizable multicellular eukaryotes-filaments of some type of algae -are 1.6 billion years old. The oldest known fossils of red algae date back 1.2 billion years (Figure 3.15), while green algae first appear 750 million years ago.

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### What Kinds of Questions Do We Ask?

- » Traditional Teaching Perspective
	- ˃ What did **you** understand?
- » Student-centered Perspective
	- ˃ What should **I** understand?
	- ˃ What *do* I understand?



### Bloom's Taxonomy



### What Should I Understand?

### » Learning Objectives

Biology: From Natural Philosophy to Darwin Chapter 2: Introduction



The Galápagos Islands in the Pacific are home to many species found nowhere else on Earth-such as this marine iquana.

#### **Learning Objectives:**

- · Identify early naturalists and their contributions to evolutionary theory.
- Analyze the role the fossil record played in the development of the concept of evolution.
- Explain the difference between homologous and analogous traits.
- Analyze how Darwin's observations of nature led to the inferences he developed regarding natural selection.
- Identify three modes of evolution.



### What *Should* I Understand?

MENU

**MEDIA** 

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In the Pacific Ocean, seven hundred miles west of Ecuador, lies an isolated cluster of extinct volcanoes known as the Galápagos Islands. On these strange outcrops are strange kinds of life. There are large birds with bright blue feet. There are scaly iguanas that leap into the ocean to eat seaweed

» Comprehension (2nd level)

- **Restate** o Report
	- Discuss o Explain
- **Describe**
- o Identify

o Recognize

o Express

- Locate
	- o Review
- » Identify early naturalists and their contributions to evolutionary theory.



### What *Should* I Understand?

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» Analysis (4th level)  $\circ$  Distinguish oDifferentiate oAppraise oAnalyze oCalculate oCompare oContrast oExamine oTest  $\circ$  Relate

oCriticize

- oExperiment
- » Analyze the role the fossil record played in the development of the concept of evolution.



- » Pre-assessment
- » Formative Assessment
- » Summative Assessment



#### » Pre-assessment Questions



> Important conceptual understanding necessary for current chapter



### » Choices include incorrect answers





#### » Formative Assessment



> Reading Comprehension



#### » Summative Assessment



- > Multiple Choice
- > Short Answer



### » Tracking Understanding



- ˃ Allows students to track their mastery of the information
	- + Study guides
- > Summaries are available to teachers



#### » Concept Maps





### » Drag and Drop







# Where Else Can We Go?

### » Provide Direct Feedback

- > Formative/Summative Questions
- > Concept Maps
- > Server-side Support

#### » Provide Community Interactivity

- > Student-Teacher Interaction
- > Peer Interaction
	- + e.g., Building Concept Maps
- » Suggestions?



### What is the Effect on Learning?

- » Ebooks and Multiple Learning Styles
	- > Audio and video clips
	- > Enhanced graphics
- » Ebooks and Flipped Classrooms
	- ˃ Numerous opportunities to delve deeper in the classroom
		- + Avida-ED
		- + SimBio
- » Effects on the Learner
	- ˃ Qualitative Study on Students' Use and Interest
	- ˃ Quantitative Study of Effect on Learning



