

# Missing Links

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Evolutionary Concepts & Transitions through Time

by

Robert A. Martin

The McDonald & Woodward Publishing Company  
Granville, Ohio

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*Missing Links*  
*Evolutionary Concepts & Transitions through Time*

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## Preface

# Preface to the Second Edition

*Missing Links* has a new publisher, McDonald & Woodward, specialty publishers in natural and cultural history. My original intent for *Missing Links* was for it to be as readily available to the general public as to college students, and I feel comfortable that in its new home its first audience will now be as well served as the second.

Some things change a lot, some a little. Since the first edition of *Missing Links* was published in 2004, the stories of life's origins, early tetrapods, dinosaurs, and hominids has changed significantly, sometimes with fascinating new discoveries such as the ancient tetrapod *Tiktaalik*, a bevy of feathered dinosaurs, and the enigmatic hominin *Australopithecus sediba*, and sometimes with new interpretations, such as the modern focus on deep sea hydrothermal vents as the likely spawning ground for early life. The terrestrial origin of whales is more firmly documented by skeletons of a new Eocene protocetid with a pregnant female showing a near-term fetus in head-down position, as in terrestrial mammals but not aquatic whales. Although the fossil history of voles has not been wracked with new discoveries that shake its foundations, the very density of fossils in this rapidly evolving group provides us with novel insights into the timing of anatomical change and the possibility of multiple origins of modern groups from separate ancestors. A new chapter documents the complex history of pocket gophers, burrowing rodents from the Meade Basin of southwestern Kansas, and another chapter considers the origin of snakes from both evidence in the fossil record and our new understanding of the role of *Hox* genes in limb formation. Finally, as additional information from long-term studies of extant animals continues to

accumulate, the more we realize the potential for rapid change within species during the lifetime of a single observer, as with the potential speciation of mosquitoes in the London underground railway system since the 1940s.

The reader will notice the absence of a chapter on plants. In the original manuscript I made the “executive decision” to limit the example chapters to animals, in part to maintain the contents within certain page limits and partly because the fossil history of plants is not as dense as that for animals. Besides, plants seem to hybridize so easily that determining fossil histories at the species level is almost impossible. The absence of a chapter on fossil invertebrates is for a similar reason; they are so developmentally and anatomically flexible that identification of fossil species and interpretation of morphological changes are problematic. The remainder of the Preface is similar to that in the first edition, with the obvious addition of the new gopher and snake chapters and a variety of comments that refine the original chapter descriptions to reflect new information and fossil material. I have also rearranged the case histories in roughly phylogenetic order.

When Darwin published his *Origin of the Species* in 1859 very little fossil material was known. Darwin himself collected many fossil specimens on his voyage around the world on H.M.S. Beagle, but they were primarily described by Richard Owen, an English paleontologist who rejected Darwin’s mechanism of natural selection for evolutionary change. Owen was a pretty active fellow; he also named the Dinosauria. In the United States, the first fossils were gathered from a marsh somewhere along the Ohio River in 1739 by a French Canadian officer, Baron Charles de Longueuil. It is a strange and sometimes ironic aspect of evolutionary science that some of those influential in the development of the modern synthesis of evolutionary theory themselves did not embrace evolution or its primary mechanisms, either because they were unaware of it or simply rejected it. A few of these include: Carolus Linnaeus, a Swedish physician and father of animal and plant classification, who believed he was cataloguing examples of God’s omnipotence; Baron Georges Cuvier, the father of comparative

## Preface

anatomy and paleontology, who was convinced that God initiated “catastrophes” to erase entire communities of organisms; Alfred Wallace, who developed the theory of natural selection at the same time as Darwin and later rejected the idea that humans could have resulted from this process; and the afore-mentioned Richard Owen, England’s premiere paleontologist. But the one-two-three punch provided by James Hutton’s *Theory of the Earth*, Charles Lyell’s *Principles of Geology*, and Darwin’s *Origin of Species* sent shockwaves through the scientific community and began a modern exploration for fossils and their meaning that continues to this day. Hutton’s work, published in 1785 and popularized by Lyell in his 1830-33 three volume tome, was particularly influential for Darwin, as Hutton’s principle of uniformitarianism, the concept that the same slow and methodical forces at work on the planet today shaped the planet in the past, provided circumstantial evidence for an ancient Earth. Fundamentalist Christians of Darwin’s time fought Darwin very strongly, for a literal reading of the Christian Bible is incompatible with both an ancient Earth and the concept of evolution. It is an amazing testimony to the power of religious influence that millions of Americans today still follow this basic credo. And one of the tenets of those who support a “creationist” model for humans and the universe is that there are no true “missing links,” extinct organisms that connect modern and ancient life in an unbroken chain through long periods of time, measured in the millions and billions of years. But we have come a long way since Darwin’s day. Thousands of expeditions have unearthed literally millions of fossils, today housed in many museums and academic institutions worldwide. Paleontologists have described fossils 3.5 billion years old, and organisms are known continuously from that point onward. Many “missing links” are recognized (though, as we shall see, a fossil “missing link” is not exactly what most creationists have in mind), and it is the primary purpose of this book to provide a compendium of this information for the general reader in the context of modern scientific inquiry.

*Missing Links* is designed to satisfy two needs. First, as represented by the case histories, it can be read purely as a compilation

of fossil histories in support of evolutionary theory. It is my hope and intention that this anthology be used in every conceivable circumstance where such information is needed, from a student classroom presentation to an intellectual religious discussion. The second usage, represented by Section I, is as a primer on evolutionary science, particularly as it applies to fossil materials. Evolution can no longer be expressed by the simple phrase “survival of the fittest.” Hundreds of scientists have worked carefully for 150 years to establish evolution as a theory that is profound in scope and universally supported, and more scientists are likely at work today on evolutionary problems than were active in the first 125 years combined. This section should also be of interest to professionals, as I present new perspectives on concepts such as punctuated equilibrium and species selection.

Evolutionary science encompasses many fields and can be extremely complicated to the novice. Consequently, I have prepared a synthesis in Chapters 1-3 of the major concepts, processes, and vocabulary necessary for a reasonable understanding of evolution, particularly as it applies to interpretation of the fossil record. Because the focus of this treatment is on transitions in the fossil record, there is little here on evolutionary genetics as practiced with extant organisms. For those interested in this area, I recommend the sections on that topic in the texts *Evolutionary Analysis* by Scott Freeman and Jon C. Herron (2007; Prentice Hall) and *Evolution* (2009; Sinauer) by Douglas Futuyma. Although it is not necessary to be familiar with the contents of Section I to consult the case histories, it will be of considerable benefit. This section begins with a chapter on how science operates as a method of knowing. Most people fail to understand that science is not limited to chemistry, biology, physics, etc., the so-called “hard” sciences. Everything we do as an adult is based on a series of experiments we performed as we were growing up. We could not function if this were not so. Hopefully, as this universal aspect of science becomes more widely known and appreciated perhaps science will not seem so mysterious. Chapter 1 also documents the ancient age of the Earth and its dynamic nature. One of the greatest and most

powerful discoveries of our time, the theory of continental drift, is reviewed. This is followed by a more specific examination of methods for dating rocks and fossils, called chronometry.

The publication of German systematist Willi Hennig's book *Phylogenetic Systematics* in 1966 led to a major revolution in the way classification is accomplished. Today, with the help of powerful computer programs such as MacClade and PAUP, we methodically examine and analyze character variation in modern and fossil organisms in order to identify relations among them. The underlying philosophy of phylogenetic systematics, or cladistics as it is sometimes known, is that classification should represent phylogeny, or the revealed genealogy of organic life. Because evolutionary processes seem to work primarily at the population level within species, and also because species seem to have morphological boundaries (albeit sometimes fuzzy ones) and are therefore recognizable units, I have provided in Chapter 2 a brief examination of the species concept, concluding that species are dynamic units, full of variation in time and space. Chapter 2 also considers the myriad influences that lead to the creation of a fossil locality and the way scientists learn about past environments. What forces affect the burial, preservation and distribution of fossils? In what ways can fossils be used to interpret past climates? In addition to these applications, fossils also can lead to an understanding about how ecological communities change through time.

Chapter 3 has been completely rewritten to incorporate more detail on almost every aspect of the evolutionary process. A revolution is underway in our understanding of evolutionary change, originating from the discovery of *Hox* gene complexes, conserved gene groups shared by all metazoans (complex organisms), and how these genes are responsible for basic body symmetry and shape. Complex changes in body form may be the result of disproportionate influence of only a few regulatory genes. Observations and processes in the lifetime of single species (variation, natural selection, genetic drift) are considered separately from patterns and processes involved in the origin of new species and subsequent radiation within clades. Can small-scale mutation in populations and intraspecific

natural selection explain life's full panorama of diversity, or are other processes, perhaps involving a selection mechanism at the species level, necessary? How do we explain long-term morphological (anatomical) trends in species? Can trends arise by random processes? Extinction, the flip side of origination, is also examined at different temporal and mechanistic scales. As the late Stephen Jay Gould often noted, contingency (chance) can have a powerful influence on the overall direction of life's history.

The case histories begin, in Chapter 4, with a scenario for the appearance of life on Earth (with contributions from Mars, if that turns out to be the case). We see how Stanley Miller and others have generated all the building blocks of complex cellular molecules, such as DNA and ATP, in the laboratory. The mixture used by Miller may not have been exactly appropriate, however, as other scientists conclude that life arose in deep sea hydrothermal vent ecosystems; strange associations of organisms that exist without sunlight.

In Chapter 5 we examine one of the great changes in the history of vertebrate animals; namely, the transition from water to land, or terrestrialization. Traditional ideas on the origin of limbs in land animals, such as possessed by the modern amphibians, proposed that hands and feet evolved to support the body on land. Not so, says Jennifer Clack of Cambridge University. Her work indicates that tetrapod (four-footed animal) limbs appeared first in fully aquatic animals! If limbs are not present for support on land, then what was their original purpose?

I almost retitled this book *Eye of the Flounder*, so excited was I over recent discoveries regarding the origin of one of Earth's most amazing groups of animals, the "flatfish," best represented by flounders, halibut, sole, and the like. During development one eye of these fishes migrates to the other side, and the adult ends up swimming on its side, with its mouth still pointing sideways. I won't spoil the story by disclosing more information here, but new fossil finds show that this condition in modern species evolved gradually from Eocene ancestors.

*Archaeopteryx* needs little introduction, but again, as in whales, there have been many new discoveries linking early birds

to their modern relatives. Chapter 7 examines these new finds in the context of a raging debate about bird ancestry. Some paleontologists, such as Robert Bakker, Louis Chiappe, and Kevin Padian, are convinced that birds arose from dinosaurs; in fact are dinosaurs, whereas another camp, led by Alan Feduccia and the late Larry Martin, think that birds originated from an earlier reptilian ancestor that may have given rise to both dinosaurs and birds. Whatever the outcome, new fossils have cemented the links between reptiles and birds. Lots of early “toothy” and feathered relatives are now known. New discoveries of fossil snakes with well-preserved partial hindlimbs prompted me to include Chapter 8 on the fossils and work by developmental biologists that help explain how limbs were lost in serpents.

Chapter 9 reviews the fossil evidence for the transition from reptiles to mammals. It is an interesting segue, involving not only modifications in thermoregulation, but also in hearing and food acquisition and processing. Were the last mammal-like reptiles endothermic? Did they possess fur? How does one define and recognize a mammal? Examination of the fossil record will show how this question is answered with the fossil material available.

Chapter 10 tells the magnificent story of whale evolution that has unfolded only in the last 20 years, complete with aquatic intermediates sporting tiny hooves on their feet! In Chapter 11 we look at the vast Cenozoic panorama of horse evolution, showing the eventual progression of changes leading from tiny forest dwelling ancestors to the large and speedy descendants of today. Thanks largely to the modern work of Bruce MacFadden and Richard Hulbert, we now can see that horses were a diverse lot, with many experiments in both size and morphology that did not survive.

Yours truly and others have chosen to work with the fossil history of the innocuous but ubiquitous rodents, in the hope that the dense fossil record of these animals will reveal the secrets of evolution, if for no other reason than that there are so many fossils available for study. Chapter 12 provides examples of short-term change in species, or microevolution, as well as a likely record of an arvicolid speciation event. In the rodents we have good fossil evidence for considerable morphological and size change at different

chronological scales. Here we can get a close-up look at how links operate, and we see that it is often a blurry mess of related populations originating in an almost helter-skelter fashion, each with its own set of characteristics and evolutionary trajectories. There is a benefit to working with a group that has a dense fossil record.

Chapter 13 continues the stories provided by the rodent record, this time with subterranean rodents from southwestern Kansas known as pocket gophers, those furry animals that made life miserable for Bill Murray in the movie *Caddyshack*. The Meade Basin record of these rodents is unparalleled for any vertebrate animal group in the late Cenozoic (last 5 million years), and here we see that despite their success today, their history is replete with species extinctions and replacements. The Kansas record also demonstrates a significant anatomical transition, from animals with rooted to unrooted cheek teeth (premolars and molars), the latter which characterizes all living pocket gophers.

Our own heritage is taken up in Chapter 14. As with the whales and birds, new hominids are being reported regularly. As I began outlining this chapter for the first time, *Australopithecus bahrelghazali* was described from three to four million year old deposits in Chad. Soon after, the amazing, diminutive *Homo floresiensis* was discovered in southeast Asia, and in 2010 *Australopithecus sediba* was described from South Africa. It is an exciting time in paleoanthropology, and as one might expect, there are probably as many theories of human relationships as there are investigators. There was an old joke that suggested there are likely as many anthropologists studying hominids as there are fossils, a past testament to a lousy fossil record, but that isn't true any more. There are now hundreds of specimens of *Australopithecus afarensis* alone.

The final chapter is one that may seem unusual in a book on missing links, but hopefully by the time the reader has made it this far its purpose will be obvious. In this chapter I consider the “smoking gun” of evolution; evolution in action during the lifetime of the reader as an observer. Missing links on a generational scale, complete with the sudden appearance of new forms, anatomical change, and the potential for new species.

## Acknowledgements

I must first acknowledge evolutionary scientists worldwide, whose diligent research provided the source of most of the information in this book. I could not cite even a small part of the tremendous written database supporting Darwin's grand theory of evolution, and I apologize to the hundreds of scientists, past and present, whose names do not appear here.

Many of my colleagues contributed in one way or another to the writing of this treatment. Pablo Peláez-Campomanes and the late Jim Honey taught me everything I know about field paleontology, from identifying likely fossiliferous sites, to stratigraphy, to field procedures to reclaim and preserve the fossils. Ted Daeschler, Robert Carroll, J. W. Schopf, Jim Hopson, Michael Bell, Richard Hulbert, Jr., Hans Thewissen, Ian Tattersall, Larry Martin, Howard Whiteman, Jennifer Clack, Alan Feduccia, Frances James, Kevin Padian, Dave Canning, and Ed Zimmerer either reviewed chapters or provided useful information and opinions for both editions. Thanks are also due Ian Tattersall for granting permission to use some of the many outstanding illustrations in his book *The Fossil Trail*. I tried out early versions of *Missing Links* in my undergraduate Evolution classes at Murray State University, and I appreciate the help provided by Tom Timmons in making the various accommodations necessary for this process.

Judy Hauck, a former editor at Jones & Bartlett, was the first individual in the publishing business to get excited about *Missing Links*, and I thank her and the staff at Jones & Bartlett for publishing the first edition. The second edition owes its existence to publication by McDonald & Woodward, and I want to thank Jerry McDonald, whose work in paleontology I have known about for many years, for recognizing the value of *Missing Links* and giving me the opportunity to produce a second edition. My extended family, Marsha, Rachel, Jeremy, and Alice, provide constant encouragement and support, and I also want to acknowledge my second wife, the late Linda L. Martin, for her many kindnesses and help in myriad ways.

