

An Overview of the Tree of Life

Joel Cracraft

Introduction

“The affinities of all the beings of the same class have sometimes been represented by a great tree. I believe this simile largely speaks the truth.” —Charles Darwin, 1859, p. 129

Long before Charles Darwin proposed natural selection as a mechanism for evolutionary change, geologists had surmised that change in Earth history must have extended over long periods of time, and the discovery of extinct organisms in many geologic strata led scientists to conclude that life itself might be ancient. At the same time, anatomists and paleontologists were comparing different organisms and using observed similarities and differences to classify them hierarchically into related groups. Thus, cats and dogs were seen to form distinct groups within carnivores (because they share carnassial teeth), and these in turn were clustered with other groups sharing similarities such as hair and mammary glands into a larger group called mammals. Darwin’s 1859 book *On the Origin of Species* provided a new conceptual framework for all these observations: life had evolved on Earth over vast amounts of time. Thus, organisms share similarities *because* they inherited them from a common ancestor.

The only illustration in Darwin’s *Origin of Species* was a hypothetical evolutionary tree depicting a branching history of species—what is now termed a phylogeny. That figure, because it was linked to a narrative explaining how organisms have evolved, established the idea of “tree thinking.” Within a few years, some of the greatest comparative biologists of the time, including Thomas Henry Huxley in England and Ernst Haeckel in Germany (who, by the way, coined the term phylogeny), began publishing phylogenies of different groups of organisms. Indeed, Haeckel attempted to synthesize what was then known about similarities into a phylogenetic tree covering all major groups of organisms.

The scientific evidence—from anatomy and paleontology to molecular genetics, behavior, and biochemistry—that has been accumulated over the last 150 years has demonstrated the fact of life’s evolutionary history. Although the phylogenetic relationships of many groups of organisms are still uncertain, that life itself has been diversifying on Earth for billions of years is as well established as other scientific notions that also once engendered debate, such as that the Sun revolves around the Earth or that Earth is a sphere and not flat.

Today building the tree of life is one of the most active areas of research in evolutionary biology (see Cracraft & Donoghue, 2004). Approximately 1.4–1.7 million living species have been discovered and described, along with countless fossil species, and systematists—those evolutionary biologists concerned with describing Earth’s species and understanding their relationships—estimate that many millions more remain to be discovered. At this time, we have studied the relationships of perhaps 75,000–100,000 species in some detail; thus reconstructing the tree of life for all species, living and extinct, will be a vast undertaking. Despite this challenge, the last decade has witnessed a substantial increase in our knowledge, not only because new forms of data (for example, DNA sequences) and technologies (gene sequences, informatics) are being used, but also because many young researchers have flocked to the discipline of systematics. We can expect, therefore, that considerable progress will be made over the next decade.

This chapter will briefly describe how systematists use comparative methods to construct the tree of life, and then it will summarize our current understanding of the evolutionary relationships among the major groups of organisms, relying heavily on the chapters in the recent summary volume *Assembling the Tree of Life* (Cracraft & Donoghue, 2004). Additional resources on tree of life research are listed at the end of the chapter.

Discovering the Tree of Life

Before describing how systematists determine the history of life, we need to define more precisely what is meant by “the tree of life.” In seeking to understand phylogenetic relationships, systematists ask the question, Are taxa A and B more closely related to each other than either is to C, where taxa (singular, taxon) are individual species or groups of species (not individual organisms)? (See figure 1) If A, B, and C are more closely related to each other than any of them is to taxon, say D, they are said to be *monophyletic*. Monophyletic groups are also called *clades* (Greek for “branch”), and two clades that are each other’s closest relative are termed *sister-groups* (figure 1).

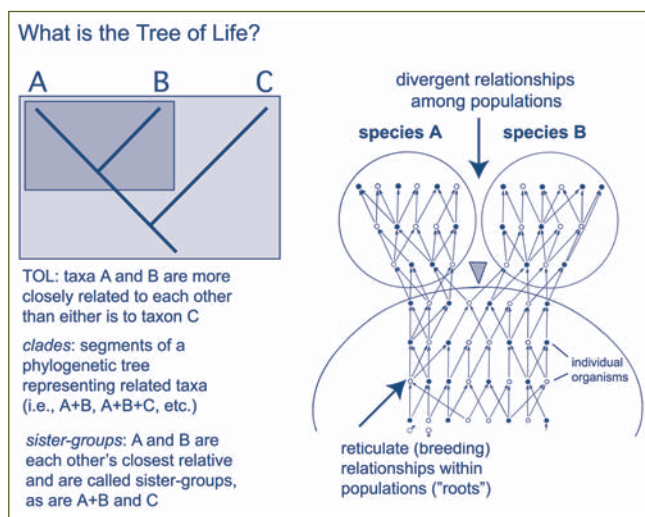


Figure 1. A general definition of the tree of life. left (a) Relative closeness of relationship is defined on the basis of a phylogenetic tree (also called a cladogram). right (b) Species arise by the geographic isolation and subsequent divergence of populations. Relationships among individuals in populations are reticulate, whereas among species they are divergent (although hybridization between species does sometimes occur).

Species arise through a process called speciation, in which a population becomes subdivided into two geographically isolated populations. Over time, these populations tend to diverge from one another and become distinct (see Zink, chapter 10). Within populations, relationships are reticulate, meaning that they represent breeding affinities among individual organisms (parents and their offspring), whereas relationships among species (taxa) are divergent, and as time goes on, clades of related species are evolved (figure 1). Seen from this perspective, the hierarchical relationships we see among species or groups of species [(A + B) + C] + D are an extension of the genealogical connections that begin with genetic relationships within populations.

Phylogenies are scientific hypotheses (conjectures), and we evaluate alternative hypotheses of relationship using evidence from shared characters including similarities in morphology, DNA sequences, behavior, or other sources of data. We accept the hypothesis, among all the alternatives being considered, that is best explained by the evidence; that is, we accept the most parsimonious hypothesis. Thus, phylogenetic analysis, like all science, is based on a rational discovery process of knowledge; it is evidenced based.

Reconstructing the Tree of Life Is a Discovery Process

Reconstructing the history of life has sometimes been called a discovery process: we discover relationships through the discovery and analysis of shared similarities or characters (figure 2). Thus, systematists will begin with a question about the relationships of a set of taxa that is usually based on their previous work or that of others. They will make decisions about the scope of the systematic problem (what taxa will be included) and what types of characters they will examine (DNA sequences or morphological data, for example) and then assemble the relevant specimen material. In the case of molecular sequences, DNA needs to be extracted from tissues, amplified using the polymerase chain reaction (PCR) to make millions of copies of the sequences to be compared, and then the resulting sequences must be aligned for comparison. If the investigator is using morphological data, then skeletons or fluid-preserved specimens are collected together and observations made.

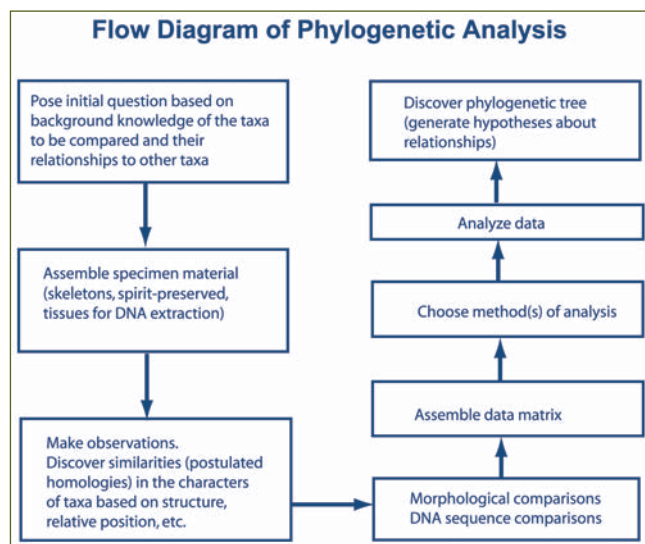


Figure 2. A flow diagram showing the reconstruction of the tree of life as a discovery process.

Observations are summarized into data matrices, with the rows assigned to each of the taxa being examined, and the columns being the individual character codings (character-states of each character). In DNA sequences, those character-states would correspond to the nucleotides adenine (A), guanine (G), cytosine (C), and thymine (T), whereas the character-states of morphological characters would usually be represented by 0, 1, 2, and so on. For example, if we were making comparisons among vertebrates, we might have a character hair and its character-states might be 0 (absent) and 1 (present).

In recent years, matrices have become quite large, often with hundreds of taxa and thousands of characters, thus it takes a computer to analyze those matrices in order to build a tree. Many computer programs are available for building trees and they differ with respect to their theoretical and technical assumptions and methods. Suffice to say, the outcome from any analysis is a phylogeny along with some assessment of how strongly the data support each node on the tree.

The History of Life on Earth

“The history of Life on Earth” summarizes current knowledge about the tree of life but with some caveats. First, our understanding of phylogenetic relationships has grown tremendously over the past decade, and currently hundreds of papers are published in dozens of journals each month, thus making the task of synthesis virtually impossible. Second, although there is general agreement on the large-scale (higher-level) relationships of organisms, there is still considerable controversy over many of these, and a review such as this can only highlight a few of the controversies. And finally, a phylogenetic tree becomes widely accepted once it is supported by the preponderance of evidence, but space limitations do not permit a full discussion of this. Additional resources are provided at the end of the chapter.

The Base of the Tree of Life

One of the early findings using DNA sequences to reconstruct the tree of life was that life is divisible into three main lineages (figure 3): the so-called true bacteria (formal name, Bacteria), the archaeobacteria (Archaea), and the eukaryotes (Eucarya). The first two groups have a simple cellular structure, whereas the Eucarya, which contain plants, animals, and numerous single-celled and multicellular organisms, all share a more complex cell with a nucleus that is

surrounded by a double membrane and many additional genetic and biochemical similarities. The archaeobacteria include the famous extremophiles, which inhabit extreme environments such as hot springs, salt flats, and deep-sea black smokers. Recent evidence shows, however, that they are ubiquitous in all environments. The true bacteria have been the subject of medical study for years because of their association with infections. They have been subdivided into many groups based on their ultrastructure, biochemical characteristics, and now their gene sequences. They have a huge undiscovered diversity in virtually all environments, and their phylogenetic relationships are still relatively poorly known.

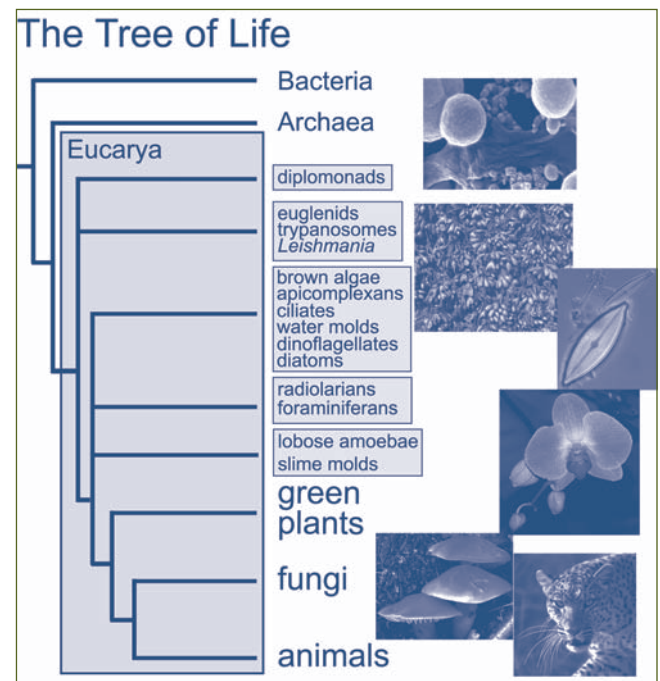


Figure 3. The major branches of the tree of life. (All photos © Joel Cracraft, except for sulfate-reducing bacteria (Labrenz, NSF Multimedia Gallery: <http://www.nsf.gov/news/mmg/index.cfm>) and diatom (Mark B. Edlund, NSF Multimedia Gallery: <http://www.nsf.gov/news/mmg/index.cfm>.)

By far, the biggest controversy through the years has revolved around where to place the root of the tree of life. Some investigators have thought the two “bacterial” groups might go together and the root would then be between them and the eukaryotes. Current data based on similarities in genetic characteristics and cellular chemistry now suggest that the Archaea and Eucarya are sister-taxa relative to the Bacteria (figure 3), but some investigators still harbor doubts.

The oldest life on Earth was bacterial-like, but determining when it first appeared has been a difficult problem (Knoll, 2003). Continents began to form

over 4 billion years ago, and by 3.5 billion years oxygen was still an insignificant component of the atmosphere. Paleontologists have found minute structures (just microns across) in sections of rock deposited at this time that have the appearance of various kinds of bacteria (filaments, rods, spheres), and if they are truly organisms and not produced by geological processes, they would indicate life is at least 3.5 billion years old. The earliest demonstrable life-forms, however, are about 1.9–2.0 billion years old.

The Base of the Eucarya

Although it is widely recognized that Earth's ecosystems are teeming with uncounted numbers of Bacteria and Archaea, nearly all of the currently described diversity on Earth is eukaryotic and can be traced back in the fossil record to about 1.8 billion years ago. There are large numbers of morphologically and genetically different microeukaryotes whose relationships to one another are still uncertain. Which one of these groups is the most basal of the eukaryotes is still debated, but the diplomonads, which include the intestinal parasite *Giardia*, are high on the list. Other lineages near the base of the eukaryotic tree are identified in figure 3 and include an array of single-celled and multicellular forms that are abundant in aquatic environments. Among the more primitive forms are the free-living photosynthetic euglenas, often studied in biology classes, as well as groups containing human parasites including trypanosomes (cause sleeping sickness) and *Leishmania* (destroy tissues like skin and cartilage).

Also among these basal lineages are many different kinds of “algae,” some of which may be related to plants, others to the fungi, or to animals. Whatever their exact relationships, most of these lineages have had a deep history. For example, fossils with substantial similarities to brown algae have been found in sedimentary rocks in China dating to 1.7 billion years ago. Inhabiting both marine and freshwater environments, “microalgal” groups are among the most diverse on Earth and they probably include many millions of species, nearly all of which are undescribed. Because many are photosynthetic, they play a crucial role in global atmospheric chemistry and climate and in the global food chain.

The History of Fungi

The “higher” eukaryotes fall into three broad groups: the green plants, fungi, and animals

(figure 3). One of the more remarkable findings from molecular sequence data in recent years is that fungi are more closely related to animals than to plants. This result is perhaps counterintuitive to most people, but it has been supported by a number of molecular studies; thus, humans are more closely related to a shiitake than to a rose!

Fungi are hugely diverse, with some experts estimating that many millions of species remain to be discovered. Most of these are extremely small or microscopic. There are two well-known groups of fungi, including the Ascomycota, or sac fungi, which contain most of the species that are symbiotic with algae to form lichens, and many that are used in food production (yeasts) and medicines (penicillin). Their sister-group is the Basidiomycota, which includes all the well-known mushrooms, both edible and poisonous.

The History of Green Plants

Green plants are characterized by the presence of chlorophyll a and b, cellulose in their cell walls, and their carbohydrates stored as starch (figure 4). The sister-group of the green plants are the red algae, and as noted above, close relatives of the plants are over a billion years old, therefore the plant lineage very likely extends that far back in time also. The phylogenetic relationships of the major groups of plants have been studied using molecular sequence data but they were first delineated by a series of shared, complex morphological specializations. Thus, as plants took to the land, they evolved reproductive specializations for terrestrial environments that were lacking in their aquatic forerunners such as green algae and basal algal-like groups (charalians). These early land plants—mosses, liverworts, hornworts—apparently appeared on Earth between 400 and 500 million years ago and quickly diversified. Relationships among these major lineages and their relationships to the vascular plants remain uncertain, however.

As their name suggests, vascular plants developed a specialized vascular tissue system to transport nutrients more effectively, and with their increasing size came the development of a central axis—a trunk. The basal vascular plants are fernlike lycophytes and the ferns and horsetails (figure 4). This latter clade is the sister-group of the seed plants, which include nearly all the familiar plants around us. The seed plants are a well-defined group (they share the seed and can produce wood, or xylem) that is known back to the Devonian period, about 280 million years ago.

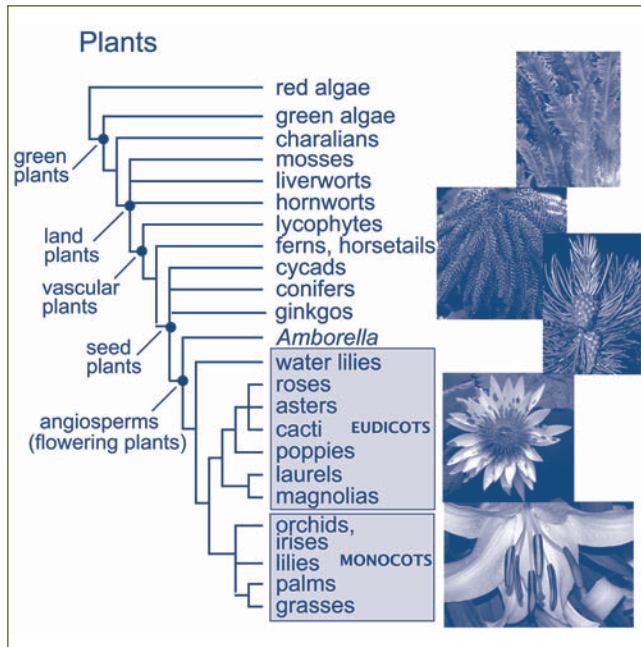


Figure 4. The phylogenetic relationships of plants. (All photos © Joel Cracraft).

Relationships at the base of the seed plants, among the cycads, conifers (pines, firs, spruces), ginkgos, and angiosperms are uncertain and hotly debated. The fossil record of cycads and ginkgos demonstrates that they were much more diverse in the past. Today conifers are important elements of ecosystems in high southern or northern latitudes, whereas angiosperms dominate in temperate and tropical environments.

The 260,000 angiosperms are by far the most diverse group of plants and their monophyly is strongly supported. They produce seeds within a floral structure called a carpel, produce an endosperm (a nutritive tissue for the developing embryo), and have additional specializations of the vascular system. The phylogeny of figure 4 simplifies the vast diversity of the angiosperms, thus many groups have been omitted. One of the more remarkable phylogenetic results of recent years is that a single species, *Amborella trichopoda* found only on the island of New Caledonia, is the sister-species to all the other angiosperms. Also near the base of the angiosperm tree are the familiar water lilies. Most of the angiosperms can be divided into two monophyletic groups, the monocots and eudicots, so named because of possessing one or two seed leaves (cotyledons), respectively. Overall, monocots are less diverse than the eudicots but nevertheless have several highly diverse groups, including orchids and grasses. Both groups have large numbers of economically important species.

The History of Animals

As noted above, recent advances in phylogenetic research have confirmed that fungi are the sister-group of the animals. The latter can be divided into the single-celled (but often colonial) choanoflagellates and the multicellular animals, termed the Metazoa (figure 5). The vast majority of the metazoans can be grouped into the bilaterally symmetrical animals, the Bilateria, which, in addition to their symmetry, have three embryological germ layers thereby leading to significantly more complexity in adult form (including their muscular, vascular, and nervous systems). Basal to the Bilateria are a number of animal groups including several kinds of sponges that are not all related to one another, comb jellies, and the anemones and jellyfish (figure 5).

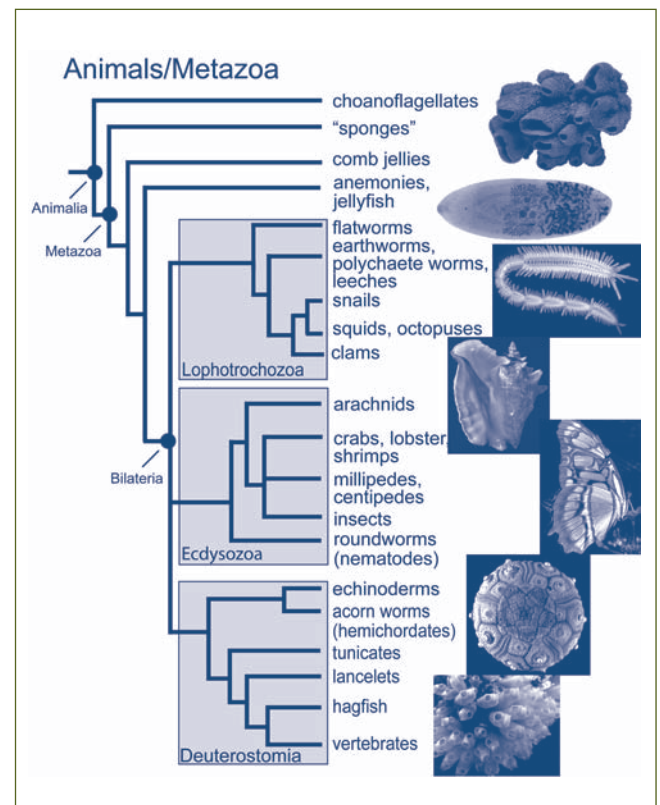


Figure 5. The phylogenetic relationships of animals. Photo credits: sponge and shell (courtesy of American Museum of Natural History), flatworm (courtesy of D. T. J. Littlewood, Natural History Museum London), polychaete worm (courtesy of Gregory W. Rouse), echinoid echinoderm (courtesy of Andrew Smith, Natural History Museum London), tunicates (courtesy of Mark Stitzer, ScubaVenture, <http://scubaventure.net/>).

Bilaterians are broadly divisible into three main groups called the Lophotrochozoa, Ecdysozoa, and Deuterostomia. All three are first known as fossils from sediments at least 530 million years old (near the time of the so-called Cambrian explosion), thus

there is little doubt that animals as a whole must be older. The monophyly of each of these groups is now generally accepted, but their interrelationships to one another and to numerous other small but distinct groups of “invertebrates” need further study (figure 5; many of these smaller clades are omitted).

The core clades of the Lophotrochozoa are the mollusks (snails, squids, octopuses, and clams) and their sister-group, the annelid worms (earthworms, the highly diverse marine polychaete worms, and the leeches), along with the platyhelminth flatworms. The mollusks have exhibited a large diversity throughout most of their history, which stretches back around 560 million years. Within the recent groups, snails and cephalopods (squids, octopuses) are more closely related to each other than either is to the bivalves (clams). The annelids are also a large group. Leeches were derived from earthwormlike forms, and both are apparently embedded within the polychaete radiation. Other lineages considered to be a part of the lophotrochozoan clade include brachiopods, bryozoans, nemertean worms, and several other small groups.

The second major group of Bilateria is the Ecdysozoa, so-called because during growth they shed an external chitinous skeleton through a process called ecdysis. The Ecdysozoa include a number of small basal groups (some of which are shown in figure 6) as well as the highly diverse arthropods. Within the arthropods are four primary clades—the chelicerates (spiders and allies), crustaceans (shrimp, lobster), myriapods (centipedes, millipedes), and the insects. The crustaceans, myriapods, and insects are united in a group, the Mandibulata, to the exclusion of the chelicerates, because they share mandibles, but relationships among these three clades of mandibulates are still a matter of controversy. Most analyses place the crustaceans and insects closer to one another than either is to the millipedes and centipedes. The problem, however, is that there is a vast array of morphologically diverse arthropods in a fossil record that extends back to the Early Cambrian (at least 520 million years ago), and when these fossils, many of which are intermediate in form among the living groups, are included in phylogenetic analyses, the results can often be contradictory.

The chelicerates have their bodies divided into two sections and have their first set of legs modified into chewing or biting structures called chelicerae. Within chelicerates, scorpions are the sister-group of spiders and mites, and horseshoe crabs are sister to all

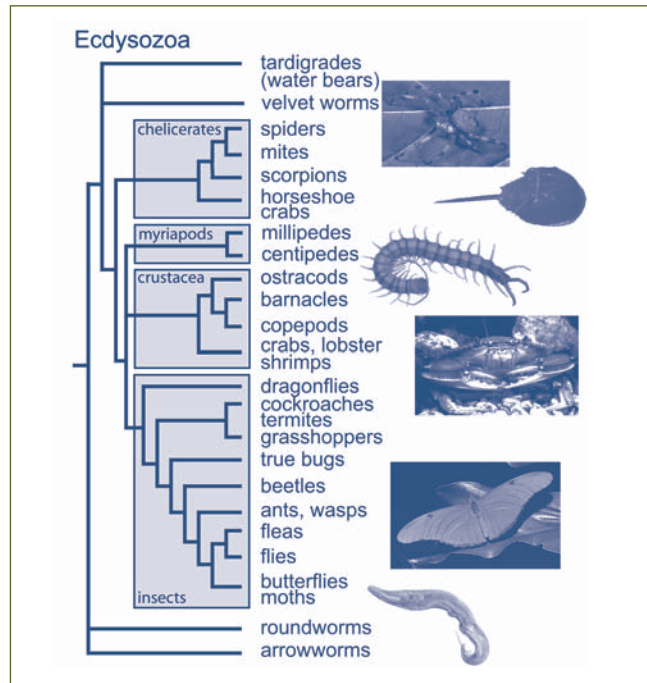


Figure 6. The phylogenetic relationships of ecdysozoans. (Photo credits: spider, horseshoe crab, centipede, and crab [courtesy of American Museum of Natural History], butterfly [© Joel Cracraft], and roundworm courtesy of D. T. J. Littlewood, Natural History Museum London.)

three. Spiders are among the most important terrestrial predators, and along with mites form one of the most diverse lineages on Earth.

Crustaceans are extremely diverse in body form due to variation in the numbers of body segments and appendages and in body size. There are many kinds of crustaceans with common names such as shrimp, crab, or lobster that may or may not be related to one another. Add to this a large and diverse fossil record, and it is easy to see why relationships are still in a state of flux, so much so that some biologists think insects may be closely related to specific lineages of crustaceans rather than to the group as a whole. Nevertheless, each of the two primary crustacean groups, the ostracods, barnacles, and copepods on the one hand, and the crabs, shrimp, and lobsters on the other, are generally recognized as being monophyletic (figure 6).

The insects (Hexapoda, named for three pairs of legs) are the most diverse group of organisms on Earth in terms of the number of species that have been described (over 1 million). As one might expect given such diversity, there still is considerable debate about their interrelationships. The tree shown in figure 6 depicts major relationships among the winged insects (Pterygota) and does not include many wingless lineages at the base of the insect tree. Most of insect

diversity is contained in four groups: beetles (at least 500,000 species); ants, wasps, and bees (150,000); flies and fleas (150,000); and butterflies and moths (150,000). Relationships among these groups are still not well understood.

The final major clade of the Bilateria is the Deuterostomia, which includes the echinoderms (starfish, sea urchins, sea cucumbers) and their sister-group the acorn worms (hemichordates) on the one hand, and the familiar chordates on the other (figure 7). Echinoderms are secondarily pentaradial (that is, they possess five radial segments) as adults, but their larvae exhibit bilateral symmetry and share a number of features with chordates including gill slits (in embryos of chordates) as well as similar sets of developmental genes, hence the relationship of these two clades is widely accepted. Chordates, including us humans, share features including a notochord (a developmentally complex stiffened rod that lies below the spinal cord in the embryo of most chordates), a specialized nervous system, as well as two hormonal glands, the pituitary and thyroid. The marine, soft-bodied tunicates (figure 7) are probably the sister-group of other chordates. Both echinoderms and tunicates are found in the Early Cambrian, at least 530 million years ago.

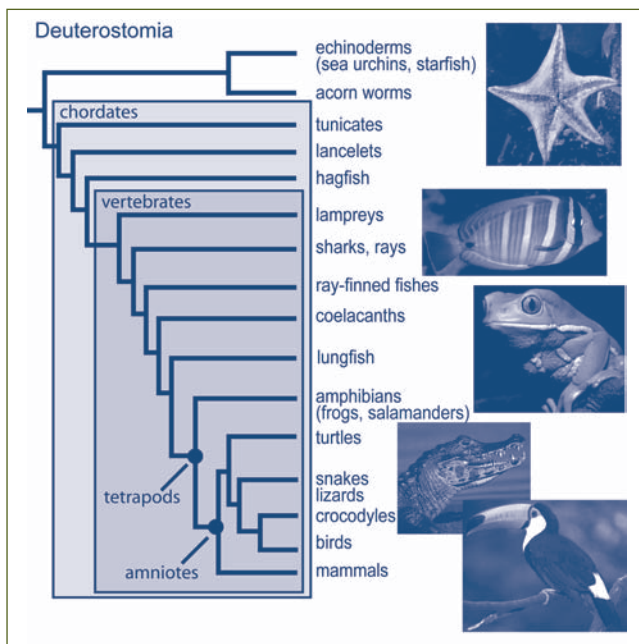


Figure 7. The phylogenetic relationships of deuterostomes. (All photos © Joel Cracraft except for ray-finned fish © Lori Zaikowski, Dowling College.)

Lancelets (amphioxus) are a small marine group of chordates that lack a head and feed by filtering out small microorganisms from the water column or

from bottom sediments. Major evolutionary changes took place with the evolution of the lineage comprised of hagfish and vertebrates, both of which share a well-developed head skeleton enclosing an enlarged brain and sense organs.

Up the deuterostome tree, relationships among the major lineages of living vertebrates are moderately well understood. Lampreys are the sister-group to the jawed vertebrates (called gnathostomes), and successive branches on the chordate tree include the sharks and rays (called Chondrichthyes, or cartilage fishes), the ray-finned fishes, coelacanth, lungfish, and then the tetrapods. Ray-finned fishes account for more than one-half of all chordate species and are abundant in marine and freshwater environments. The pectoral (anterior) and pelvic (posterior) pairs of lobe-fins characteristic of coelacanth and lungfish were evolutionarily modified into the fore- and hind limbs of tetrapods. The majority of early tetrapods were aquatic, and it was not until the evolutionary “invention” of the complex amniote egg (figure 7; amniotes), with its complex series of membranes, large amount of yolk, and modified shell, that a fully terrestrial lifestyle could emerge. This transition to land took place around 325–350 million years ago.

Amniotes can be divided into two major clades, the lineage leading to mammals on the one hand, and the reptile lineage on the other. There are a large number of fossil taxa extending back as far as 300 million years ago that are more closely related to mammals than to any reptile (hence their name, mammal-like reptiles). Within the reptile lineage, turtles appear to be the most basal branch, although the evidence for this is still not completely satisfactory. As is well known, birds are very close relatives of theropod dinosaurs such as *Tyrannosaurus*, but their closest living relatives are the crocodiles and alligators.

Conclusions: Why the Tree of Life Is Important

Evolution as fact

The incessant statements by anti-evolutionists that evolution is just a theory promote a misunderstanding about the process we follow in accumulating knowledge about the world around us and they infuse an anti-intellectual atmosphere into the public schools regarding the subject of evolution. Is the conclusion that Earth is not flat but an ovoid sphere just a theory? Is the conclusion that Earth revolves around the Sun just a theory? Is the conclusion that

malaria is caused by the microorganism *Plasmodium* just a theory? Even creationists would, though perhaps begrudgingly, admit to the notion that, yes, these are facts, they are true statements we make about the world around us. We think we know these things. And we do, because if we treated these conclusions with the same skepticism as creationists do evolution, then there would be little reason to doubt that in traveling from New York to Hawaii we might fall off the end of the world, or in sending a spacecraft to Jupiter it would not arrive (because the laws of physics might be strange if Earth were the center of the solar system), or that sequencing the genome of *Plasmodium* in search for a cure to malaria would be a complete waste of money.

The point is, of course, that knowledge advances using a scientific method, namely, we pose ideas (theories, hypotheses, conjectures) that attempt to explain some phenomenon and we test those ideas by looking at the empirical world. If we do that long enough, and consistently find no reason to reject the idea, then we say it is “true,” a fact, something we know.

The notion of evolution is no different. Science has now accumulated so much evidence life has evolved on Earth that it is indeed a fact to the scientific community. And this evidence and conclusion are so inextricably connected to the other sciences—geology, physics, chemistry, astronomy—that to deny evolution is to reject the very foundations of all the sciences. Evolution is the only rational, scientific explanation for the tree of life.

Tree of Life Research as Science

Evolutionary science is no different from other sciences in that we may have overwhelming support for a conclusion, but we might not know everything there is to know about it. Returning to the example above, we might know it is a fact that *Plasmodium* causes malaria, and we might know many of the mechanisms of that causation, but that does not mean medical science is through studying *Plasmodium* or seeking a cure for malaria.

This chapter has summarized evidence for the fact of a tree of life, but it also has noted that many relationships are still provisional and in need of more data to corroborate, or refute, them. Some of the relationships depicted in figures 3–7 are undoubtedly incorrect, but we can expect these uncertainties will be clarified as new evidence accumulates. This has been the history of systematics research over the past

decades. Thus, the hagfish and lampreys were once united in their own group, but current evidence suggests that lampreys are more closely related to other vertebrates. Many other examples could be cited. It is therefore worth stressing to students that our understanding of the history of life expands much like it does in the other sciences, through raising ideas (hypotheses, etc.) and testing them with new observations.

The Tree of Life as a Basis for Biological Comparison

All of biological knowledge is founded on making comparisons (see Donoghue, chapter 7). Observations made in isolation of other knowledge usually are incomplete, but in the context of comparison those observations take on new meaning and can lead to generalizations. The fact that organisms have evolved over time, and that those descended from a common ancestor share features not found in more distant relatives, makes comparison a very valuable tool for predicting the unknown from the known. Thus, if a newspaper reports the discovery of a new species of mammal, and if you know something about mammals through observation and comparison, you can predict almost immediately that the new species will have hair, mammary glands, and a single bone in the lower jaw, among other characteristics. Moreover, as we sample more and more diversity—fossils as well as living taxa—and gather more and more comparative character information, our predictions can become much more precise. Thus, it is pretty obvious that without knowing how these different groups are related to one another, comparisons will be difficult to make and even more difficult to interpret.

Coda: Knowing the Tree of Life Saves Lives

All of this has major implications for society, as many chapters in this book can attest. Tree of life research has become critical for the success of the medical sciences, forensics, environmental management, and other disciplines. It is no exaggeration to say that the many uses of phylogenetic understanding, along with basic evolutionary biology, are saving lives on a daily basis and are creating economic prosperity. This is why knowing the tree of life is so important to discover and so important to teach in our schools.

An Annotated Bibliography

Cracraft, J., & Donoghue, M. J. (Eds.). (2004). *Assembling the tree of life*. New York: Oxford University Press.

This is the most up-to-date summary of tree of life research, with chapters on all major groups of organisms written by leading systematists.

It also contains a number of chapters on the importance of phylogenetic research to society. While many chapters are technical, many will be of interest to a general audience.

Darwin, C. (1859). *On the origin of species by means of natural selection*. London: Murray.

Dawkins, R. (2004). *The ancestor's tale*. New York: Houghton Mifflin Co.

This is an engaging wander through the history of life by a master of narrative and science writing. In addition to talking about organismal phylogeny, it includes a large amount of information about natural history and evolution.

Knoll, A. H. (2003). *Life on a young planet*. Princeton, NJ: Princeton University Press.

This is a readable account of early life on Earth. It details the fossil evidence and environmental conditions surrounding early life and focuses on the Cambrian explosion, at a time when many major groups of organisms first appeared around 530 million years ago.

Margulis, L., & Schwartz, K. V. (1998). *Five kingdoms: An illustrated guide to the phyla of life on Earth* (3rd ed.). New York: W. H. Freeman.

This book contains a wealth of information about the diversity, structure, biology, and ecology of all major groups of organisms. Although it does maintain an old-fashioned approach to classification and does not have much discussion of phylogeny, it is still an indispensable reference.

Tudge, C. (2000). *The variety of life*. New York: Oxford University Press.

A readable guide to the history of life with numerous phylogenetic trees, although some are a bit out of date. This is probably the best summary of life's phylogeny written for the layperson.

Appendix: General Resources on the Tree of Life

Web search engines can find countless sites devoted to various groups of organisms. Many specialists have their own sites, and a lot of phylogenetic information on specific groups can be found by Web searching. Here are some general resources.

Assembling the Tree of Life: Harnessing Life's History to Benefit Science and Society

This brochure, produced at the request of the National Science Foundation, describes how understanding phylogeny benefits society. It is written for a general audience and would be very appropriate for classroom teaching. It can be downloaded from <http://ucjeps.berkeley.edu/tol.pdf>.

Tree of Life Web sites: General

There are two key Web sites that are gateways to information about the tree of life and both are essential resources for students and teachers:

- *The Tree of Life Web Project* (<http://tolweb.org/tree/phylogeny.html>). The Tree of Life Web Project is the most comprehensive site on the tree of life. Individual scientists have authored Web pages on various groups of organisms. Not all are equally detailed or up to date, but the site is ever-changing and there are links and bibliographies for most groups.
- *University of California Museum of Paleontology* (<http://www.ucmp.berkeley.edu/>). This is one of the most important resources about the history of life and evolution. It has a lot of good information about various groups and their fossil record.

- *The Tree Thinking Group* (<http://www.lrdc.pitt.edu/donovan/>). This Web site is put together by Sam Donovan of the University of Pittsburgh and has a number of posters on tree thinking that can be downloaded. In addition, it points to a lot of valuable resources on the tree of life and phylogenetic analysis.

Theory and Methods of Phylogenetic analysis

Several Web sites provide easily understandable introductions to phylogenetic analysis (cladistics) and the reconstruction of evolutionary relationships. These include the following:

- *University of California Museum of Paleontology* (<http://www.ucmp.berkeley.edu/clad/clad1.html>).
- *The Society of Australian Systematic Biologists*
The society has two sites: see <http://www.science.uts.edu.au/sasb/glossary.html> for a glossary of cladistic terminology and <http://www.science.uts.edu.au/sasb/WestonCrisp.html> for a general introduction to cladistic methodology.
- *ReefQuest Centre for Shark Research* (<http://www.elasmo-research.org/education/classification/cladistics.htm>). ReefQuest also has an introduction to cladistic methodology.
- *Diana Lipscomb* (<http://www.gwu.edu/~clade/faculty/lipscomb/>). Diana Lipscomb provides a link to a PDF file of her basic guide to phylogenetic analysis, which is a good general resource.

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