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1

Evolution's New Narrative

The most obvious realities are the ones that are often the hardest to see and talk about.

—DAVID FOSTER WALLACE, *THIS IS WATER*

Humans are storytellers. We use observations to weave narratives explaining social trends, economic trends, world history, and the trajectory of people's lives. If done well, narratives provide a realistic framework for understanding that tells us much more than facts alone. Of course, scientists use narratives too. Scientific narratives are compact summaries, often using metaphor, that encapsulate our understanding and shape our thinking about how the natural world operates.

The key premise of this book is that the current, conventional narrative for evolution, which can be traced back to Charles Darwin, is outdated. I am not casting doubt on the fact of evolution, which is common ancestry for all of life. I am saying, however, that the conventional narrative for common ancestry, or common descent, has not kept pace with new knowledge and discoveries about evolution's many and disparate paths. My

purpose in this book is to explain why the conventional view is outdated, to portray a new narrative, and to explore why the new narrative matters.

The short version of the conventional narrative describes life as one big family linked by common ancestry. All of us, from bacteria to kelp, condors, and people, are fellow travelers through time, sharing our deepest and oldest roots. The path of common ancestry in this narrative is a sprawling series of splitting events. A single species splits to become 2, those 2 species become 4, which become 8, then 16, then 32, and so on, with bifurcating branches for millions of species filling the wide canopy of life's evolutionary tree. This narrative and the tree metaphor reflect Darwin's statement: "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."¹ In this view, the course of common ancestry is diagramed as a tree, with dividing branches denoting species, and is linked to the process of natural selection, which favors those individuals and groups enjoying greater reproductive success. With Darwin's keen observations of species in nature, his compelling development of natural selection as the mechanism for evolutionary change, and his detailed narrative regarding change among organisms, evolution became the explanation for life's proliferation. Branching tree diagrams had long been used by naturalists in their classifications, grouping similar kinds of organisms, but evolution by natural selection finally provided the natural mechanism giving rise to these relationships, something that had been sorely missing.²

As useful as this branching, tree-based view has been for evolutionary understanding, scientific narratives are dynamic and must change if significant new findings emerge. The time has come to shift our understanding of the evolutionary narrative.

The change in evolution's narrative that I advance here emphasizes greater sharing of genetic materials among different species, and a greater role for the influence of species on their mutual genetic change. I use "horizontal evolution" as a broad umbrella term to cover the various processes for this genetic integration among life-forms.

In vertical evolution genetic material passes from parents to progeny. By contrast, horizontal evolution often entails transfer of genes that is *not* from parents to progeny. Horizontal evolution occurs with variable frequency among different species and at different times. Though we are all well aware of human parents passing their genes to offspring, most of us don't know much of the copious evidence coming to light for horizontal evolution, even within our own past. It is buried in our genomes, as a result of events ranging from ancient horizontal gene transfers from viruses to relatively recent hybridization among different species of *Homo*. The bias of our experience makes it easy to miss the radical plot twists that horizontal evolution knits into the narrative of change covering all species, including our own.

By taking both horizontal and vertical evolution into account, we can better understand the phylogeny for all of life, the overall pattern of genealogy, not simply as a tree but as a network—a network of life.³ This network resembles the tree familiar to us from the conventional model of evolution, but it adds horizontal connections among branches. The network includes both divergence and integration among species and provides a more detailed view of evolution.

Biology has a lot of specialized terms. So, I provide a cheat sheet with quick and simple definitions in table 1.1. A few frequently used terms deserve mention here. "Species" is a concept I use to denote different kinds of organisms. However, there is

Table 1.1. Simple definitions of terms

Branch	The lines in a phylogenetic diagram denoting lineages of organisms or genes
Clade	A phylogenetic group including a common ancestor and all of its descendants, and no others
Classification	A grouping of species or other taxa based on their traits
Coevolution	Heritable change due to species' influences on one another
Core genome	The set of genes shared by all individuals in a species or group (<i>see pan-genome</i>)
Decentralization	Removing central control or influence; enhancing integration and network effects (in this book, heritability is not restricted to that from parents)
DNA	A double-stranded molecule made of nucleotides and carrying genetic information
Endosymbiosis	Symbiosis in which one of the symbiotic organisms lives inside the other
Epigenetics	The study of how environment and behavior affect the way genes work, as with the intracellular environment affecting expression of genes
Genome	An organism's complete set of genetic materials
Holobiont	Assemblage of species including a host and all those living in and on it
Hologenome	All the genomes of all the species in a holobiont
Horizontal evolution	Transmission of genes that is not from parents to progeny; may entail processes of merger, hybridization, recombination, and horizontal gene transfer
Horizontal gene transfer	Genetic exchange between different species
Hybridization	The mating of individuals from different sexual species; analogous to recombination in asexual species
Individual	Single entity; may apply to cells, organisms, taxa, holobionts
Introgression	The transfer of genes between species as a result of hybridization
Lineage	A series of organisms (or genes or taxa) connected by a continuous line of descent
Merger	Joining of two species into one; can result from hybridization and endosymbiosis
Mobile genetic elements (MGEs)	Genetic material that can move within a genome or between species; often helps mediate its own movement (<i>see box 4.2</i>)
Mutation	Change in the DNA sequence of an organism

Table 1.1. (continued)

Natural selection	Differential survival and reproduction of individuals due to heritable variation
Network	Phylogeny based on lineage splitting and joining
Network of life	Phylogeny based on lineage splitting and joining for all life
Pan-genome	The complete set of genes present in a species or group, regardless of their absence in any one individual
Phylogeny	Diagram of genealogy, showing relationships among genes, species, or other taxa
Plasmid	DNA molecule that replicates separately from other DNAs in a cell
Prokaryote	A single-celled organism that lacks a nucleus and other membrane-bound structures
Recombination	The exchange of DNAs between different asexual organisms; analogous to hybridization among sexual species
Replicator	A DNA or RNA molecule that can copy itself on its own or with help
Reticulation	Another term for horizontal evolution
RNA	A single-stranded molecule made of nucleotides, differing from DNA, carrying genetic information
RNA world	A hypothetical stage in life's early evolution with RNA molecules arising before DNA and proteins
Speciation	Process or events giving rise to new species
Species	A taxon including all organisms of the same kind, able to exchange genes; no simple definition can be applied to all life forms
Species radiation	Rapid origin of multiple species from a single progenitor species
Substitution	Replacement of one nucleotide in a DNA sequence with another
Symbiogenesis	Evolutionary change due to long-term stable symbiosis
Symbiont	An organism living in symbiosis with another
Symbiosis	Relationship between organisms living in close association
Taxon/taxa	Any unit used in classification of organisms (species, genera, families, orders, kingdoms); all are human constructs
Technology	Applied scientific knowledge
Tree	Phylogeny based on lineage splitting
Vertical evolution	Transmission of genes from parents to progeny
Virus	A mobile genetic element (see above) that encodes structural proteins encasing its own genome

no single definition of species that can be easily applied across all life-forms.⁴ I use the term “lineage” to denote temporal sequences of groups of organisms. We could, for example, discuss the human lineage as including all individuals going back ten thousand years, or trace its ancestry even further, including all individuals going back ten million years to an ancestor among the primates. “Taxon” (plural: “taxa”) is a general term and can be applied to any group of organisms, whether the group is a population, species, genus, or something more inclusive.

Looking Back

Now that I have laid out the book’s purpose, let’s back up a bit. How have our views and narratives changed? Evolution is the ultimate story about life on Earth, and wondering is arguably one of our oldest habits. What kinds of life exist and why? What do they do and how do they do it? Do new forms arise, and if so, how? How do humans fit into the picture? How did we get to Darwin’s general narrative? This is a vast topic, and I will visit just a few mileposts.

A fascinating early glimpse into human knowledge about life’s diversity comes from Ötzi, also known as the Tyrolean Iceman. Ötzi was born about 5,300 years ago and died, apparently murdered, at the age of 45. With graying brown hair and a thin beard, his five-feet-four-inch, 110-pound body lay frozen and well preserved in a glacier for millennia. He was spotted by hikers in 1991 high in the mountains along the Italian and Austrian border, as his icy crypt melted.

Ötzi spent his life hunting and shepherding in the lush valleys and rugged Alpine terrain of the Ötztal Alps. By necessity, he had an expert’s knowledge of nature. Based on his possessions and clothing, he was ingeniously equipped for survival, stemming

from his cultural inheritance, native intelligence, and millions of years of natural selection of humans. We're ignorant of Ötzi's views on life's history, though we can safely suppose the topic came up around campfires and elsewhere, and that supernatural forces were invoked at least occasionally. We can, however, look at Ötzi's dealings with life's diversity as providing a narrative of his practical views on the living world. The summary would be: I'll use my wits and knowledge of the natural world to survive and perhaps raise a family.

Ötzi and his contemporaries were skilled in propagating domesticated plants and animals, carrying on the agricultural revolution that began about 12,500 years ago. They selected individual plants and animals for future breeding based on their traits and vigor. Often called artificial selection, this is actually natural selection in human hands. Ötzi's leggings were made from goat hides, and his coats and a loincloth were sheepskin patches stitched together with twisted tendon strips. His cap was a fitted piece of brown bear hide worn hair-side out. His shoes, nearly waterproof, had roe deer upper parts, soles made from brown bear hide and laces from cattle hide. He carried a lightweight net for trapping small animals made from the pliable, strong inner bark fibers, called bast, from several different tree species.

Ötzi carried masses of dried birch polypore fungus, *Piptoporus betulinus*, on two narrow leather laces. When eaten, this fungus induces diarrhea and has some antibiotic and anti-inflammatory properties. No doubt, Ötzi attributed some benefit to the fungi he carried, and he may have been self-medicating with these as a treatment for his heavy whipworm infection.

These ancient scraps, all found on or near Ötzi's corpse as the ice melted, reveal his extensive knowledge of what we now call biological diversity as vital to his survival. He depended on other species for his food, clothing, shelter, and medicine

and in planning for survival in harsh environments. And it has always been so throughout human history. We don't know anything of his supernatural beliefs, but it seems he understood clearly that his life and the lives of various other species were intertwined.

Let's move ahead about three thousand years to 340 BCE and consider the Greek naturalist and polymath Aristotle. He was the first to choose inquiry about life's diversity for its own sake and leave us a record of his studies. Most of Aristotle's writing appears as informal notes, though scholars estimate those represent just 20 percent of his actual writings, the rest being lost. Aristotle's pioneering efforts, despite errors and inclusion of some folktales and nonscience, set a high standard. So high, nothing of comparable insight and scope appeared for over a thousand years.

Aristotle's work centered on direct observation in the wild and dissection of animals. Based on his writings, he dissected at least 110 different species, including bats, octopi, dolphins, and chameleons. He used the wealth of facts gained in these detailed dissections and comparisons to better understand the distinctive kinds of life, their forms and their functions.⁵

Aristotle's years of study led him to see similarities and a gradation in the differences among species, or forms, of organisms. He thought living and nonliving entities could be ordered along a scale of vitality, mobility, and, for some species, a potential based on development. He wrote: "Nature proceeds little by little from things lifeless to animal life in such a way that it is impossible to determine the exact line of demarcation. . . . [A]fter lifeless things in the upward scale comes the plant, of which one will differ from another as to its amount of apparent vitality; . . . there is observed in plants a continuous scale of ascent towards the animal. . . . [T]hroughout the entire animal scale there is a

graduated differentiation in amount of vitality and in capacity for motion.”⁶

Aristotle's concept of a scale for life is simultaneously vague and bold. There is no metric for the scale; there are no units for degrees of vitality or mobility. But the idea of relating all life-forms, as variants along a common thread, is entirely new. It also breaks with prior classification methods that his contemporaries used outside of biology on topics of mathematics, astronomy, and philosophy. It is only outlined verbally, but his vision was detailed enough and logical enough to gain a strong following over time.

Aristotle mentioned names of about 230 different animals in his writings. Although he didn't explicitly assign them all to positions on a scale, we can, with a bit of imagination, depict his vision by putting some species into a rough sequence, starting with what he considered the “plant-like” invertebrate animals and continuing from there. Not in a straight line, but zigzagging, sometimes wildly, and tracing an arc of generalized progression in complexity and organization.

Using Aristotle's own study species, we can begin with sea anemones and sponges, and move successively to hard-shelled animals with limpets and mussels, soft-shelled animals with crabs and lobster, soft-bodied animals with cuttlefish and octopus, insects with ants and butterflies, fishes with gobies and parrotfish, snakes with water snakes and vipers, egg-laying tetrapods with tortoises and chameleons, birds with bee-eaters and ravens, and mammals with otters and humans.

Aristotle's rough scale for natural entities, from minerals to plants and then animals, eventually gave rise to the idea of the *scala naturae*, or great chain of being, which became the dominant organizing concept for understanding living diversity for nearly two millennia.⁷ The *scala naturae* was often considered

as arranging species in sequence of increasing perfection or complexity, with the humans at the top of the animal scale, and just below deity, although extending the scale of the *scala naturae* to heaven was not at all what Aristotle had in mind. Aristotle was committed to explaining the natural world based on natural causes, without invoking the supernatural. This commitment was not held by many who followed him, especially those in positions of power, helping to explain why progress in the study of biological diversity was so slow in the ensuing years.

We now jump ahead to eighteenth-century botanist Carl Linnaeus. Like Aristotle, Linnaeus wanted to describe and organize all known life-forms. He championed the use of binomials in taxonomy, consisting of genus and species names. *Homo sapiens* in our case. Before Linnaeus, species names were jargon-filled strings of description trying to be diagnostic. For example, the Latin plant species name *Plantago foliis ovato-lanceolatis pubescentibus, spica cylindrica, scapo tereti* (in English: “plantain with pubescent ovate-lanceolate leaves, a cylindrical spike, and a terete scape”) became simply *Plantago media* in Linnaeus’s treatment. He understood that names couldn’t function as species identification guides, given the pace of new species’ discovery.

Between 1735 and 1766 his book *Systema naturae* went through 12 editions, in which he classified about 9,000 species of plants and 4,400 species of animals. What had been a slim volume of 12 pages became a three-volume series of 2,400 pages. Modern taxonomies still begin with his writings, and the idea of ranked categories of classes, orders, and genera is still in broad use, though not without controversy.

At the time, the dominant narrative for explaining life’s diversity was biblical creation by God, and the number of species and their forms did not change. Though Linnaeus was a creationist and devout deist, his astute observations of variation

within and among species led him, in his latter years, to doubt this view. He had witnessed the origins of new plant species via hybridization (different species interbreeding) in his extensive garden experiments. He and his students saw many wild plants intermediate in form between known species and considered them to be new species of hybrid origin. The twelfth edition of *Systema naturae* omitted a claim that Linnaeus had made in earlier editions: that new species do not form. This implicitly allowed the possibility of natural processes leading to the origin of new species. So, although he was a creationist, he also understood that some new species had arisen, naturally, since the creation.

Next in this selective review of evolution's changing narrative is the work of Charles Darwin, born 31 years after Linnaeus died. Darwin is well known as the founding father of evolutionary biology. Though less well known, British naturalist Alfred Russel Wallace, who studied and developed his ideas independently from Darwin, was a codiscoverer of natural selection. Both linked the concept and process of natural selection to change in organisms over time, providing the key mechanism, natural selection, to unlocking the modern view of life's evolution in their extensive writings. Wallace even expressed a similar view to Darwin's branching tree, describing relationships among species as involving "branching of the lines of affinity, as intricate as the twigs of a gnarled oak."⁸ Though they did publish together in 1858, Darwin's notebooks of 1837 show he had been developing the core ideas 21 years earlier. Darwin framed human evolution as another instance of material process and change. Wallace, however, held that humans owed much of their mental and spiritual faculties to "an unseen universe—a world of Spirit . . . to which the world of matter is altogether subordinate," rather than natural selection.⁹

As noted earlier, the short version of the current scientific narrative for evolution, laid out by Darwin, describes life as one family, with all species related by means of splitting or branching events. This Darwinian tree view for evolution reflected the species classifications used by previous biologists, going back at least to Aristotle. That is, preexisting classifications for plants and animals, based on similarity alone, gained the compelling explanation of evolution. This narrative about natural process brought a newly dynamic and unifying vision of life's history on Earth.

The cultural impact of Darwin's narrative for human origins—the idea that all life, including humans, shares common ancestry—was immediate, striking at the heart of nonscientific narratives regarding the human story. Though controversy continues in some circles, the fact of common ancestry for all life including humans hasn't been a scientific controversy since Darwin's time. This does not mean our knowledge is complete. Far from it. There are many aspects of life's evolution that remain to be discovered or reconsidered and integrated into our growing knowledge.

Evolutionists through the mid-twentieth century predominantly studied animals and, to a lesser degree, plants, and the processes they discovered were placed front and center in evolution's overarching narrative. The conventional narrative has long emphasized that new species arise by branching off from others. This was a foundational insight from Darwin: early examples of speciation as a branching process, with one species splitting into two or, in cases of a species radiation, more than two, include the mockingbirds and finches that Darwin studied on the Galapagos Islands.¹⁰

A key, limiting aspect of the conventional evolutionary narrative is its inherent centralized view. In the conventional

approach each new species receives all its genes, and all the features they encode, from a single parental species—one centralized source. Centralization is baked into the narrative based on branching tree diagrams, which show evolutionary relatedness, or genealogy. These phylogenies show single species splitting into two, over and over again. Our knowledge of evolution has progressed significantly since Darwin, however, revealing a great deal of horizontal evolution. But even for many who know that unconventional, decentralizing events sometimes happen, like the genetic exchange between different species (as in horizontal gene transfer), the overarching narrative of evolution remains conventional.

How does the new narrative differ? Evolution's new narrative depicts common descent for all life's species as a more decentralized network, where branches can both split and join. With a bit more imagination, the new narrative and network for all life are envisioned as a vast tangled system of streams, variously dividing, joining, meandering, and dividing again, as it carries and integrates species and their genes through time, with succeeding generations linked by currents and networks of heritability. The relative frequency and consequences of these networking mechanisms will be described in following sections and chapters. Table 1.2 highlights differences between the conventional and new narratives for evolution.

In the past, some have sought to summarize evolution as a two-step process: first mutation and second natural selection favoring beneficial mutations. These remain key features, but an even broader pair of processes, in keeping with the new narrative for evolution, is that of divergence and integration, with mutation and selection operating within both. In visualizing the basic diagram of life's genealogy, we need to see divergence and

Table 1.2. Comparison of trends for the conventional and new narratives for evolution

	Conventional Narrative	New Narrative
Pattern of genealogy (phylogeny)	Splitting of branches in an evolutionary tree	Joining and splitting of branches in an evolutionary network
Pattern of phylogeny applies to	Mostly organismal species	Organismal species, genomes, gene families, genes, mobile genetic elements (MGEs), endosymbioses, hybridizations, recombination, horizontal gene transfer events
Brief prose rendition of the narrative	“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” (Darwin)	Life’s evolution may be represented as a system of tangled streams, variously dividing, joining, and dividing again, as they carry lineages of organisms and their genetic materials through time, with succeeding generations linked by currents of heritability
Evolutionary tempo	Mostly gradual, uncommonly episodic	Often gradual, often episodic; horizontal evolution being capable of faster change with more impact, compared with single base mutations and vertical evolution
Heritable material	Centralized, meaning genes are received from parents only or nearly so	Decentralized, meaning genes are received from parents and, potentially, many other organisms
Heritability of acquired traits?	No or minor	Often, depending on the species
Key mechanisms	Vertical evolution and natural selection acting on variation in DNA sequence mutations among individuals	Same as conventional view, plus horizontal evolution (hybridization among species, endosymbioses, horizontal gene transfer, recombination among different bacteria and archaea)

integration simultaneously. Both are real and can coexist within groups of organisms.

The need for this new narrative stems not from any single recent discovery or eureka moment for a person or team, but from the cumulative weight and synthesis of many discoveries about the functions and evolution of biological diversity, some dating back to the nineteenth century and many others based on current science. In recent years there have been increasing calls for change from the conventional view, given these new discoveries. Evolutionary and molecular biologist W. Ford Doolittle was early to spotlight the problem: "If chimerism or lateral gene transfer cannot be dismissed as trivial in extent or limited to special categories of genes, then the history of life cannot properly be represented as a tree."¹¹ Bringing the broad outlines of evolution's new narrative into better alignment with current science by taking horizontal evolution into account alongside vertical evolution improves our thinking about life's past and its future, including our own.

The Means of Horizontal Evolution

Horizontal evolution occurs along a continuum. This ranges from direct sharing of genetic material among different species, at the more material end, to mutual genetic influences among species, known as coevolution by natural selection, at the less material end. The three primary means of direct sharing are: (1) hybridization among sexual species and recombination among microbes, (2) the joining or merger of species, and (3) horizontal gene transfer.

To visualize this, let's map vertical evolution and these three processes of horizontal evolution on a phylogenetic network, with time advancing from the bottom to the top (figure 1.1).

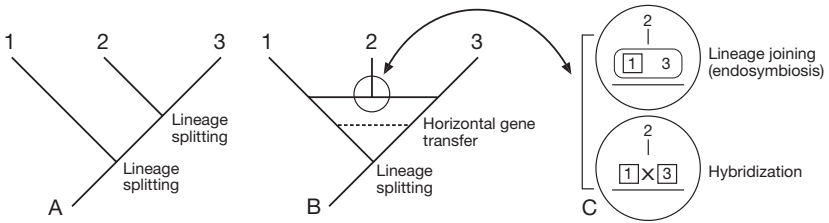


FIGURE 1.1. Reading evolutionary (phylogenetic) relationships from (A) a tree and (B) a network. Time progresses from the bottom up, and the splits closest to the bottom are the oldest. In A, species 2 and 3 are closest relatives (sisters). In B, species 2 arises from two possible scenarios. Horizontal gene transfer is shown as a dotted horizontal line between species 1 and 3. C shows the two possible scenarios within the circle at the base of species 2 in B, either lineage joining (*top*—an individual of species 1 swallowed by an individual of species 3) or species hybridization (*bottom*—an individual of species 1 hybridizes with an individual of species 3). See table 1.1 for definitions of terms.

Figure 1.1A shows two lineage splitting events (vertical evolution) on a tree, with species 2 and 3 being most closely related. Figure 1.1B shows lineage splitting between species 1 and 3 at the bottom, followed by horizontal gene transfer as a dotted line, and then horizontal evolution between species 1 and 3 giving rise to species 2. This latter horizontal evolution is diagrammed in figure 1.1C as either joining or hybridization. The terminology cheat sheet in table 1.1 provides helpful definitions.

Let's consider the same three processes of horizontal evolution, in the order given above. Hybridization occurs when individuals of different sexually reproducing species interbreed. This leads to mixing of genes between the species, known as introgression. In recent years, the study of large genomic datasets has shown that introgression is much more common than previously thought. Domestic crops offer a clear example

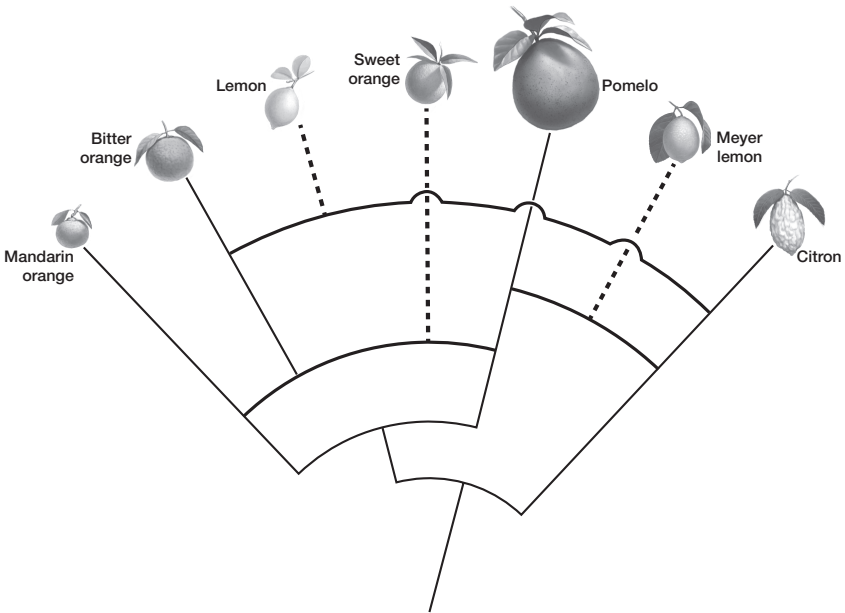


FIGURE 1.2. Phylogenetic network showing evolutionary relationships among citrus trees. Species that have hybrid origins are shown with dashed lines, and dark lines connect their parents. For example, mandarin orange trees hybridizing with pomelo trees gave rise to sweet orange trees. Similarly, pomelo trees hybridizing with citron trees gave rise to Meyer lemon trees.

Drawing modified from Curk, F., Ollitrault, F., Garcia-Lor, A., Luro, F., Navarro, L., and Ollitrault, P., 2016, "Phylogenetic Origin of Limes and Lemons Revealed by Cytoplasmic and Nuclear Markers," *Annals of Botany*, 117(4):565–83.

of hybridization in action. Figure 1.2 shows the outcome of hybridization among some citrus tree species. Many modern cultivars are the result of intentional hybridization followed by selection for variations in features like taste, cold-hardiness, and disease resistance. Recombination within and among bacteria

and archaea is analogous to sexual reproduction and hybridization, and is discussed in chapters 2 and 3.

The joining or merger of species begins as interactions, including symbioses, among individuals from different species that become obligate and genetically integrated over time. A primary mechanism for joining of species lineages is endosymbiosis. This occurs when one symbiont resides inside another. The difference between joining and hybridization is depicted in figure 1.1C. Some of the most consequential innovations in life's 3.8-billion-year history stem from a joining of previously distinct lineages by endosymbioses. This includes the origins of two essential components of cells: mitochondria found in all animals, plants, and fungi, and chloroplasts found in plants.

The third process is horizontal gene transfer. This is the movement of genetic material between organisms, outside of its vertical transfer between parents and progeny. Discoveries of horizontal gene transfer over the past 50 years have provided some of the biggest changes in our understanding of evolution in recent times, and it is now recognized as a dominant mode of evolution among microbes.¹² Most if not all genes in the genomes of all bacteria and archaea (the oldest and most inclusive groups of single-celled life) have experienced horizontal gene transfer in their past. Horizontal gene transfer is comparatively rare in plants, fungi, and animals; however, it is being discovered in them with increasing frequency. Given that early lineages of all multicellular life-forms arose with the help of horizontal gene transfer among bacteria and archaea, horizontal gene transfer ranks as a key feature in life's evolution and now an important part of the new narrative. For a quick and partial view of the pervasive nature of horizontal gene transfer, see figures 1.3 and 1.4. The former shows instances of horizontal gene transfer into plants, and the latter shows horizontal gene

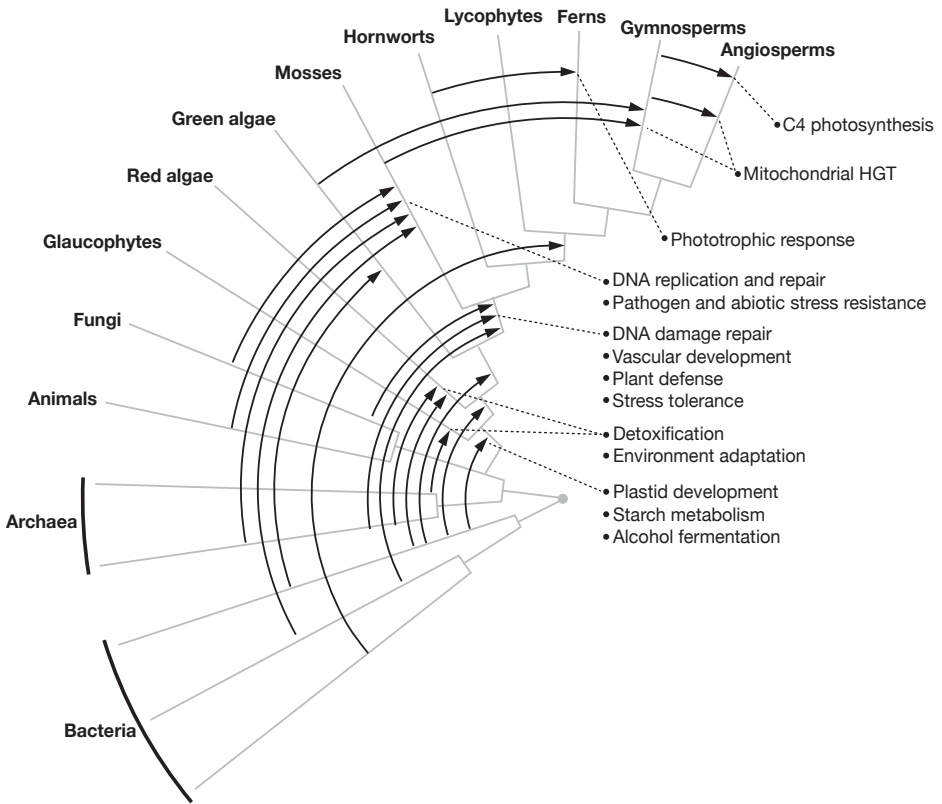


FIGURE 1.3. Horizontal gene transfer (HGT) into plants from bacteria, archaea, animals, and fungi. Arrows begin at donor groups and point to recipient groups.

Drawing modified from figure 5 of Yue, J., Hu, X., Sun, H., Yang, Y., and Huang, J., 2012, "Widespread Impact of Horizontal Gene Transfer on Plant Colonization of Land," *Nature Communications*, 3:1152; see also Soucy, S. M., Huang, J., and Gogarten, J. P., 2015, "Horizontal Gene Transfer: Building the Web of Life," *Nature Reviews Genetics*, 16(8):472–82.

transfer among select bacterial species, resulting from transfer of small DNA molecules called plasmids.

These three processes—species hybridization, species joining, and horizontal gene transfer—result in a decentralizing of the material of inheritance. Decentralization is a key tenet

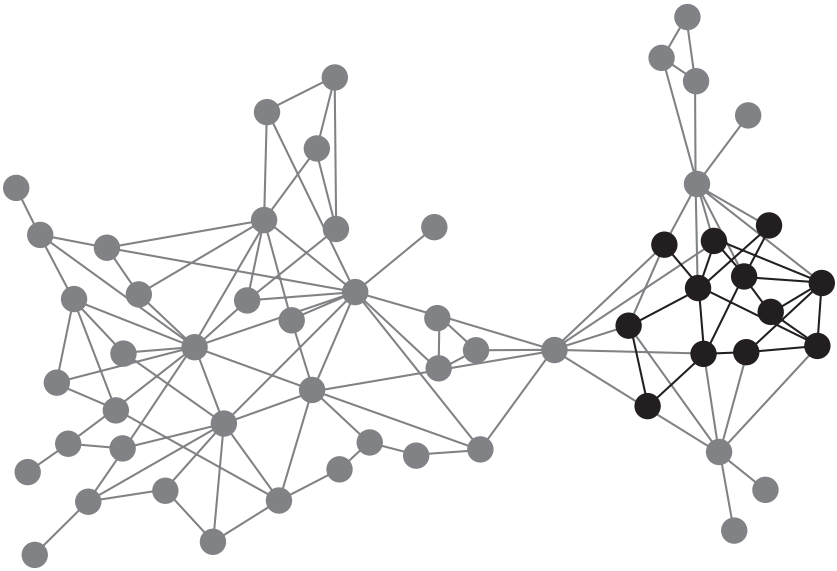


FIGURE 1.4. Unrooted phylogenetic network, in which the lines indicate horizontal gene transfer among bacterial species, represented by dots. Horizontal gene transfer events here are mediated by plasmids, which are small DNA molecules that replicate separately inside bacterial cells. Each dot denotes a separate species in a large phylum of bacteria known as Proteobacteria, which includes the genera *Escherichia*, *Salmonella*, *Vibrio*, *Helicobacter*, and others. Differences in shading of dots indicate different taxonomic classes.

Drawing modified from Redondo-Salvo, S., Fernández-López, R., Ruiz, R., Vielva, L., de Toro, M., Rocha, E. P., Garcillán-Barcia, M. P., and de la Cruz, F., 2020, “Pathways for Horizontal Gene Transfer in Bacteria Revealed by a Global Map of Their Plasmids,” *Nature Communications*, 11(1):1–13.

of the new narrative of evolution. Many species can and do get their genes from one or more different species. This differs from the conventional view, in which a new species derives its genetic material from one, central parental species. Horizontal evolution’s strong decentralizing forces, both past and

present, are much more than a trivial detail. Its pattern is opposite and complementary to that of conventional branching. Its consequences within the narrative are at least twofold. Horizontal evolution can catalyze change within species as well as a dramatic proliferation of species. It does not subsume the conventional narrative, but shows it to be inadequate. Modernizing evolution's narrative better represents current science, and makes the understanding to be drawn from the narrative richer and more accurate.

Decentralization as a concept has proven useful in understanding the relative success of various strategies in governance, economics, and technology. And its application to the evolution of biodiversity, particularly its potential adaptive and maladaptive features, will be developed in chapter 2. To visualize this decentralization of heritability, see the example phylogenetic network in figure 1.1*B*. It differs from a phylogenetic tree in that lineages have genealogical links to more than one other species.

The fourth process under the umbrella of horizontal evolution is coevolution of species by natural selection. This happens over time, for example, between flowers and their pollinators, between predators and their prey, and between pathogens and their hosts. Thus, deeper flower nectaries select for longer bills in hummingbirds, and greater virulence in pathogens selects for greater resistance in their hosts. Figure 1.5 provides more examples. By definition, coevolution yields heritable, genetic change among species over time, similar in the long run to the direct mechanisms of genetic sharing noted above.

All species are subject to coevolution to some degree; however, its impact in driving life's evolution is often under appreciated. The new narrative for evolution emphasizing integration of genetic materials must include coevolution, as it shines a

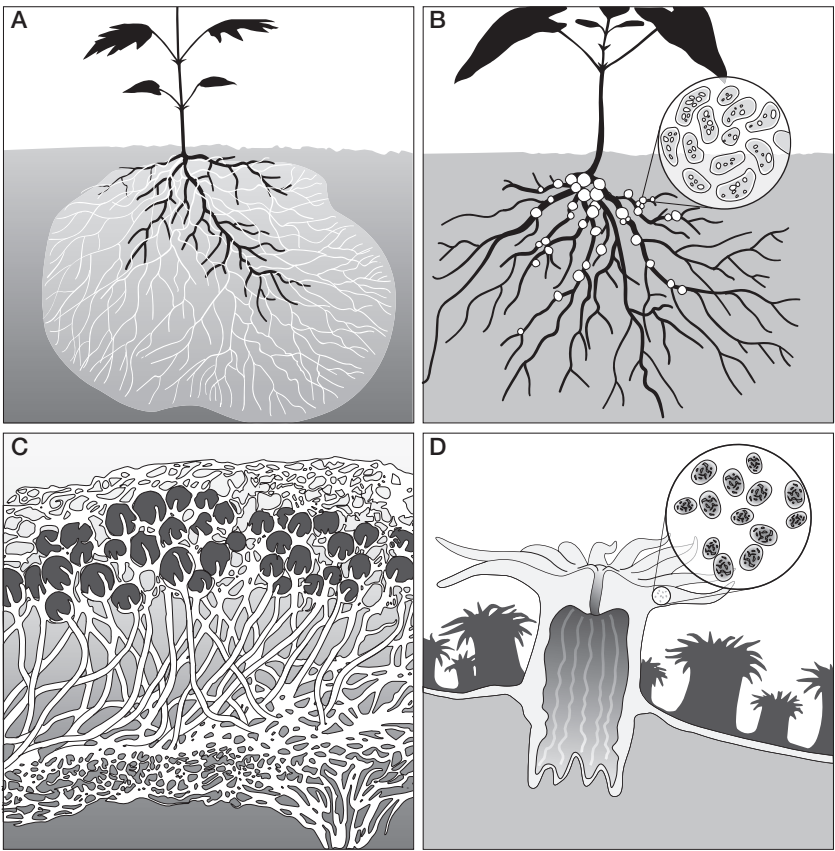


FIGURE 1.5. Examples of coevolution for different species. *A*, Mutual influence of fungi and plant roots yielding mycorrhiza, in white, which aid plant nutrition; *B*, bacteria and plant roots yielding root nodules, which house nitrogen-fixing bacteria; *C*, fungi and bacteria or algae yielding lichens; *D*, algae and the small animals called polyps, which build corals. Examples *B–D* are also endosymbioses, with one species living inside another.

necessary light on coevolution as the process by which species' ecological and behavioral interactions lead to mutual and heritable genetic changes in their form and function. As such, coevolution aligns conceptually with the other processes under the umbrella of horizontal evolution. Coevolution is a primary theme in part II of this book, which explores why evolution's new narrative matters.

The Network of Life

A simplified graphic of life's story—the origins and evolution of species—is shown in figure 1.6. The braided stream represents heritable information in the form of DNAs, which animate and flow through succeeding generations of all organisms. Bacteria and archaea are the two forms of single-celled microbes (prokaryotes) and gave rise to eukaryotes, a group that includes the rest of all known organisms. No diagram can show the entirety of life's history. Doing so would require tracking the reproductive efforts of countless individual organisms and genes through time. Further, experts estimate that extinction has claimed over 99 percent of all the species that have ever existed, erasing much of the molecular record. But still, the record of change unlocked by comparison of genomes among current species is richly detailed, and the relationships shown among these primary groups are increasingly well supported.¹³

The groups named in figure 1.6 are presented in table 1.3, which gives estimated numbers of extant species for the groups and a characterization of the extent of horizontal evolution for the lineage due to hybridization, joining, and horizontal gene transfer. The designations of high, medium, and low indicate relative importance and role in diversification of the group.



FIGURE 1.6. Life's phylogenetic network represented as a system of tangled streams, variously dividing, joining, and dividing again, as they carry lineages of organisms and their genetic materials through time, with succeeding generations linked by currents of heritability. Time proceeds from background to foreground. Note eukaryotes arising from within archaea.

All the primary groups shown are substantially impacted by horizontal evolution. Their lifestyles, their bodies, and their genomes are all deeply influenced by its integrating mechanisms. Some groups more than others, of course, and at some times more than others.

Vertical evolution and conventional branching patterns remain key to the new narrative, especially among animals, but they are woefully insufficient to explain the entire genealogical network of life. Agreement for the new narrative with current research findings requires new emphasis on genetic and organismal integration. Seeing diagrams of both vertical and horizontal evolution together is like gazing at a world map on a school classroom wall with the country and state borders

Table 1.3. Comparison across organismal lineages of estimated numbers of extant species and relative extent of past horizontal evolution

	Estimated Number of Species (% of total for nonviruses) ¹	Relative Extent of Either Sexual Hybridization or Asexual Recombination	Relative Extent of Joining/ Key Benefit	Relative Extent of Horizontal Gene Transfer
Bacteria and archaea	1.746 billion (78%)	High	Low	High
Animals	163.2 million (7%)	Low	Low/ cellular energy	Low to moderate
Plants	0.340 million (<0.5%)	Moderate	Low/ cellular energy and photosynthesis	Moderate
Fungi	165.6 million (7%)	Moderate	Low/ cellular energy	?
Protists	163.2 million (7%)	Moderate	Low to moderate/ variously cellular energy and photosynthesis	Moderate
(Viruses) ²	187 million	High	Low	High

Sources: Larsen, B. B., Miller, E. C., Rhodes, M. K., and Wiens, J. J., 2017, "Inordinate Fondness Multiplied and Redistributed: The Number of Species on Earth and the New Pie of Life," *Quarterly Review of Biology*, 92(3):229–65; Locey, K. J., and Lennon, J. T., 2016, "Scaling Laws Predict Global Microbial Diversity," *Proceedings of the National Academy of Sciences of the USA*, 113(21):5970–75; Lefkowitz, E. J., Dempsey, D. M., Hendrickson, R. C., Orton, R. J., Siddell, S. G., and Smith, D. B., 2018, "Virus Taxonomy: The Database of the International Committee on Taxonomy of Viruses (ICTV)." *Nucleic Acids Research*, 46(D1):D708–17; Rohwer, F., 2003, "Global Phage Diversity," *Cell*, 113(2):141; Geoghegan, J. L., and Holmes, E. C., 2017, "Predicting Virus Emergence amid Evolutionary Noise," *Open Biology*, 7(10):170189.

1. Estimating numbers of species on Earth is difficult, requiring assumptions and extrapolations. This table follows Larsen et al. ("Inordinate Fondness") for animals, plants, fungi, and bacteria, totaling 2.238 billion species. A recent estimate for archaea of 20,000 species (Tahon, G., Geesink, P., and Ettema, T. J., "Expanding Archaeal Diversity and Phylogeny: Past, Present, and Future," *Annual Review of Microbiology*, 75 [2021]:359–81) does not add significantly to the estimate for bacteria alone. The paper by Locey and Lennon ("Scaling Laws") predicts a much higher number of roughly 1 trillion microbial species alone (including bacteria, archaea, and microscopic fungi), estimates not shown in this table, using a scaling approach. Despite differences in estimates, a common finding is that microbes vastly outnumber animals, plants, and nonmicroscopic fungi.

2. There are no suitable estimates for numbers of species for all viruses as a group. The International Committee on Taxonomy of Viruses currently recognizes 6,950 species (Lefkowitz et al., "Virus Taxonomy"); however, most virus diversity remains undescribed. Rohwer ("Global Phage Diversity") estimated roughly 100 million species for phage viruses, a virus group that infects bacteria and archaea. Geoghegan and Holmes ("Predicting Virus Emergence") estimate 87 million virus species infecting eukaryote species. Locey and Lennon ("Scaling Laws") predict 100 billion "microbial" species (bacteria, archaea, and microscopic fungi only, excluding viruses or microscopic eukaryotes) using scaling laws.

clearly drawn, and then superimposing another map showing the highways and the airplane, train, and ferry routes that cross the borders and seas. This is a richer, more connected map.

Scientific advances in resolving life's evolutionary story have been accompanied at nearly every step by discovery of additional complexity. Our understanding of the network of life will always be a work in progress. Because our data and analyses are improving. And because the network is dynamic, growing and changing, even as you read this. New lineages are always emerging or disappearing, and some genes are always being moved somewhere. This is vastly more common among viruses and bacteria than among vertebrates, but still the network evolves. Most nascent organismal lineages and genetic transfers are likely to be ephemeral, but some may last, either by chance or by natural selection favoring adaptation.

The new narrative uses the metaphors of networks or webs as patterns of relationship because these are more appropriate for describing evolution than that of strictly branching trees. Analyses and description of phylogenetic trees are more appropriate for some species (most eukaryotes) and less so for others (bacteria and archaea), where horizontal evolution is more common. Evolutionary trees will always be useful and are deeply embedded in evolutionary discourse. But for overarching narratives, networks that combine vertical and horizontal evolution are much more accurate. As I will discuss later, the new narrative also better informs thinking about the environment, health, and conservation. A variety of popular misconceptions related to evolution and phylogeny are outlined in table 1.4. Their corresponding "better conceptions" often reflect evolution's new narrative as well.

Some will object to elevating the importance of horizontal evolution as an explanation and driver of life's diversification.

Table 1.4. Common myths about evolution, phylogenetic trees, and life

Misconception	Better Conception
Phylogenetic trees and rooted networks show evolutionary progress, usually advancing from species on the left to those on the right	The ordering of tips has no meaning regarding progress; all tips denoting extant species are of equal age relative to shared common ancestors
Species arise by splitting only, with one becoming two	Species can also merge, with two becoming one
Some living species are ancestors of other living species	Living species are cousins, not ancestors
Species are consistently, clearly defined	In many cases, designating species is difficult
Evolution progresses from primitive forms to advanced	Evolution can yield both increased and decreased complexity
We've discovered most or all of Earth's unique life-forms (species of organisms)	The rate of discovery of new life-forms and variants is as high as ever, in large part because of molecular sequencing efforts
Viruses are not alive	Viruses reproduce, carry genetic instructions, and evolve, and many biologists do consider viruses as alive or in a grey zone; life is a process (see chapter 4)
Inheritance of acquired features doesn't exist	Inheritance of acquired features is integral to horizontal evolution and, to a lesser degree, immune system evolution; the term carries historical baggage
All organisms including humans are intelligently designed	Organisms change over time by processes of evolution and often include inefficient features

I understand the reluctance, but suspect it reflects a primary focus on groups such as vertebrates, where horizontal evolution is rare. It helps to note that frequency and importance (or consequence) are not the same. The horizontal evolution events early in life's history (entities joining) associated with the emergence of eukaryotes have had greater consequences for diversifying life than vertical evolution (entities splitting) among vertebrates alone. Elevating horizontal evolution, however, does not diminish the importance of vertical evolution. Horizontal evolution is often most reliably identified against a backdrop of vertical evolution. The two are complementary in revealing the complex patterns of relationship among life-forms.

The methods of phylogenetics for estimating genealogy remain vital as they are needed to evaluate vertical evolution and, in doing so, to expose horizontal evolution. The tangled networks of relationships occur at several levels of biological organization: among species, among individual organisms, and among their genes and entire genomes. Though recovering these networks of relationships requires increasingly large datasets (mostly molecular) and analytical tools, the findings explain more than relationships alone. They map the ancient and ongoing integration among life-forms.

Finally, I want to call attention to two more differences in the implications of the new and conventional narratives for life's evolution (see table 1.2). First, recognizing the importance of horizontal evolution places new focus on the episodic nature of evolution's tempo. Events of joining and horizontal gene transfer are relatively sudden compared with the conventional scenario of more constant, smaller-scale, single-DNA-base substitutions. Second, horizontal evolution entails inheritance of characteristics acquired during an individual's lifetime. Horizontal gene transfer into a single bacterium can be inherited

by its progeny. This is reminiscent of, but quite different from, the older historical conception of Lamarckian inheritance, whereby physical traits of organisms acquired during their lifetimes could be inherited by their progeny. Genes and their mechanisms of inheritance were unknown when inheritance of acquired traits was entertained by biologists like Lamarck and Darwin. Nor was there any detailed understanding of key differences between body cells (soma) and reproductive cells (sperm, eggs). Regardless of what we call it, the reality of many acquired traits becoming heritable is now clear. This stems not just from the mechanisms of hybridization, joining, and horizontal gene transfer discussed here, but from mechanisms associated with epigenetics (changes in the expression levels of genes), immune system capacity, and genome editing as done by organisms themselves.¹⁴ Though detailed review of the findings from each of these fields of study is beyond the scope of this book, they fit better with the new than with the conventional narrative for evolution.

Why Has It Taken So Long?

Why has it taken so long for evolution's new narrative to gain traction among nonspecialists, the public, and even many biologists? Key discoveries about horizontal evolution have been hiding in plain sight for a very long time. Darwin knew of exceptions to the metaphor of a "great tree" for the evolution of different life-forms, even as he first applied the term. Animal breeders, like Darwin the pigeon fancier, and avid gardeners all knew that hybridizing among species could lead to new forms. Similarly, many modern biologists have seen through their own research that the tree metaphor and accompanying narrative of serial branching are insufficient or even misleading as

descriptors of evolution. My arguments here are, in many ways, a rear-guard and after-the-facts action to address the narrative.

There are of course many reasons for the delay. Some likely reasons stem from differences in the timing and pace of scientific advances across different disciplines. Still other reasons concern obstacles to cultural change, inside and outside scientific communities. Perhaps the enduring fact of common ancestry for life may have helped to shield an outdated narrative. For the first century after Darwin and Wallace, most evolutionists studied animals and plants, and the mechanisms of change seen in them were taken as examples that could be extrapolated for the evolution of all life-forms. But, in hindsight, that was mistaken. The great diversity and ubiquity of microscopic, single-celled organisms remained to be discovered.

We also like to see ourselves as the star of any story that includes us. But consider how far removed our species is from an average, representative species of life's diversity. We are one among millions if not billions of species, depending on how species are defined, and very few are like us. Even the complete set of vertebrate animal species, about 66,000 strong, represents a paltry fraction of life's diversity. The vast majority of species and organisms, now and across time, are single-celled microbes. And it is their modes of change and proliferation, varied as they are, that dominate by frequency across the 3.8-billion-year history of life.

The attention we humans give to microbes, even now, is still largely focused on our relationships with pathogens or species used in industry. The vast majority of microbes are unseen and unnamed. Out of sight and out of mind. This is despite the fact that microbes pioneered in oxygenating the Earth's atmosphere, making it habitable for our kind, and in evolving the fundamental molecular and genetic mechanisms that facilitate

(continued...)

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