

“Tree Thinking”:

The Rhetoric of Tree Diagrams in Biological Thought

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Abstract: Tree-like visualizations have played a central role in taxonomic and evolutionary biology for centuries, and the idea of a “tree of life” has been a pervasive notion not only in biology but also in religion, philosophy, and literature for much longer. The tree of life is a central figure in Darwin’s *Origin of Species* in both verbal and visual forms. As one of the most powerful and pervasive images in biological thought, what conceptual and communicative work has it enabled? How have the visual qualities and elements of the tree form interacted with biological thinking over time? This paper examines the pre-Darwinian history of tree images, the significance of Darwin’s use of such images, and the development of tree diagrams after Darwin. This history shows evidence of four separate traditions of visualization: cosmological, logical-philosophical, genealogical, and materialist. Visual traditions serve as rhetorical contexts that provide enthymematic backing, or what Perelman calls “objects of agreement,” for interpretation of tree diagrams. They produce polysemic warrants for arguments in different fields. The combination of the genealogical tradition with the cosmological and the logical changed the framework for thinking about the natural world and made Darwin’s theory of evolution possible; the later materialist tradition represents the “modernization” of biology as a science.

Keywords: evolutionary biology, rhetoric of science, tree of life, visual rhetoric, visual tradition

Introduction

In December 2014, a team of 200 scientists from 80 labs published eight studies of avian genomes in the journal *Science*, simultaneously with 20 additional papers in other journals, all the

results of a coordinated effort to understand the evolutionary history of birds. One of the major results showed that modern birds originate from only four dinosaurian lineages that survived mass extinction 66 million years ago, as demonstrated by a massive computer-generated tree diagram (Jarvis *et al.*, 2014).¹ Tree diagrams have been widely used by biologists for decades to understand the evolutionary history of biological organisms. They are perhaps the most important tool for explaining how, through a long, gradual process of mutation and adaptation, a dinosaur can become a bird. This particular tree and the associated projects make new arguments about avian evolution, many of which were widely reported in popular media: for example, that falcons are more closely related to parrots than they are to other birds of prey such as eagles, owls, and vultures; that all modern birds are descended from a dinosaurian ancestor that had once had teeth but lost them 116 million years ago; that a “big bang” of bird speciation occurred shortly after the extinction of the dinosaurs 66 million years ago, when most types of modern birds appeared; and that song-learning evolved three separate times (Jarvis *et al.*, 2014; Pennisi, 2014; Zhang *et al.*, 2014).

What is novel about this evolutionary tree are the data that were used to generate it: as emphasized in the flagship paper (Jarvis *et al.*, 2014), the relationships were built from whole-genome data, rather than a set of morphological characteristics or a few selected genes or proteins. In their introduction to the *Science* issue, the authors claim that the massive amount of data used to generate this tree resolves some long-standing disputes about the “timing and topology of [bird species’] radiation,” that is, the time in history these species evolved and how they are related to each other (Zhang *et al.*, 2014). Erich Jarvis, one of the lead researchers on this breakthrough project, explained in an interview with *Scientific American* that this new tree “contradicts morphology-based trees. It contradicts mitochondrial trees. It supports more trees based upon nuclear genes, although those trees weren’t highly resolved and this one is” (Mirsky, 2014). The tree’s new features raise new questions and generate new arguments regarding the complicated evolutionary history of the avian class; it thus acts not only as an illustration of the data that generated it, but also as an inventional tool.

¹ See figure 1 in Jarvis (2014), available at <http://science.sciencemag.org/content/346/6215/1320/tab-figures-data>.

Tree-like visualizations have played a critical role in taxonomic work for centuries, and the idea of a “tree of life” has been a pervasive notion not only in biology but also in religion, philosophy, and literature for much longer. It is a central figure in Charles Darwin’s *Origin of Species* in both verbal and visual forms. In summarizing his argument about natural selection, Darwin says this, in a widely quoted passage:

The affinities² of all the beings of the same class have sometimes been represented by a great tree . . . As buds give rise by growth to fresh buds, and these if vigorous, branch out and overtop on all sides many a feebler branch, so by generation I believe it has been with the great Tree of Life, which fills with its dead and broken branches the crust of the earth, and covers the surface with its ever branching and beautiful ramifications. (pp. 129–130)

One of Darwin’s earliest intimations of the idea that would become the *Origin* was a tree-like diagram in an 1837 notebook. And although Darwin used only one tree diagram in the entire *Origin*, Alan Gross has argued that it is so central that a “view of the *Origin* as a book with one diagram is mistaken; it is really a diagram so complex that it takes a whole book to unfold its meaning” (2007, p. 67). Darwin himself considered the diagram so central to his argument about how species arose that he insisted on its necessity with his publisher, calling it “*indispensable* to show the nature of the very complex affinities of past & present animals” ([1859b]).³

Since Darwin, “tree thinking” has become central to biology, and the tree has become “the single most powerful and most often used image of evolutionary history,” (Archibald, 2014, p. 22); entire textbooks are devoted to generating and interpreting such diagrams. The term “tree thinking” was introduced by Robert O’Hara to epitomize the explanatory task of converting questions of state into questions of process (1988b), a conversion the rhetorician might think of as a change of stasis from existence to cause. In other words, instead of treating the question “why are flamingos pink?” as a question about the present state of pinkness (to which the answer is diet and metabolism), the evolutionary biologist must learn to think of it as a question about history and change (how and

² We will have more to say later about this term “affinities.”

³ We are indebted to William Kimler for pointing this out to us.

when did pinkness become a species trait?). A 2005 perspective essay in *Science* claims that evolutionary trees, or phylogenies, “have become an essential element of modern biology,” pointing for example to their multiple uses in the AIDS epidemic. The authors note that the field of phylogenetics “is complex and rapidly changing, replete with a dense statistical literature, impassioned philosophical debates, and an abundance of highly technical computer programs” (Baum *et al.*, 2005, p. 979). Another team of biologists notes that “Our conception of evolution and our interpretation of phylogenetic trees are intimately linked . . . How we interpret phylogenetic trees directly impacts our understanding of evolution” (Omeland *et al.*, 2008, p. 854). As cognitive and inventional tools, evolutionary tree diagrams are ripe for rhetorical inquiry. They have been continually adapted and modified for different rhetorical situations in response to a changing discipline and to changing media. With rhetoricians turning their attention to the role of visuals in science, it seems worthwhile to take a closer look at the role of tree diagrams in evolutionary thought.

What we aim to do here is to extend Gross’s discussion of Darwin’s diagram by placing it into the historical context of the development of tree diagrams in the biological sciences both before and after Darwin. Given its endurance and its centrality to biological thought, we are interested in understanding what rhetorical role the visualization of the “tree of life” has played in the development of evolutionary thinking. As one of the most powerful and pervasive images in biological thought, what conceptual work and what communicative work has it enabled? What does the tree form “mean”? How have the visual qualities and elements of the tree form changed over time as they have interacted with developing biological issues? We propose to address these questions by examining the pre-Darwinian history of tree images, the significance of “tree-thinking” in Darwin’s thought, and the rhetorical work of the major forms of post-Darwinian tree diagrams. Through tracing this history, we see evidence of four separate traditions of visualization: a cosmological tradition, a logical-philosophical tradition, a genealogical tradition, and a materialist tradition. These traditions are not consistent with each other; they arose for different reasons, inform different ways of reading the meaning of the tree form, and thus influence the way we think visually about biological relations. They represent historically contingent assumptions that condition the meanings of the images they produce. Their differences have led to problems that the sciences of phylogenetics and systematics are still dealing

with. In short, evolutionary tree diagrams have been a central rhetorical mechanism in the emergence of evolutionary theory, as these visualizations and their changing forms and interpretations shaped and constrained scientific thinking about the natural world.

Visual Rhetoric and Tree Diagrams

Tree diagrams are used to show structured relationships, including hierarchies (such as organization charts), classifications (such as branches of knowledge or computer file structures), and process or chronology (such as decision trees, flowcharts, or genealogies). There is little agreement on what a tree diagram must look like: whether it must be oriented with a root at the bottom or can be inverted or presented sideways. Manuel Lima's book on tree diagrams takes a broad approach, including not only vertical and horizontal trees but also multidirectional, radial, rectangular, and other forms that do not look much like trees at all but do serve the function of "portray[ing] hierarchical structures" (2014, p. 11). Gunther Kress and Theo van Leeuwen's discussion of the semiotic capacities of tree diagrams focuses on their role in classification (1996, pp. 79–89). However, they complicate their discussion by distinguishing two structures of representation: trees that are narrative, presenting "unfolding actions and events, processes of change, transitory spatial arrangements," and trees that are conceptual, presenting "generalized and more or less stable and timeless essence" in terms of "class, structure or meaning" (1996, pp. 56, 79). Narrative structures have "vectors," that is, directionality, whereas "conceptual structures never do" (1996, p. 57). There is thus a fundamental ambivalence in the tree image, and as Kress and van Leeuwen note, such diagrams "can blur the boundaries between the dynamic and the static" (1996, p. 84). In fact, as we shall see in what follows, this ambivalence dogs the long history of tree of life diagrams, and it echoes the change of stasis from existence to cause required by "tree thinking," as noted earlier.

Two recent studies in the developing literature on the visual rhetoric of science address tree of life diagrams directly. One study examines tree diagrams in contemporary public communication about biological evolution. Han Yu evaluated 218 diagrams from 145 articles in popular science magazines, finding that many do not accurately represent the principles of evolutionary biology and are likely to be misinterpreted by their public audiences (2018). Our research suggests that the reasons for this situation are historically

complicated: that the misinterpretations result in part from scientific debates about evolutionary theory itself and in part from the competing visual traditions that influence the construction and interpretation of these diagrams.

We have already mentioned the other study, Gross's deeply contextualized discussion of the conceptual and rhetorical work done by the tree diagram in Darwin's *Origin*. Gross sees Darwin's achievement in this diagram not only as a distillation of the book's entire argument but also as an important step in making biology a truly modern science (2007, p. 62). In later work with Joseph Harmon, Gross characterizes modern science as "Heideggerian," based on the philosopher's view of science as objectifying the world into a "picture" or image; Heidegger, they say, was the first philosopher "who saw clearly that visualization was central to the sciences" (2014, p. 19). In their account of Heidegger, objectifying the world as a picture turns it into "spatiotemporal magnitudes of motion" that can be expressed as "a calculable nexus of forces" (quoted in 2014, pp. 7, 13, 27). They thus connect visualization with calculation as essential to modern science, and we will see this relationship foregrounded in what we have called the "materialist" tradition of tree diagrams, which developed in the early 20th century.⁴

Many studies on visual rhetoric in science concern the relationships between the verbal and the visual aspects of an argument and the differing affordances of these two modes,⁵ or as Gross and Harmon put it, the "division of communicative, semiotic, and epistemic labor between words and images" (2014, p. 31). Although J. L. Lemke has observed that the verbal mode excels at expressing the "typological," that is, creating categories and expressing differences and relationships, whereas the visual mode excels at the "topological," that is, expressing continuous change, covariation, spatial relationships, and dynamic emergence (1998, p.

⁴ By our term "materialist," we mean to invoke scientific materialism, not rhetorical new materialism. Scientific materialism (sometimes called "physicalism") is an older (17th-18th century) monist view holding that existence or reality consists only of spatiotemporal matter (Stoljar, 2017), whereas contemporary new materialism, also monist, aims to combine or blend dualisms such as subject/object, culture/nature, mental/physical, and the like (for example Gries, 2015).

⁵ Jonathan Buehl includes a very helpful survey of this material (2016, pp. 14-20).

87), tree diagrams challenge this division of cognitive labor, since as noted earlier they can show (or posit) categories (or types), as well as process and change.

Because the verbal and visual modes are so distinct and so differently capable, Gross has claimed that “rhetorical theory as it is traditionally conceived cannot be legitimately ‘stretched’ to include the visual. Just as does the verbal, the visual requires treatment that is *sui generis*” (2009, p. 149). As a result, he adopts dual coding theory from cognitive psychology, which posits that verbal perception and visual perception require two separate cognitive processing systems, with different representational units and different associative systems that produce different responses; he grounds his analytical system for visuals on Gestalt psychology and Peircean semiotics (Gross, 2009; Gross & Harmon, 2014). However, we are reluctant to dispense with rhetoric as an approach to understanding scientific visualization. And there is some precedent for retaining it: after all, if Heidegger emphasizes the visual, so does Aristotle, according to George Kennedy (Aristotle, 2007, p. 222). But we will also introduce three more recent witnesses to support our case.

The first witness for the defense of rhetoric in scientific visualization must be Jeanne Fahnestock’s work on figuration. In spite of her statement that the visual is an area in which “the discipline of rhetoric itself needs to be enriched to hold up its part in the rhetoric of science” (2005, p. 279), she has demonstrated that patterns used to describe verbal expression and arguments, such as antithesis and *incrementum*, can also describe visualizations (1999). She points out, for another example, that parallelism “is a mental perception that can be produced visually as well as verbally,” and those productions, as “formal devices,” can reinforce an argument that is based on a series of supporting examples (2003, pp. 124-125).

A second witness is the work by Lynda Walsh on topical systems in science. She shows that in inventing and composing visuals for research publication, researchers rely on rhetorical *topoi*, which she defines as “beliefs, norms, values, and commonplaces that shape . . . discourse” (2018, p. 6); examples of important scientific *topoi* used this way include change over time, comparison, and degree. Moreover, Walsh makes the case that some *topoi* can be found in multiple semiotic modes (the verbal, visual, and gestural, which she calls “channels of communication”); she thus challenges the

necessity for dual coding theory and hypothesizes that “the processes of visual invention and composition are fundamentally continuous and are scaffolded on top of basic cognitive operations” (2018, p. 25).

Our third witness for the utility of rhetoric in understanding scientific visuals is Jonathan Buehl’s book *Assembling Arguments*, which shows how the verbally oriented rhetorics of Chaim Perelman and Kenneth Burke can illuminate scientific visualization (2016). Of particular interest to us is Buehl’s emphasis on what Perelman and Olbrechts-Tyteca call the starting points of argument, or “objects of agreement” (2016, pp. 30-32), as ways of explicating the functions and effects of scientific visuals. The “objects of agreement” that serve as starting points include agreements about the real (facts, truths, and presumptions) and agreements about the preferable (values, *topoi*, and hierarchies). Such agreements lie in the background of verbal argument, as well as in the visual contributions to argument, often unexpressed and implicit. We suggest that they can serve as what Toulmin calls “warrants” or “backing,” that is, the premises upon which interlocutors are understood to agree and which help to constitute an “argument field” such as a scientific discipline (1958). Such agreements are not limited to discrete, propositional facts or maxims but tie into wide networks of prior knowledge, cultural memory, and belief systems about the way the world is and the way it should be. As premises to enthymemes, whether expressed or presumed, they condition orientations to inquiry and expectations about results. Thomas Kuhn called these community-defining agreements “disciplinary matrices,” suggesting that they include symbolic generalizations (or scientific laws), metaphysical paradigms (which include models and metaphors), values, and exemplars (or model problem-solutions) (1962, pp. 182-187). Burke ties these background agreements specifically to language, to the way that our terminologies direct our attention in particular ways and thus “screen” or filter our perceptions and interpretations; he claims that what “we take as observations about ‘reality’ may be but the spinning out of possibilities implicit in our particular choice of terms” (1966, p. 46).

Our point here is that visualizations, like verbal expressions, are used and interpreted in contexts that are complexes of such agreements, and our hypothesis for the discussion that follows is that what we identified above as “traditions” of visualizing the tree of life serve rhetorically as enthymematic premises for interpreting

tree diagrams—that is, as prior agreements about the real and the preferable that serve as backing or presumptions about what a particular diagram can mean, how it means, and how it functions in a line of thinking about biology. As historians of scientific imagery Lüthy and Smets observe, “The meaning of a given image can only be grasped in the context of the epistemological, metaphysical and social assumptions within which it is embedded” (2009, p. 398). A tradition, in the sense we are using it, is an historically sedimented configuration of such assumptions or “objects of agreement”; these assumptions make the tree of life a familiar concept that already has a set of possible meanings, reflecting and reinforcing that same configuration. The fact that such traditions provide interpretive contexts for not only the visual but also the verbal components of argument helps explain how they reinforce each other.

Our term “visual traditions” has affinities with the ways that others have taught us to understand images in historical context. For example, Roland Barthes, speaking about photography and images in advertising, notes that there is a “historical grammar of iconographic connotation,” that is, a “cultural code” that informs a photograph’s “connoted message” (1977, pp. 22, 46). Art historian Michael Baxandall examines how Italians in the 15th century, both painters and public, “attended to visual experience in distinctively Quattrocento ways and how the quality of this attention became a part of their pictorial style,” summarizing these as a socially conditioned “period eye” (1988, pp. 27, 29). More generally, the great art historian Erwin Panofsky emphasizes that the interpretation of three strata of visual meaning (primary subjects, conventions, and symbols) must be “supplemented and corrected by an insight into historical processes the sum total of which may be called tradition” (1955, p. 39).

We hope our notion of visual-rhetorical traditions can complement and perhaps extend recent discussions of critical approaches to visual rhetoric, like those of Cara Finnegan (2010) and Laurie Gries (2015). To take Finnegan’s discussion, for example, traditions, as we are conceiving them, influence all five of the approaches she identifies: the production, composition, reproduction, circulation, and reception of tree-of-life diagrams (2010, p. 252). Although Gries has a somewhat similar scheme (with a particular focus on circulation), she also emphasizes several principles of rhetorical new materialism (such as becoming and virality) that draw attention to the dynamic, emergent nature of images and their future transformations (2015, pp. 86-87). Our

emphasis on traditions pulls in the reverse direction, toward the past, providing a deep intertextual framework for production, composition, reproduction, circulation, and reception.

Tree Diagrams before Darwin

The pre-Darwinian history of the tree of life shows this image to be more complex and polysemic than the simple tree form might suggest. In the first place, the history is a very long one, with the pre-historical mythologies of many cultures using a tree of life motif, in both verbal and visual forms (Hacking, 2007, pp. 224-225; Hellström, 2012, pp. 245-246; James, 1966). For example, many artifacts from ancient Assyria show a highly stylized tree form representing a sacred tree of life (Lima, 2014, pp. 16-17), the Nordic tradition features the “world-tree” Yggdrasil that supports the earth and the heavens,⁶ and the creation story in the *Book of Genesis* makes reference to a tree of life in the Garden of Eden. This verbal image became deeply embedded in Christian iconography, being visualized in illuminated manuscripts, sculpture, and decorative architectural elements throughout Christian Europe. Beyond signifying life itself, and the sustenance of human life in particular, the tree image came to represent the specific relationship between the earthly and the divine worlds, a hierarchical set of connections between the low and the high, the imperfect and the divine. This is the tradition of visualization that we are calling “cosmological.”

The cosmological tradition is epitomized in the *scala naturae*, or Great Chain of Being, a representation that is sometimes more ladder-like than tree-like, as the name suggests. This image, primarily in verbal form, is “one of the half-dozen most potent and persistent presuppositions in Western thought,” according to Arthur O. Lovejoy (1936, p. vii). The *scala naturae* represents the universe as “composed of an immense, or . . . of an infinite number of links ranging in hierarchical order” from barely existent up to the perfect being, with each link differing from those above and below it by the “‘least possible’ degree of difference” (Lovejoy, 1936, p. 59). It has sources in both Plato’s idea of the Good and Aristotle’s attempts to systematize the natural world, but it is most fully developed in Christian neo-Platonism (Lovejoy, 1936, p. 61). Some visualizations show the chain as a ladder or stairway, but the

⁶ See <https://publicdomainreview.org/collection/yggdrasil-the-sacred-ash-tree-of-norse-mythology>.

version in Figure 1 shows the cosmos as a tree-like structure, arrayed in hierarchical ranks, from devils at the bottom, up through plants, animals, fish, birds, humans, and angels, to the deity at the top, all connected by a single chain held in the right hand of the deity falling down through the center.

Lovejoy claims that the Great Chain of Being reflects three principles of world-ordering: plenitude (that is, it includes all possible forms of existence), continuity (there are no gaps), and “unilinear gradation” (a single hierarchy), with a vertical scale of perfection, or actualization of goodness (1936, pp. 58-59, 61). Lovejoy also notes that the Great Chain of Being incorporates contradictory notions: from Plato both otherworldliness and its opposite, and from Aristotle both “the habit of thinking in discrete well-defined class-concepts and that of thinking in terms of continuity, of infinitely delicate shadings-off of everything into something else” (1936, p. 57). These contradictions can be read from the diagram. It shows the relationship between the divine realm and the material world as a link in the continuous chain similar to that between the animate and inanimate worlds; this continuity is in tension, however, with the depiction of discrete levels clearly distinct from one another. In Lemke’s terms, the Great Chain of Being attempts to be simultaneously typological and topological (1998). We can also see that it is, in Kress and van Leeuwen’s terms, primarily conceptual, showing a stable structure of the cosmos, but at the same time there is a narrative-like trajectory, drawing us upward toward the perfection of the divine.

The cosmological tradition of tree-thinking survived in Enlightenment efforts to rationalize the natural world, as natural philosophers like Linnaeus, Buffon, Lamarck, Diderot, Cuvier, and Darwin’s own grandfather, Erasmus Darwin (Bowler, 1989), struggled to understand the grand harmonious plan assumed both by natural theologians and by rational mechanists to structure the universe. One visual example is provided by Charles Bonnet’s “Concept of a Ladder of Natural Beings,” 1745.⁷ This diagram is a simple vertical ladder, with overtly religious imagery removed and only observable phenomena included, from fire, air, water, earth, and metals on the bottom rungs; to plants, insects, shellfish,

⁷ From *Traité d’Insectologie*; available at <https://commons.wikimedia.org/wiki/File:BonnetChain.jpg>.



Figure 1. The Great Chain of Being, from the *Rhetorica christiana* by Fray Diego de Valades (1579). Wikimedia Commons. Retrieved from <https://commons.wikimedia.org/w/index.php?curid=33603873>

serpents, fish, birds, and quadrupeds on higher rungs; and humans at the top. Bonnet emphasizes the principle of continuity, confident that “missing links” will be found: “Shall we judge of the chain of beings by our present knowledge? . . . The gap that we find between the vegetable and the mineral will apparently some day be filled up . . . to demonstrate the admirable gradation there is between all beings” (quoted in Lovejoy, 1936, p. 233). His diagram, then, is an expression of confidence in the principle of continuity. Both these figures show higher and lower orders of being, but they indicate no other relationships (i.e., no branching) or chronology: as depictions of a permanent creation, there is no need for an historical dimension.

Even today, the *scala naturae* persists in contemporary biology. In the words of the title of a recent article in the journal *Evolution: Education and Outreach*, “The great chain of being is still here” (Rigato & Minelli, 2013). As the authors claim, “We should not expect in the current professional literature in biology, and evolutionary biology in particular, any survival of *scala naturae* thinking, or of the corresponding language” because of its hierarchy and its “complete lack of historical perspective. . . . These expectations, however, fail to be supported by facts” (Rigato & Minelli, 2013, p. 1). This data-mining study of over 60,000 biological articles published in major biology journals between 2005 and 2010, found “ladder” language in over 1000 of the articles, such as “higher” and “lower,” “primitive” and “advanced” forms of life, and placement of humans as “highest.” A similar critique in *Nature* notes that many presentations of evolution “mirror the great chain by viewing the process as progressive” and by habitually placing the human species at the top of visual representations (Nee, 2005; see also Omland *et al.*, 2008). Likewise, Yu’s study of popular science magazines, mentioned earlier, found visual orientations that “promote an incorrect, progressive reading of evolution” (2018, p. 100).

Closely related to the *scala naturae* is the second visual tradition, the representation of logical relationships in tree form. Logic trees are usually traced to a 3rd-century verbal description by Porphyry in his introduction to Aristotelian logic (*Isagoge*), where he explains genus–species relationships as a sequence of hierarchical subordinations, or as analysis by dichotomous division; this work became the basis for most medieval instruction in logic. The earliest visual representation of this set of relationships in the Western tradition occurred in the 9th century (Hacking, 2007, p. 232), but

such tree diagrams became ubiquitous only in the 13th century, beginning with Peter of Spain's influential work on logic written around 1235. According to Ian Hacking, Peter "clearly understood the logical form of his diagram [as] . . . not merely a representation of a text of Porphyry's" but as a "relationship of abstraction" (2007, p. 245), with the most abstract and inclusive category at the top, and a descending series of dichotomous divisions into more and more concrete categories. The 14th-century logic diagrams of the prolific Ramon Llull are less abstract and more tree-like, elaborated and ornamented with roots, branches, and leaves (Hacking, 2007), such as the one in Figure 2 from a 1512 edition of his *Logica Nova*, representing one version of medieval scholasticism. This tree represents from the top: being or substance, divided into essential and accidental; essence divided into corporeal and incorporeal; the corporeal, divided into animate and inanimate; the animate, divided into rational and irrational; and the (rational) human, divided into representative individuals, Plato and Socrates; with question (or inquiry) at the root (see Hacking, 2007, p. 248).

Logic trees are similar to the *scala naturae* in some ways but quite different in others. Since both represent eternal and universal relationships, neither has any place for chronology. In the vertical dimension, both represent hierarchy: of abstraction, or logical inclusion, in the former case and of perfection in the latter. But they are also quite different in that the *scala naturae* does not represent relations of inclusion from one level to another: angels do not "include" humans, whereas substance includes all of material reality.⁸ Although the principles of plenitude and continuity hold that there is a gradation between entities on each level in the Great Chain of Being, the relations of inclusion in the logic tree mean that the levels must be quite distinct from one another. Furthermore, in the horizontal dimension, the *scala naturae* indicates numerousness: there are many plants, birds, fish, humans, but fewer angels, and just one perfect divinity at the top. In contrast, logic trees in the Porphyrian tradition restrict themselves to dichotomous division, a practice consistent with Plato's practice of

⁸ Loosely. There are differences between Aristotle and his Christian medieval interpreters; and Aristotle wasn't completely consistent, but for him substance is matter plus form (Robinson, 2018, p. 2.2.2).

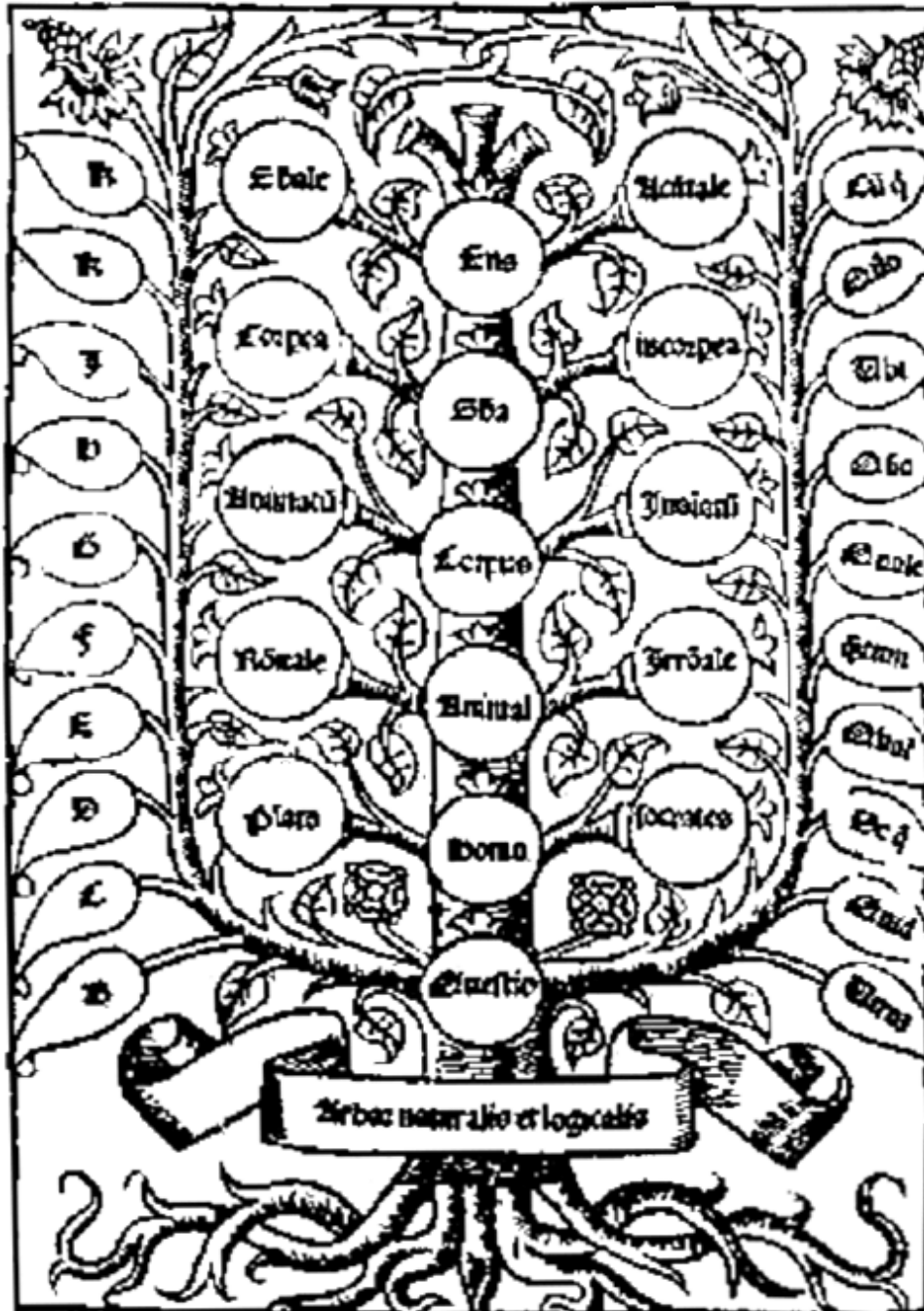


Figure 2. Raymond Llull's Arbor naturalis et logicalis (Tree of nature and logic), from *Logica Nova* (1305), 1512 edition. Wikimedia Commons. Retrieved from [https://commons.wikimedia.org/wiki/File:Arbor_scientiae_\(Ramon_Llull\)_using_A_porphirii_structure.png](https://commons.wikimedia.org/wiki/File:Arbor_scientiae_(Ramon_Llull)_using_A_porphirii_structure.png)

dialectic and Aristotle's early thinking on logic and metaphysics.⁹ Thus, there are only two entities at each level, both of which are included in one of the two entities at the level just above.

Centuries later, we see the influence of logic trees in the work of early modern natural philosophers, who were familiar with medieval logic from their own schooling. Given their assumption that the natural world is an orderly system, logic, that is, the method of dichotomous division, seemed the best tool for finding that order (Mayr, 1982, p. 159). Thus, we find the bracketed table, or dichotomous diagram, a distinct visual genre, appearing in the 16th century to organize knowledge in many fields; according to Pietsch, who shows several examples, its earliest use to show similarities and differences among organisms was a 1555 classification of wading birds (see also Lima, 2014, p. 102; 2012, p. 11).¹⁰ Perhaps the most influential user of the bracketed table was Carl Linnaeus, who had excelled in the study of logic at school (Mayr, 1982, p. 173). As one historian notes: "Linnaeus's system of classification owes much to scholasticism . . . [it] was simply the result of filling in the abstract Tree with the names of actual species" (Franklin, 1986, pp. 246, 252).

Linnaeus aimed to represent the rational plan of divine creation within his classification system, an ambition revealed in the title of his first work, the monumental *Systema Naturae*, published in 1735 and republished in many continually expanded editions during his lifetime; he had, according to Ernst Mayr, an "obsession to classify" (1982, p. 172). He began with 18th century assumptions: that species were stable, that the relationships among them would reflect a single orderly system, and that this system would be a linear hierarchy much like the *scala naturae*. Many of his works include bracketed tree diagrams, and the example in Figure 3 shows dichotomous division used to map out the plant kingdom through

⁹ In his later works on biology, Aristotle came to realize that dichotomy would not suffice to classify the complexity of the plants and animals he observed (see Aristotle, 1961, pp. I.iii.643b610-615; Leroi, 2014, pp. 111-113). Interestingly, we will see dichotomy reappear in cladograms of the 20th century.

¹⁰ Bracketed tables were used in many other applications, with what Walter Ong calls a "cult of dichotomies" reaching a peak in the work of curricular reformer Peter Ramus and his followers in 16th-century France, primarily in the pedagogy of dialectic (1983, pp. 202, 199).

CLAVIS SYSTEMATIS SEXUALIS.

NUPTIÆ PLANTARUM.

Actus generationis incolarum Regni vegetabilis.

Florescentia.

PUBLICÆ.

Nuptiæ, omnibus manifestæ, aperte celebrantur.

Flores unicuique visibiles.

MONOCLINIA.

Mariti & uxores uno eodemque thalamo gaudent.

Flores omnes hermaphroditi sunt, & stamina cum pistillis in eodem flore.

DIFFINITAS.

Mariti inter se non cognati.

Stamina nulla sua parte connata inter se sunt.

INDIFFERENTISMUS.

Mariti nullam subordinationem inter se invicem servant.

Stamina nullam determinatam proportionem longitudinis inter se invicem habent.

- | | |
|----------------|------------------|
| 1. MONANDRIA. | 7. HEPTANDRIA. |
| 2. DIANDRIA. | 8. OCTANDRIA. |
| 3. TRIANDRIA. | 9. ENNEANDRIA. |
| 4. TETRANDRIA. | 10. DECANDRIA. |
| 5. PENTANDRIA. | 11. DODECANDRIA. |
| 6. HEXANDRIA. | 12. ICOSANDRIA. |
| | 13. POLYANDRIA. |

SUBORDINATIO.

Mariti certi reliquis præferuntur.

Stamina duo semper reliquis breviora sunt.

- | | |
|----------------|-------------------|
| 14. DIDYNAMIA. | 15. TETRADYNAMIA. |
|----------------|-------------------|

AFFINITAS.

Mariti propinqui & cognati sunt.

Stamina coherent inter se invicem aliqua sua parte vel cum pistillo.

- | | |
|-------------------|-----------------|
| 16. MONADELPHIA. | 19. SYNGENESIA. |
| 17. DIADELPHIA. | 20. GYNANDRIA. |
| 18. POLYADELPHIA. | |

DICLINIA (a *δῖς* bis & *κλῖν* thalamus f. duplex thalamus.)

Mariti & Feminae distinctis thalamis gaudent.

Flores masculi & feminei in eadem specie.

- | | |
|---------------|----------------|
| 21. MONOECIA. | 23. POLYGAMIA. |
| 22. DIOECIA. | |

CLANDESTINÆ.

Nuptiæ clam instituuntur.

Flores oculis nostris nudis vix conspiciuntur.

- | |
|------------------|
| 24. CRYPTOGAMIA. |
|------------------|

CLAS

Figure 3. Linnaeus's "Key to the Sexual System" of the Plant Kingdom, from *Systema Naturae*, 10th ed., 1758. This bracketed diagram uses dichotomous division based on medieval logic trees. Botanicus.org Creative Commons License. Retrieved from <http://botanicus.org/page/586756>.

reproductive morphology. Mayr notes that he chose reproduction as the basis for his scheme of classification because it represented the “working plan of the creator” (1982, p. 178).

Sideways trees such as this begin with an all-inclusive category on the left, breaking into smaller, more exclusive groups towards the right. The axes are turned 90 degrees from the earlier examples: the vertical axis is diversity or plenitude; the horizontal axis is logical inclusion or abstraction. Again time is not represented, as the primary motivation is to demonstrate groupings of similarity in a timeless system; thus, in Kress and van Leeuwen’s terms, they are purely classificational, with no narrative vector. Unlike the *scala naturae* or later branching diagrams but like the logic diagrams, there is no assumption of continuity between the divisions. But the principle of plenitude from the *scala naturae* is a driving force in the background, as the evidence of the diversity and fecundity of the natural world, revealed by the age of exploration and colonization, piled up in the great collections of the European naturalists, including Linnaeus’s own experimental garden in Uppsala and the royal collections in Paris with which French naturalists Buffon and Cuvier both worked. Linnaeus’s classifications and taxonomies brought order to the “threat of total chaos” and led to the “unprecedented flowering of taxonomic research” in the 18th and early 19th centuries, making Darwin’s work possible (Mayr, 1982, p. 173).

But Linnaeus’s work contained inconsistencies, and these inconsistencies are grounded in his acceptance both of the principles of plenitude and continuity and of the discontinuities required by scholastic logic (Mayr, 1982, p. 172), as well as the strong presumption that species were sharply differentiated natural and eternal entities (Lovejoy, 1936, p. 227). But it gradually became apparent to the 18th century naturalists that a single ladder or scale just could not account for the diversity of the organic world (Lovejoy, 1936, p. 202; Ragan, 2009); that whatever the principle of ordering was, it could not be perfection, especially among plants, since it was difficult to see how one plant was more perfect than the next (Ragan, 2009); and that species might not be as fixed and permanent as assumed, given the evidence of hybridizing and of the development of multiple varieties by breeding. It was under these conditions of “crisis” (Ragan, 2009) that the third tradition of visualizing the tree of life became important. This is the genealogical tradition.

Genealogies, which represent family relationships as a tree, are distinctly different from both cosmological and logical tree representations because one of their dimensions (usually the vertical) represents time, a consideration absent from the other two. The genealogical tree has Biblical roots, with its apparent origin in a passage in *Isaiah* (11.1)¹¹ predicting the descent of the Messiah and later depicted in Christian iconography as the Jesse tree, showing the genealogy of Jesus as descended from Jesse, the father of King David. The earliest such visual representation has been traced to the early 12th century (Hacking, 2007), after which they become “one of the most widely visible of medieval diagrams” (Franklin, 2000), in illuminated manuscripts, stained glass windows, and church sculpture.¹² Most commonly, these images depict Jesse asleep at the bottom, with a tree or vine growing out of his side, subsequent ancestors layered on branches above him (the number depending on the pictorial space available), the Virgin at or near the top, and Jesus with or above her (Hacking, 2007, p. 229; Lima, 2014, pp. 32, 36). The vertical dimension thus depicts both time and continuity or relatedness, and since Jesse trees were never inverted, with Christ at the bottom (Klapisch-Zuber, 1991), they have a narrative directionality like that of the Great Chain of Being.

Genealogical trees became important in secular contexts as ways to establish the claim to legitimate succession by a ruler and to sort out inheritance and marriage arrangements among the royal houses of Europe. The latter need was served by trees of consanguinity, which show blood relationships within a family. Church canon law forbade marriage within seven degrees of separation until 1215, when it was reduced to four, in part because the interrelated royal houses of Europe had such limited options for marriage. The earliest extant tree of consanguinity dates from the 9th century (Hacking, 2007, p. 228; Lima, 2014, p. 32). The earliest genealogical trees, dating from the 11th century, take the form of a single line of succession, much like the listing of “begats” in the

¹¹ The *Gospel of Matthew* begins with a detailed genealogy of Christ, listing 14 generations from Abraham to David, 14 generations from David to the Babylonian captivity, and another 14 generations to Christ (Matthew 1:1-17).

¹² Many examples are included in Lima (2014) and on Wikimedia Commons, including the oldest stained glass Jesse tree, at Chartres Cathedral, dated 1145; see https://commons.wikimedia.org/wiki/File:France_Chartres_JesseTree_c1145_a.JPG.

Bible; because the inheritance system in feudal society was based on lineage, the “antiquity and continuity of one’s line” was “the fundamental structural mechanism of power and social reproduction” (Klapisch-Zuber, 1991, p. 107). These trees tended to begin with the founding ancestor at the top and the current generation at the bottom, consistent with language of “descent,” but Klapisch-Zuber argues that the narrative trajectory of the Jesse tree, with the origin at the bottom and Christ at the top, “breath[ed] new life into the arboreal metaphor” and “turn[ed] the trees around,” (1991, p. 120). Thus, by the 15th and 16th centuries, European genealogical trees tended to be organized with the past at the bottom and the top of the tree emphasizing not the singular line of succession but rather power through ascent and proliferation (Klapisch-Zuber, 1991, pp. 108–112).

Genealogical trees were also put to use in other historical enterprises, in particular the effort to understand the diversity and origins of human languages. European exploration of what is now India revealed similarities between Sanskrit and the ancient European languages, Greek and Latin, leading to proposals in the latter half of the 18th century that these ancient languages had a common source. These observations, and a religious interest in discovering the “*lingua Adamica*,” the hypothesized original tongue, led to the development of historical linguistics (Hoenigswald, 1962). The first genealogical tree of languages was apparently published in about 1800 (O’Hara, 1996, p. 84), showing primitive languages at the bottom and the more “advanced” languages (modern English and French) at the top.¹³ In 1850, German philologist August Schleicher published a systematic study of European languages in which he described language development as an evolutionary process and “spoke of the Indo-European languages in terms of family relationships” (Koerner, 1972, pp. 260-262). He called his approach *Stammbaumtheorie*, family-tree theory, using tree diagrams to show groups of historically related languages. Although he was aware of much work in natural history (and later made much of the resonances between his work and Darwin’s), Schleicher may have developed his approach to language from his education as a classical philologist, trained to create manuscript stemmata according to the doctrine of shared errors (Hoenigswald, 1962, p. 8). His teacher, Friedrich Ritschl, worked also on human genealogy (Maher, 1966, p. 8), so

¹³ This diagram is reproduced at https://blogs.princeton.edu/graphicarts/2011/08/tree_of_language.html

this tradition of tree diagrams may have served as a direct model for this form of representation in linguistic inquiry.

In any case, the late 18th and early 19th centuries saw a flourishing of tree diagrams, as naturalists attempted to discover and represent the plan of the natural world, the “natural system” they were convinced had produced the diversity that seemed to increase with each discovery. Pietsch reproduces many of these diagrams and explains the hypotheses they represent. For one example, Figure 4 shows a genealogy of strawberries from 1766 that attempts to account for anomalies observed in the royal gardens at Versailles by a horticulturalist, who observed that “the genealogical order is the only one nature indicates, the only order that fully satisfies the mind” (quoted in Pietsch, 2012, p. 27). The diagram shows the wild strawberry at the top with other varieties and their presumed or observed lines of descent.

Biological thinking and visualization during this period were influenced by the developing science of geology. In the early 19th century, geologists developed visualizations that both represented and theorized geological structures and processes, including diagrams of vertical sections of the earth, abstractions from what one sees on the rock face of a quarry (Rudwick, 1976, p. §iv); these diagrams of strata were ladder-like, in the manner of those depicting the Great Chain of Being, but with a vertical scale representing not perfection but rather both space and time. For example, an 1840 geology textbook included a paleontological tree of life that is the first representation of geological time in a diagram of plant and animal relations (Pietsch, 2012, pp. 69–70, Fig. 54). The discovery of geological time, the study of fossils in geological strata, and the development of the science of paleontology are all a part of what Lovejoy calls “the temporalizing of the Great Chain of Being,” which he characterizes as “one of the principal happenings in eighteenth-century thought” (1936, p. 244). Against great intellectual and religious resistance, there was a spreading acceptance of the idea that nature was not immutable, that the natural system had not been created once and for all but rather had a history. Geologists, surveyors and mining engineers, and biologists slowly came to the conclusion that the earth itself had a history, a “deep history” (Rudwick, 2005): that geological strata were evidence of a time sequence and that the lowest strata, bearing fossil organisms quite unlike any living plants or animals, were the oldest (Mayr, 1982, p. 320). In 1796, Georges Cuvier, at the National Museum in Paris, published a comparison of fossil

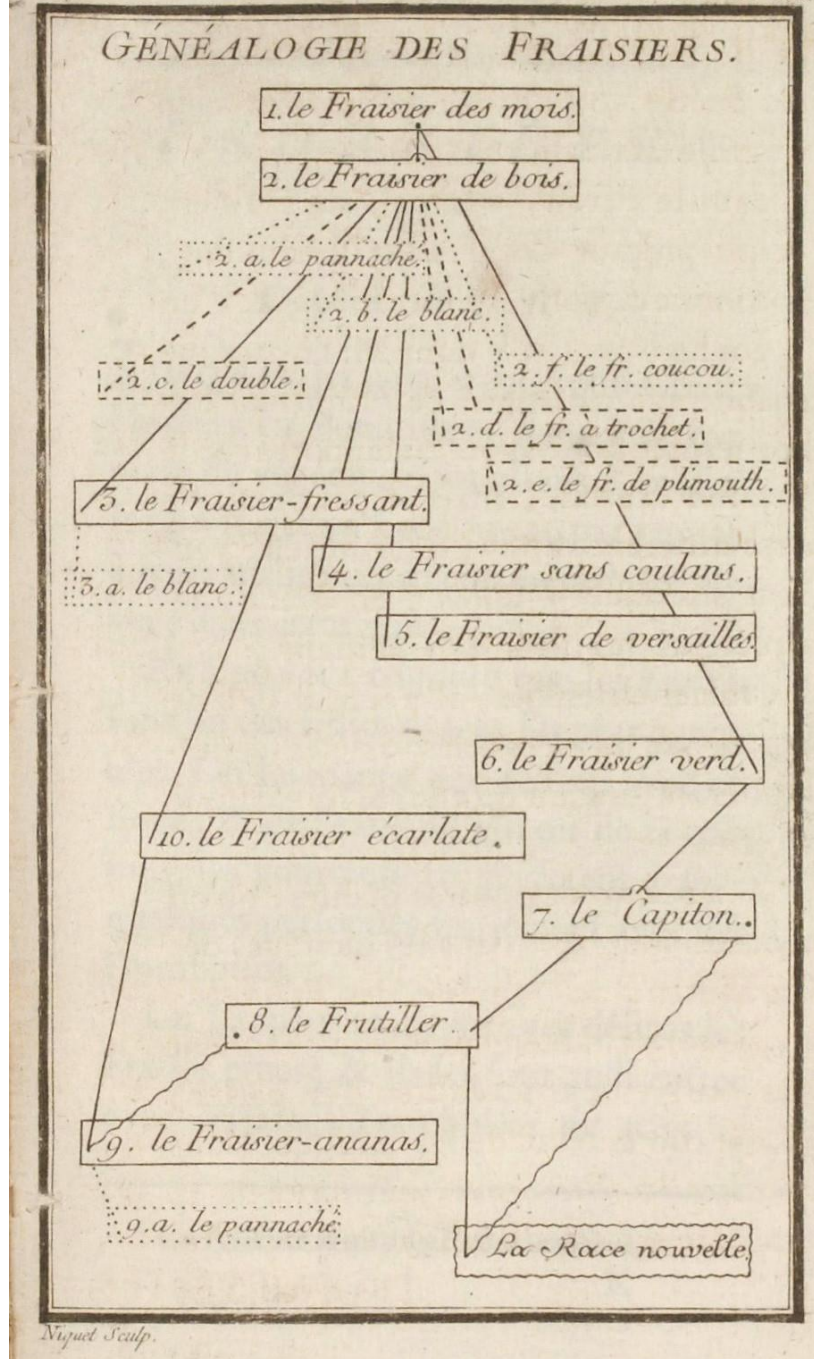


Figure 4. Généalogie des Fraisiers (Genealogy of Strawberries), from *Histoire Naturelle des Frasiers* by Antoine-Nicolas Duchesne, 1766, facing p. 228. Hortalia: Bibliothèque de la Société Nationale d'horticulture de France. Retrieved from <http://bibliotheque-numerique.hortalia.org/items/show/789>.

elephants (the new world mastodon and the Siberian mammoth) with living African and Indian elephants, concluding that they were four distinct species, with the fossil species apparently extinct; his subsequent 1812 four-volume work on fossils is now regarded as the “founding document of vertebrate paleontology” (Reiss, 2009, p. 90). Extinction was a radical notion, inconsistent with faith in a benevolent and omnipotent Creator, but one that connected geology and biology and helped give a genealogical meaning to biological tree diagrams, “temporalizing” them, in Lovejoy’s terms.

The many tree or tree-like biological diagrams produced during this period represent a set of experiments in classification and ordering, attempts to discover and describe the relationships among the multitudinous entities of the natural world. These relationships, premised on the principle of continuity, were called “affinities,”¹⁴ a term used to denote relationships of similarity. A key assumption driving the efforts of 18th-century naturalists was that affinities among species would define the natural system (O’Hara, 1991, p. 258; Ragan, 2009, § “The Search”); as Mayr notes, “There was a conviction that . . . [affinity] reflected some kind of causal relationship” (1982, p. 202). Thus, much of the work of these naturalists was directed to figuring out just which similarities were true affinities (such as those between penguins and ducks or auks) and which were mere analogies that did not reveal true relationships (such as those between penguins and seals). As late as 1856, Alfred Russel Wallace, in a paper titled “Attempts at a Natural Arrangement of Birds,” remarks that ornithologists are in pretty good agreement about the major classification of birds, based on structure and “economy” (behavior) but that for the large class of perching birds (*passeres*), “No systematist has been satisfied with the arrangements of his predecessors, and, after an endless variety of divisions and subdivisions, we are as far off from any generally accepted system of arrangement as ever” (1856, p. 195). There follows a detailed discussion of the erroneous affinities that have been postulated between hummingbirds and sun birds, concluding that “In the case of these two families, a mere outward

¹⁴ This term has a complex history. It was used in church law (as early as the 14th century) to describe relationship by marriage (in contrast to consanguinity, relationship by blood), in linguistics (as early as the 16th century) to describe similarities between languages, in chemistry (17th century) to describe attraction between substances, and in 18th-century biology to refer to resemblances among organisms (Oxford English Dictionary, 2012).

resemblance appears to have been universally mistaken for an affinity” (1856, p. 196). Figure 5 is one of the two tree-like diagrams Wallace offers in this paper after more discussion of the various true and false affinities in this group: “We have now completed a very brief and imperfect review of those families which we conceive can be separated from the mass of *Passeres* to form the tribe of the *Fissirostres* [the order that includes nightjars, swallows, and kingfishers], and in the accompanying diagram we have endeavoured to represent at one glance their various affinities” (Wallace, 1856, p. 205).

In this diagram, Wallace explains, “It is intended that the distances between the several names should show to some extent the relative amount of affinity existing between them; and the connecting lines show in what direction the affinities are supposed to lie” (1856, p. 206). The diagram is thus not chronological but shows what could be a cross-section of a genealogy at a specific moment in time. That Wallace may well have been thinking along these lines is strongly suggested by his publication of just a year earlier, in which he offers “the Law which has regulated the Introduction of New Species.” Observing that none of the explanations offered since the time of Linnaeus for the great diversity and geographic distribution of animals and plants has been satisfactory or has managed to keep up with the constant addition of new facts, Wallace notes that recent geological discoveries regarding the age of the earth and the “long and uninterrupted series of changes which it has undergone” can throw “a great light” on the problems of biology (1855, p. 184). The law he deduces from the facts of geography and geology is that “Every species has come into existence coincident both in space and time with a pre-existing closely allied species.” This law, he says, means that “the natural series of affinities will . . . represent the order in which the several species came into existence, each one having had for its immediate antitype [predecessor] a closely allied species existing at the time of its origin” (1855, p. 186). In effect, Wallace acknowledges the role of time in biology. Moreover, he thinks about the chronological processes involved as being tree-like: “The species [are] so numerous and the modifications of form and structure so varied, arising probably from the immense number of species which have served as antitypes for the existing species, thus produc[ing] a complicated branching of the lines of affinity, as intricate as the twigs of a gnarled oak” that “the whole difficulty of the true Natural System of classification becomes apparent to us” (1855, p. 187). He concludes that “the analogy of a branching tree

Diagram of the Affinities of the Fissirostres.

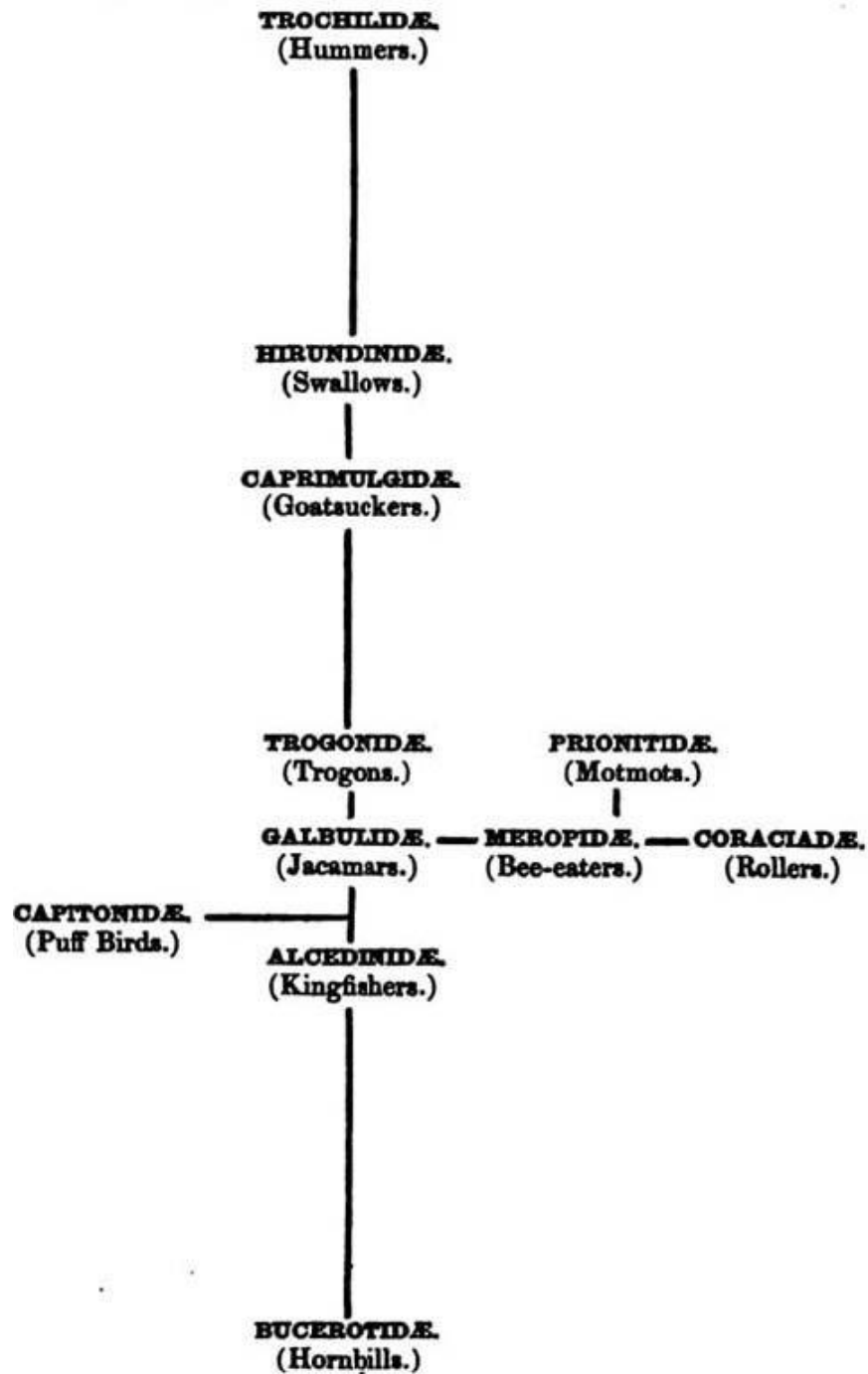


Figure 5. Diagram of the Affinities of the Fissirostres (Wallace, 1856, p. 205). U.S. National Library of Medicine, Open-i. Retrieved from https://openi.nlm.nih.gov/detailedresult.php?img=PMC2793248_1745-6150-4-43-19&req=4.

[is] the best mode of representing the natural arrangement of species and their successive creation” (1855, p. 191).¹⁵

The use of tree diagrams in pre-Darwinian biology is very much more complex than we have been able to portray here (Hellström, 2012; O'Hara, 1988a, 1991, 1996; Pietsch, 2012), but we have said enough to make the point that the tree diagram is not a simple, self-evident visual representation of anything. It can be constructed and read in multiple ways, and these are tied intimately to prevailing philosophical, cultural, and religious beliefs, which we have called, collectively, “traditions.” The cosmological tradition of visualization assumed that biological tree diagrams represented affinities that were signs of a divine order; the logical tradition saw affinities as relations of morphological and functional similarity that reveal the nested hierarchical structure of the system of nature; and the genealogical tradition made it possible to think that affinities were relations of descent. The lines, nodes, branches, and orientations on a tree diagram thus mean quite different things within these three traditions. We suggest that the combination of the genealogical tradition with the cosmological and the logical changed the framework for thinking about the natural world and made the theory of evolution possible.

The Role of Tree Diagrams in Darwin's Evolutionary Thought

We have already mentioned that the “tree of life” is a central figure, in both verbal and visual forms, in Darwin's argument in *The Origin of Species*. And indeed there has been significant research and commentary on Darwin's use of tree diagrams (A. Gross, 2007; A. G. Gross, 2006; A. G. Gross & Harmon, 2014; Hellström, 2012). So our aim in this brief section will simply be to position Darwin's use of the image within the framework we have used above. Darwin's explanatory project was two-fold: to demonstrate that modern species had descended from earlier ones and to show how this could be so, that is, to find a mechanism for descent with modification (Dennett, 1995, p. 39). His solution involved random variation of features within a breeding population, continuity or

¹⁵ This paper, which includes no diagrams, is not the one that spurred Darwin to publish in 1859 but a precursor to the 1858 paper that did so (Rosen, 2007).

inheritability of variations, overproduction of offspring, and “natural selection” produced by competition for survival.

Gross argues that Darwin’s overall argument is skillfully epitomized in the diagram included in the *Origin*: “once we understand the diagram, we understand Darwin,” he claims, adding that “its combination of conceptual complexity and graphic simplicity remains impressive” (2006, p. 97). The diagram, shown in Figure 6, is a schematic genealogical tree, or rather several trees, with differing amounts of branching, showing the (distant) past at the bottom and the present at the top; horizontal lines mark out equal measures of time, and dotted lines connect the generations of organisms. The trees are hypothetical, showing abstract ancestors and descendants rather than any specific organisms, such as birds or strawberries. Darwin’s explanation of the diagram culminates in the passage quoted in our introduction about the “great Tree of Life” (Darwin, 1859a, pp. 129–130).¹⁶

Later in the *Origin*, Darwin observes that “Naturalists try to arrange the species, genera, and families in each class, on what is called the Natural System,” and he then asks, “But what is meant by this system?” (1859a, p. 413). His answer is that

the natural system is founded on descent with modification; that the characters which naturalists consider as showing true affinity between any two or more species, are those which have been inherited from a common parent, and, in so far, all true classification is genealogical; that community of descent is the hidden bond which naturalists have been unconsciously seeking, and not some

¹⁶ Gross (2006, pp. 90–96) and Hellström (2012, pp. 235–236) both detail the tree diagrams in Darwin’s notebooks, over 20 years before the *Origin*, demonstrating the inventional role they played in Darwin’s thinking. Both Hellström (2012, p. 235) and O’Hara (1996, p. 81) note that the diagram in Darwin’s 1837 notebook is probably the first genuinely evolutionary tree diagram. This diagram can be viewed in an online exhibition at the American Museum of Natural History (<http://www.amnh.org/exhibitions/past-exhibitions/darwin/the-idea-takes-shape/i-think>) and in context of the complete 1837 notebook at <http://darwin-online.org.uk/content/frameset?itemID=CUL-DAR121.-&viewtype=image&pageseq=1> at p. 36. It is also reproduced in Gross (2006, p. 92).

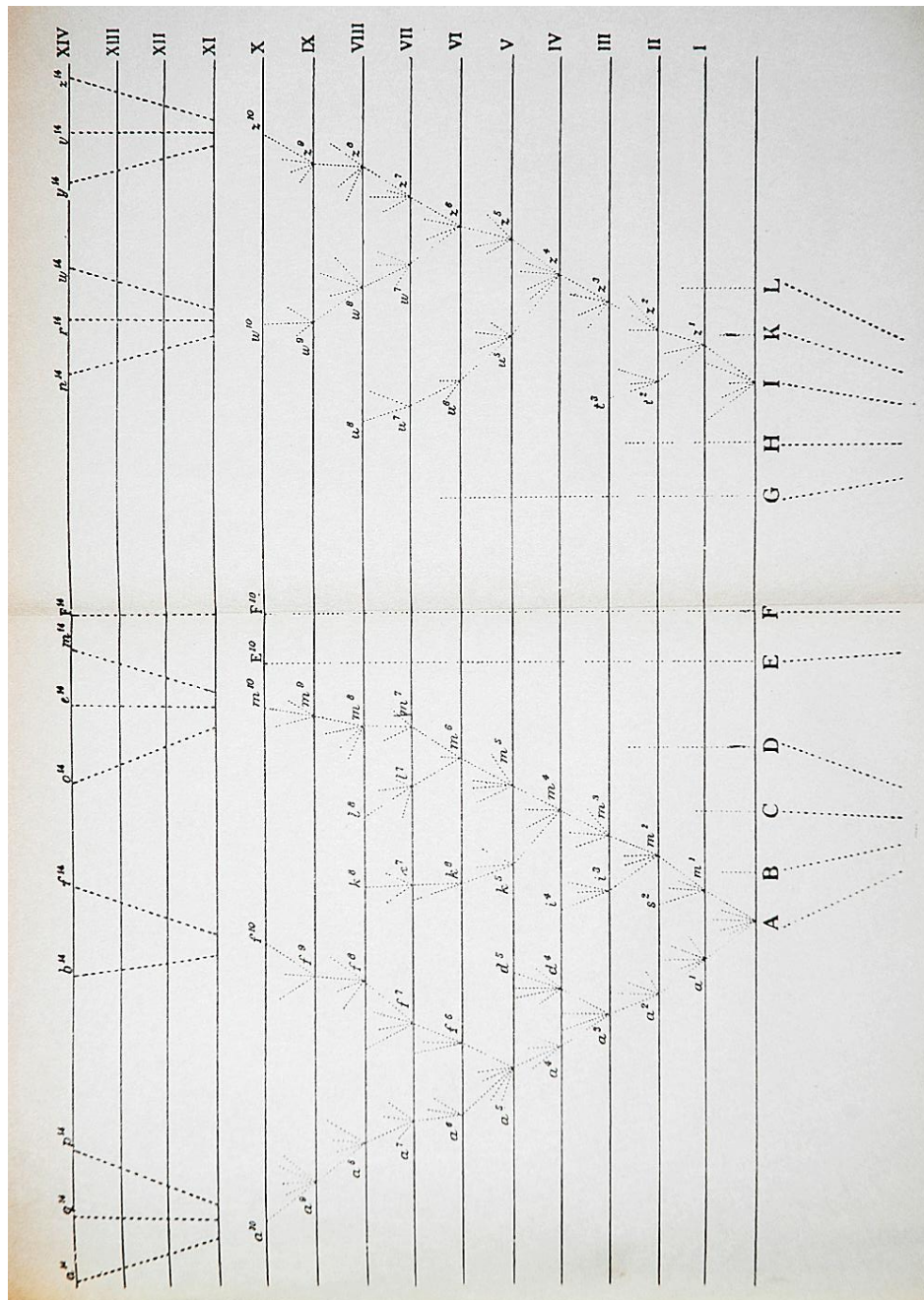


Figure 6. Darwin's Tree Diagram in *The Origin of Species* (1859), facing p. 116. Wikimedia Commons. Retrieved from https://commons.wikimedia.org/wiki/File:Darwin_divergence.jpg.

unknown plan of creation, or the enunciation of general propositions, and the mere putting together and separating objects more or less alike. (1859a, p. 420)

As Burke points out, Darwin emphasizes the principle of continuity between humans and other animals (indeed, all of life), whereas those with a more theologically inflected terministic screen require discontinuity and hierarchy (1966, p. 50), and this is precisely the difference visualized in the genealogical and the cosmological traditions.

Gross argues that Darwin's diagram combines genealogical trees with the "geological column," in which time is portrayed in the vertical space both of geological strata and of the diagram on the page (A. Gross, 2007, p. 75; A. G. Gross, 2006, p. 96); the connection with geology provides the bottom-up orientation of the tree diagram, but for Darwin the narrative vector is one of time, not cosmological perfection. Our point is that only against the context we have presented involving the long and influential traditions of cosmological and logical tree diagrams can we truly appreciate Darwin's argumentative achievement here, the revolutionary nature of his rejection of both of those traditions that had so strongly influenced previous tree diagrams. Darwin's diagram insists that we must understand affinities as evidence of descent and ancestry, that the natural system is not a hierarchical classification but rather a set of family relationships. It draws on a different visual tradition, requiring us to see the tree of life in a new way.

Tree Diagrams After Darwin

The use of genealogical tree diagrams became widespread in many fields of biology in the decades after Darwin, being especially useful in vertebrate biology as comparative anatomists and paleontologists worked to understand extensive dinosaur finds (Ragan, 2009). As Mark Ragan concludes, the genealogical tree diagram after Darwin became a "landmark not only of biology . . . but of modern intellectual and visual culture as well" (2009, § "Conclusion"). Nevertheless, we also find remnants of the cosmological and logical traditions surviving in many of these images, and, in the early 20th century, the emergence of diagrams deriving from our fourth tradition of visualization, the materialist.

The most notable of the later 19th-century diagrams are the many trees published by Ernst Haeckel, the German naturalist,

philosopher, and illustrator. Haeckel was first exposed to Darwin's ideas in 1861 and quickly became one of his strongest supporters and popularizers. Unlike Darwin's abstract diagram, those of Haeckel were specific, "palaeontologically grounded" attempts to map the relationships among actual organisms and known and hypothesized ancestors (quoted in Richards, 2014, p. 162).¹⁷ Haeckel was the first to publish a tree showing a single origin for plants, animals, and protists (Pietsch, 2012); he coined the word "phylogeny" (Dayrat, 2003) and proposed the "biogenetic law" that "ontogeny recapitulates phylogeny," an idea that is no longer accepted (Dayrat, 2003; Richards, 2014). His books, published in multiple editions and translated into many languages, were influential and sometimes controversial.

Haeckel's tree diagrams range from simple line diagrams and bracketed lists to a "phylogeography" (a branching tree superimposed on a map) and elaborate multi-branching pictorial trees showing the relations of various groups of plants and animals. The most famous and most frequently reproduced (Pietsch, 2012, p. 100) is the "great oak" family tree of humans (Figure 7). Originally published in German in 1874 and intended for a general educated readership, this is perhaps the most pictorial of all Haeckel's trees. It is distinctive, also, in recalling earlier images of the *scala naturae*, which it does in at least two ways. First, the thick trunk dominates the page, diminishing the importance of the short, twiggy branches and focusing the attention on the dramatic vertical line connecting the human race, at the top, to its progenitors in the trunk below. Second, the vertical scale, or y-axis of the image, marked out by dotted horizontal lines, is labeled not with units of time, as Darwin's was, but with the major classifications of living creatures, single-celled organisms at the base, followed by invertebrates, vertebrates, and mammals at the top. Thus, although Haeckel was known as "the German Darwin," this diagram reverts to a pre-Darwinian scheme, in which the vertical axis is a scale of progress, not unlike the Great Chain of Being. Six of the 20 trees by Haeckel that Pietsch reproduces have y-axes that are labeled, but this is the only one in which the labels are not geological time-periods. Haeckel's Darwinism, according to Dayrat, is complicated by a residual commitment to the *scala naturae*, to a conviction that

¹⁷ Haeckel was a colleague and friend of Schleicher, the philologist mentioned earlier, with whom he shared many ideas, including ideas about *stammbaumtheorie* (Dayrat, 2003; Richards, 2014).

PEDIGREE OF MAN.

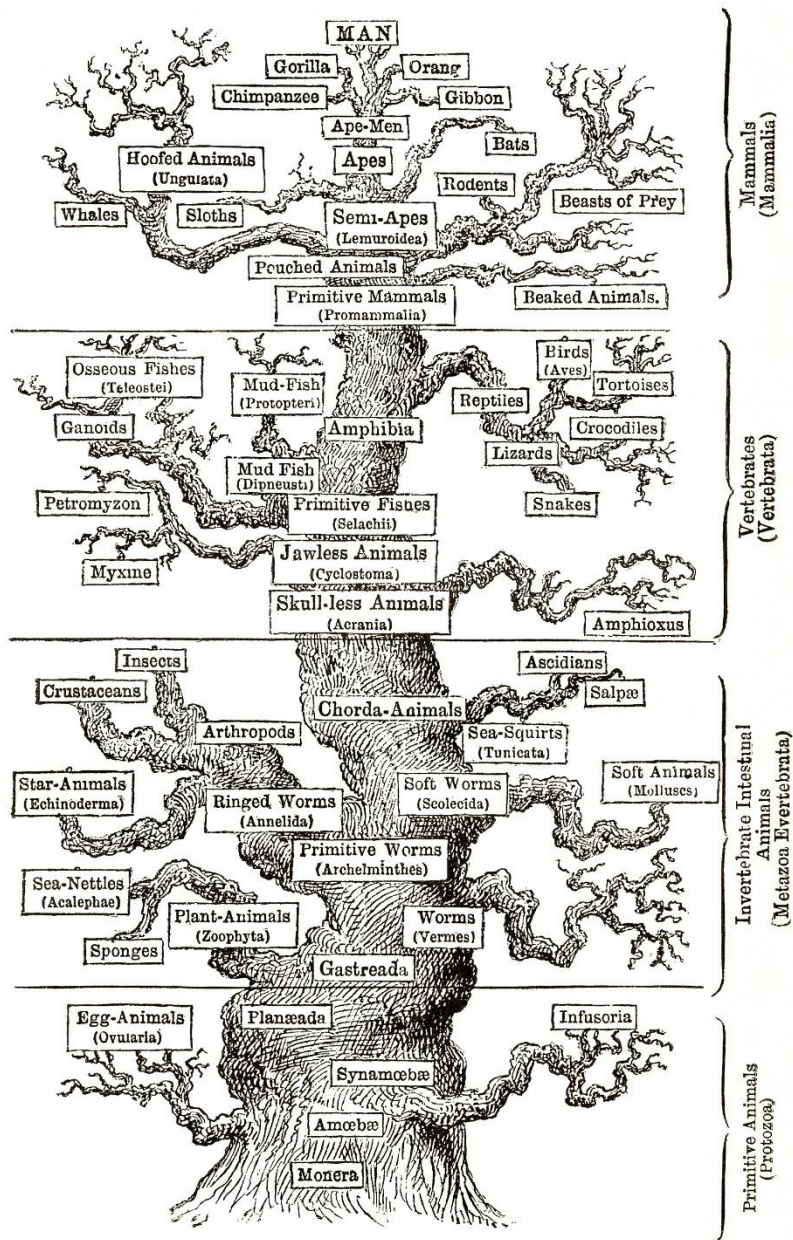


Figure 7. Haeckel's "Pedigree of Man" from *The Evolution of Man: A Popular Exposition of the Principal Points of Human Ontogeny and Phylogeny*. New York: Appleton & Co., 1897. Wikimedia Commons. Retrieved from https://commons.wikimedia.org/wiki/File:Pedigree_of_Man_English.jpg.

“organisms are ordered along a scale of progress from lower to higher organisms” (2003, p. 526). Haeckel called his diagrams *stämmebaume*, or pedigrees, not phylogenies; that is, “the information conveyed . . . was the succession of main stages along the trunk,” not the pattern of branching (Dayrat, 2003, pp. 524, 526). His diagrams, of which the “great oak” is just the most dramatic example, trace the pedigree of a particular species or group back through its progenitors; Haeckel considers this as the ontogeny of a species, in contrast to the embryological and developmental ontogeny of a particular organism¹⁸ and in contrast to a phylogeny, which would show the species in a larger evolutionary context (Richards, 2014, pp. 141-142). To many observers the design produces a non-Darwinian teleological effect, with humans as the ultimate product of evolution, rising out of the succession of more primitive life-forms.¹⁹

The cosmological tradition died hard, and in the book where this diagram appeared, on the sensational topic of *The Evolution of Man*, it had a clear rhetorical appeal, the teleology compensating for the radical notion that humans were descended from “lower” forms of life. Haeckel has been accused of inconsistency and muddleheadedness in his attempt to blend Darwinian genealogy with German Romanticism (Dayrat, 2003, pp. 523, 526; Richards, 2014, p. 263),²⁰ and we can see the result in the ambivalence of this particular image, which is both cosmological and genealogical. Such polysemy can be rhetorically productive, as Leah Ceccarelli has argued (1998), so it may not only reflect the ambivalence of Haeckel’s own thinking but also appeal differently to popular and to scientific readers and allow scientific readers to preserve familiar religious ways of thinking even as it invokes the science of paleontology. And in fact, non-Darwinian teleology (a narrative

¹⁸ Haeckel produced many diagrams of this type as well, showing the embryological development of various species. See Fahnestock’s discussion of this type of diagram (2003).

¹⁹ It should be noted that Richards resists this interpretation, not recognizing the visual and intellectual imprint of the *scala naturae* that Dayrat describes (Richards, 2014, pp. 141-142, 161-162).

²⁰ Haeckel has also been accused of supporting social Darwinism and scientific racism, but these charges are controversial (see Richards, 2014, pp. 270-276, 448-453).

vector of “progress”) continues to influence evolutionary biology well into the 20th century (Ruse, 2009, 2013a).

In the early 20th century, biologists began to construct tree diagrams using specific, observable characteristics to hypothesize relationships among different species of plants and animals. Many of these were published mid-century by William King Gregory, using morphological characteristics such as teeth, cranial shape, and hand shape in primates (see Pietsch, 2012, pp. Figs. 163, 164, 172, and 173). But perhaps the earliest tree of this type was published by Peter Chalmers Mitchell in 1901 showing the intestinal tracts of birds (Figure 8). Mitchell’s tree uses drawings of intestinal tracts as the nodes, showing presumable phylogenetic relationships as branches. This tree is significant as it was one of the first to use a single, specific characteristic to create a phylogeny *of that characteristic*; this type of diagram would later be called a “character-state tree.” Mitchell cautioned that a character tree did not necessarily represent the phylogeny of any other character or even the phylogeny of “these impermanent combinations of characters that we call species” (quoted in Pietsch, 2012, p. 150).

In Mitchell’s focus on the details of specific characters we can see early evidence of our fourth tradition of visualization in tree diagrams, the materialist tradition. His apparent anxiety about his character trees being misinterpreted as true phylogenies of species (and about the “species” concept itself) is emblematic of a widespread concern that the taxonomic methods of the late nineteenth and early twentieth centuries lacked any “rigorous methodology (especially compared with the newly developing fields of genetics and experimental embryology)” (Cracraft & Donoghue, 2004, p. 1) and relied too much on “the intuitive judgment of the expert and even on artistic and pragmatic criteria” (Pietsch, 2012, p. 255). Indeed, there were “serious problems” in biological classification at this time and no agreement on standards for recognizing higher taxa (such as family, order, class) (Mayr, 1982, p. 221). The need for more inductive empirical methods that could supplant traditional reliance on deduction from *a priori* principles (Hull, 1988, p. 117) was met by a number of transforming developments in biology. One of these developments occurred in 1900 when English botanist William Bateson delivered a paper to the Royal Horticultural Society reintroducing the work of Gregor Mendel (Ruse, 2013b, p. 273). Over the course of the next several decades, Mendel’s work on the inheritance of dominant and recessive traits was reconceptualized in the context of Darwinian

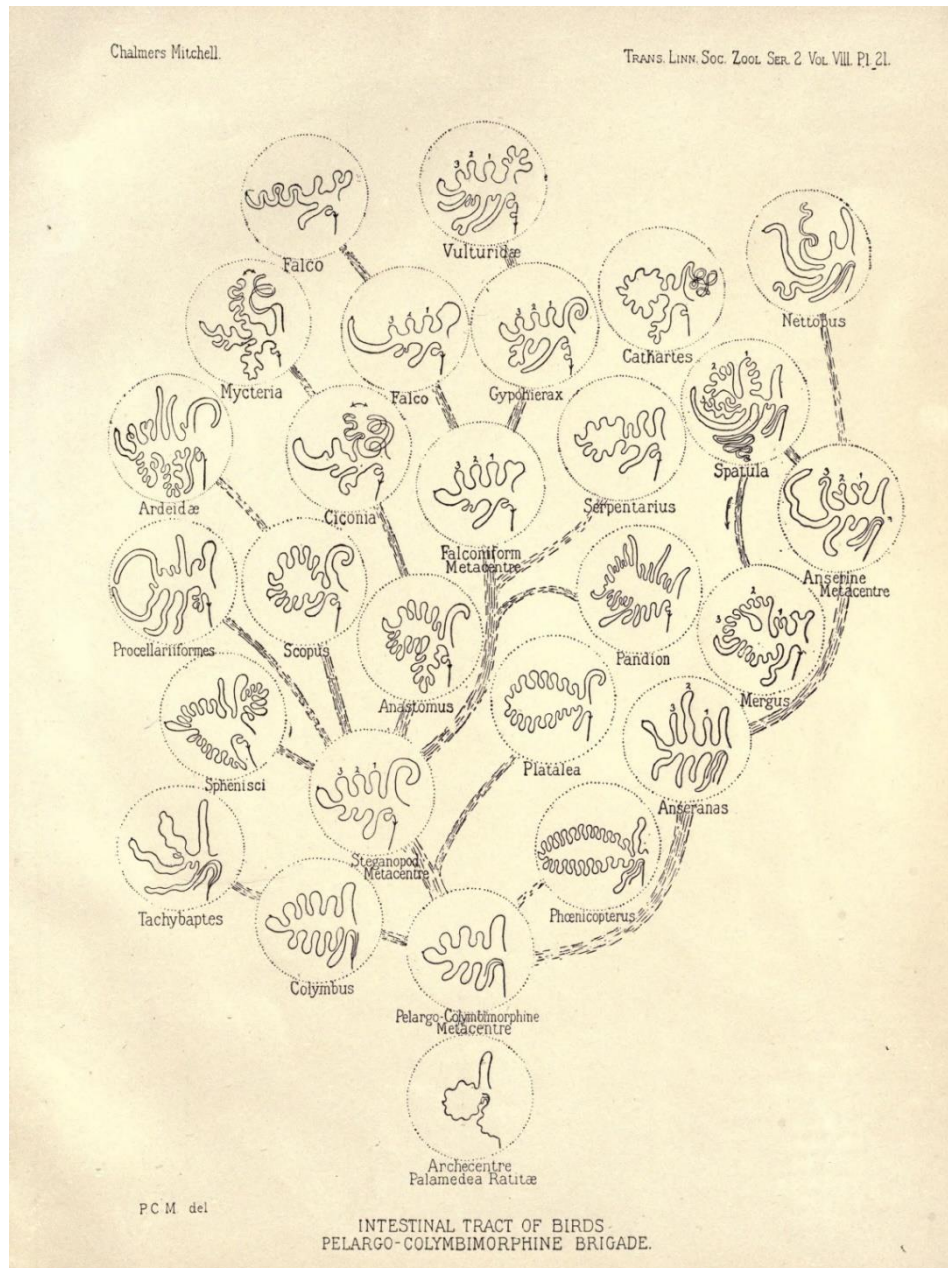


Figure 8. Intestinal Tract of Birds, an Early Character-State Tree (Mitchell, 1901, n.p.). Biodiversity Library via Wikimedia Commons. Retrieved from

https://commons.wikimedia.org/wiki/File:On_the_intestinal_tract_of_birds_BHL23877816.jpg.

evolution to create a theory of genetics extending to entire populations (Ruse, 2013b).

A second development was the development of the Hardy-Weinberg equilibrium principle. Working independently in 1908, G. H. Hardy, in England, and Wilhelm Weinberg, in Germany, demonstrated mathematically that the frequencies of alleles (genetic variants) in a population would remain constant over time when there are no other intervening factors, such as mutation, selection, or immigration. Scientists could now calculate the effects of mutation rates or selection pressures to see how genetic variation spreads through a population over time, potentially leading to a speciation event. This law provided one more major step towards the quantification of the biological sciences and a view of species as the result of measurable genetic forces.

Historians of science have characterized the move to quantification and calculation as definitive of modern science, with biology the last of the natural sciences to become modern in this sense (or “Heideggerian” in Gross’s sense), as the 19th century’s natural history became the 20th century’s phylogenetics and systematics. James Wynn has examined the developing role of mathematics in biological argument during the 19th century, showing how Darwin’s and Mendel’s ideas about variation, evolution, and heredity helped transform biology “from a predominantly qualitative science to one with a vital, mathematical component” in the late 19th and early 20th centuries (2012, p. xvi). As Wynn argues, Darwin’s reading, correspondence, and notebooks show him determined to provide quantitative evidence for the patterns of change that underlie his theory of evolution, and it was only his haste to publish in the wake of Wallace’s publications that forced him to leave the mathematical detail out of his “summary,” the *Origin* (2012, pp. 36-64). And noting “the increasing centrality of visuals to scientific communication and thought, a centrality more and more evident as the nineteenth century unfolded,” Gross connects quantification to visualization as together indicative of the “wholesale objectification of the world” by science (A. Gross, 2007, pp. 52, 53).

In their study of scientific image-making from the 18th through the early 20th centuries, Lorraine Daston and Peter Galison present a visual history that informs what we are seeing with tree diagrams at this juncture and provide another rationale for what we call the “materialist tradition” of visualizing the tree of life. They conclude

that scientific epistemology moved from an 18th-century “truth-to-nature” ideal for visual representation to an ideal of “mechanical objectivity,” emerging in the mid-19th century, and finally to “trained judgment” in the 20th century. The “truth-to-nature” ideal underlies the 18th-century ambitions to reveal the “natural system” through abstract representations of its logic derived from the selective observations of the expert; these visuals “characteristically praised the regularity of God’s laws as . . . worthy of admiration” (2010, p. 68). Daston and Galison use Linnaeus as the paradigm example of commitment to “truth to nature,” as seen in his dichotomous and essentializing diagrams. What Daston and Galison refer to as “mechanical objectivity” seeks to “repress the willful intervention of the artist-author [i.e., the image maker], and to put in its stead a set of procedures that would, as it were, move nature to the page through a strict protocol, if not automatically” (2010, p. 121), and this ambition underlies the materialist trend in tree diagrams. Further, as we have found with the traditions of visualizing the tree of life, Daston and Galison note that the three epistemic ideals do not replace each other successively but rather proliferate and compete: “Each successive stage presupposes and builds upon, as well as reacts to, the earlier ones” (2010, p. 18).

What we call the “materialist” tradition in visualizing evolutionary trees, then, is a reflection of Heideggerian or modern science and of the ideal of mechanical objectivity.²¹ The sources of this tradition lie not in social practices like genealogy, or in religion or logic, but rather in older sciences such as physics and chemistry. The developments in biology that enabled thinking about inheritance and variation in statistical terms and about genetics as a predictable process subject to calculation presented new opportunities for understanding the “tree of life” because they ostensibly provided a

²¹ Two readers of this paper have pointed to similarities between what we are calling the “materialist” and “logical” traditions because the Porphyrian logic tree is a schema for the material universe. These two traditions may represent the same ambition (i.e., to map relations of physical reality), but we believe the differences are more significant. First, of course, trees in the logical tradition do not include the dimension of time, which is an important aspect of the materialist tradition even when not directly mapped; for example, insofar as they are “rooted,” the logical trees begin with a timeless abstraction, and the materialist trees begin with at least an implied common ancestor. Second, trees based in the logical tradition are a priori, deductive systems, whereas materialist trees are (or at least aim to be) empirical and inductive.

basis in quantifiable physical reality for creating phylogenetic and taxonomic tree diagrams. Despite the appearance of greater objectivity in this tradition, however, this part of the story is complex and rife with controversy,²² and we can cover just a few highlights below. We will focus on the ways in which tree diagrams became “objective” and “materialist,” that is, on their basis in various methods of physical measurement and calculation.

The methodological problems of biological classification provoked two conflicting responses that drew on the new quantitative and material understandings of biology to produce new types of tree diagrams. The first, using observable morphological characteristics, is known as phenetics, or numerical taxonomy. This approach aimed to quantify degrees of similarity between organisms by using multiple morphological features; they thus generally rely on measures of correlation. The earliest diagrams of this type, identified by Pietsch as the earliest produced by numerical methods (2012, p. 256), were published in two papers in 1957 and 1958 by Charles Michener and Robert Sokal, who used an “IBM tabulator” (Michener & Sokal, 1957, p. 143). They examined 122 characters within 97 species of bees in four genera with the specific aim of developing a method to “remove some of the subjective bias from taxonomy” (1957, p. 162).²³ One distinctive feature of the tree diagrams in both papers is the quantitative scale on the y-axis, which is not time but rather the correlation coefficient of the multiple characters examined (in effect, a measure of “affinity”). Figure 9 reproduces one of these diagrams, showing the correlation-based relationships—or degrees of evolutionary divergence—of species in one genus of bees. The y-axis is the correlation coefficient multiplied by 1000; the numbers at the tops of the branches designate bee species, and the correlation between any two species can be read on the y-axis at the level where the branches connect; the dashed horizontal lines are somewhat

²² For a detailed history of the “taxonomy wars” of the 1960s and 1970s, see Hull (1988), especially Ch. 5.

²³ Such removal was not complete, however, as each character was assigned from 2 to 8 possible states, some of which were the presence or absence of a feature (color, for example), some being measurable (length or width of a part or ratio of two measurements), and some of which were impressions (shape, degree of convexity, density) (Michener & Sokal, 1957, pp. 139-141, Table 132).

“arbitrary” indications of how one might use these data to distinguish genera (1957, p. 157).

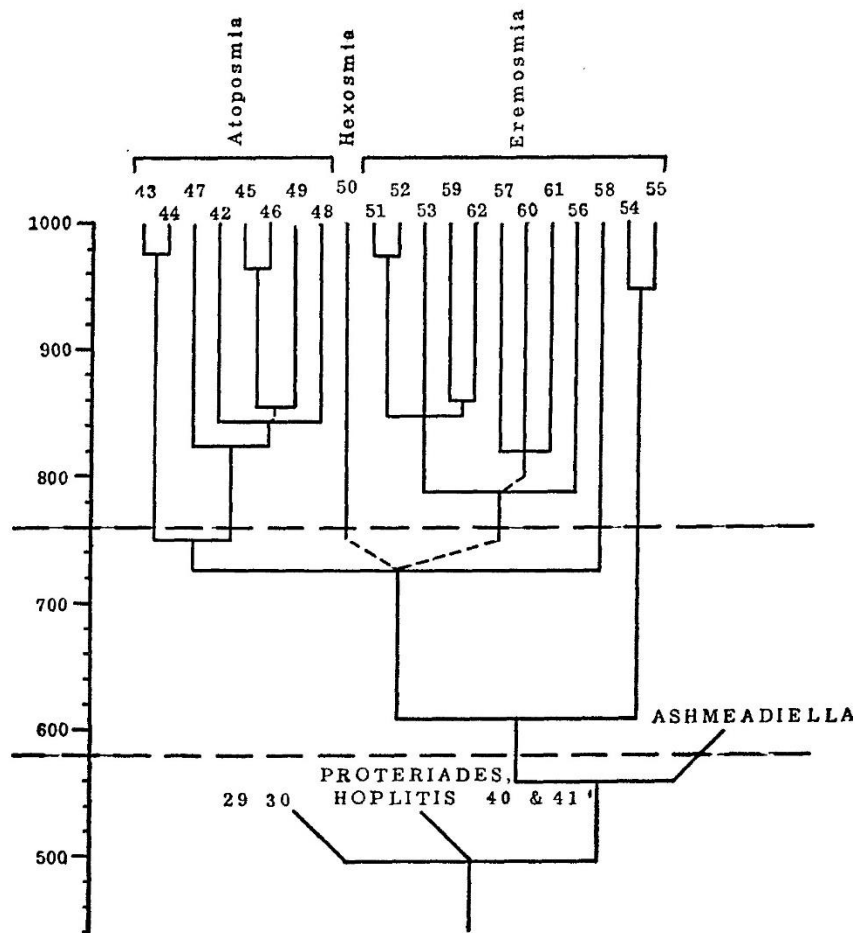


Figure 9. Diagram of relationships for the genus *Anthocopa* obtained by the weighted variable group method. Republished with permission of John Wiley & Sons, from “A quantitative approach to a problem in classification,” by Charles D. Michener and Robert R. Sokal, in *Evolution* 11, 1957, Fig. 7, p. 148; permission conveyed through Copyright Clearance Center, Inc.

Michener and Sokal observe that their diagrams correspond well with previously accepted taxonomy but caution that they “represent relationships in a static, non-historical sense” (1957, pp. 148, 149), so this is a family tree of living relatives, not of ancestors. The authors struggle with the dilemma, carried over from the 19th century, that a taxonomy or a tree diagram “cannot always show both common descent and evolutionary divergence” (1957, p. 156),

the former representing the Darwinian genealogical tradition in tree diagrams (a narrative diagram) and the latter a holdover of the logical, Linnaean tradition (a conceptual diagram). In fact, the two authors disagree on which is preferable. Michener prefers a “more or less subjective approach,” using information gained by quantitative analysis but modifying it with knowledge of phylogenies and adapted for the “convenience” of a classification system. Sokal advocates “uniform and objective standards” based on quantified relationships for establishing categories (1957, pp. 156-157). Another issue that troubled Michener and Sokal was how to weight the various characteristics within a correlation. Although some characteristics carry more information about evolutionary history, others are more useful in representing evolutionary divergence, that is, they represent intuitive gaps between categories. Phenetics usually weighted each characteristic equally, a solution that satisfied no one. In Mayr’s judgment, phenetics ultimately failed because it basically ignored phylogenetic information (1982, pp. 223-225).²⁴

Phenetics lost favor to the second new approach to objective biological classification, which became known as cladistics. Working at about the same time as Michener and Sokal, Willi Hennig, a German entomologist, proposed that classifications should be based exclusively on genealogy. Calling his approach phylogenetic systematics, Hennig conceived of phylogeny as a series of dichotomies by which ancestral groups produce two daughter groups (Mayr, 1982, p. 226). Classification, he held, should be based on such monophyletic groups, or “clades.” The degree of relationship between groups is determined by recency of common ancestry, not by similarity or correlation of characteristics. Cladistic analysis relies on determining which characteristics shared between groups are ancestral (“primitive” characteristics, also called plesiomorphies) and which developed more recently (“derived” characteristics, also called apomorphies). Shared derived characteristics, or “synapomorphies,” are evidence of recency of relatedness (Cracraft & Donoghue, 2004). The resulting diagrams are called “cladograms.” Figure 10 shows an early version of Hennig’s diagram explaining how monophyletic groups are analyzed according to shared derived characteristics. In this figure, each monophyletic group (labeled A, B, C, and D) is determined by an apomorphous, or derived, characteristic, marked by a black

²⁴ Hull tells a more complex failure story about the personalities and social dynamics involved (Hull, 1988).

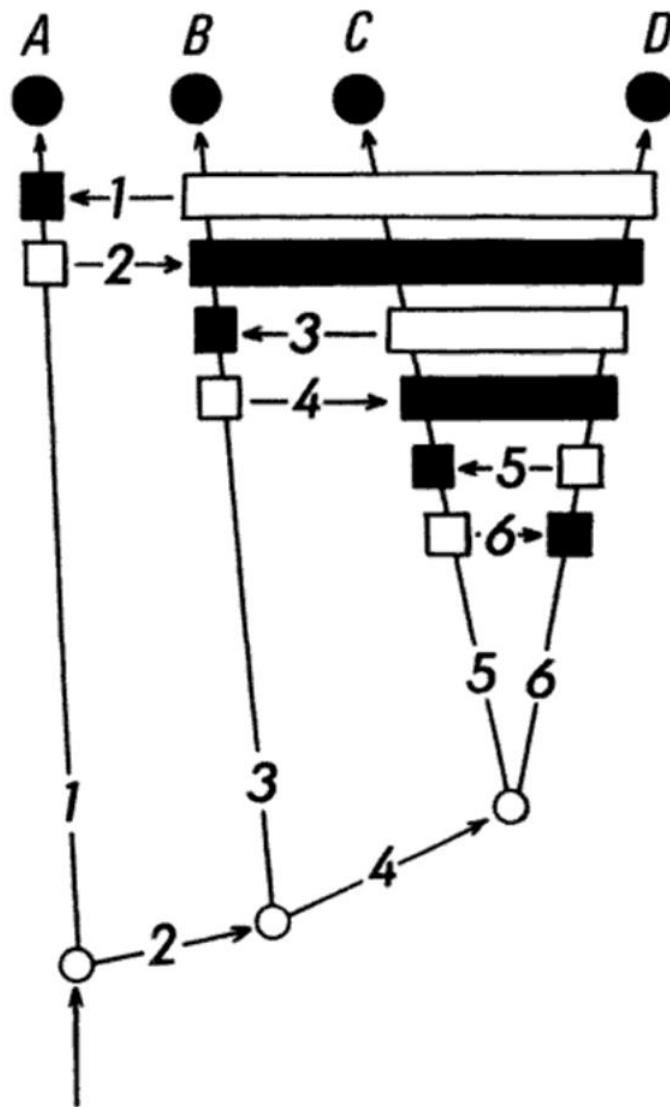


Figure 10. Willi Hennig, "Scheme of Argumentation of Phylogenetic Systematics." The open rectangles are primitive characteristics and the black rectangles are derived characteristics. The letters designate monophyletic groups, which are distinguished by shared derived characteristics; the numbers by the boxes designate traits and the lines show when each trait arose relative to others. From *Phylogenetic Systematics*, p. 91, Fig. 22, copyright 1979, Board of Trustees of the University of Illinois. Used with permission of the University of Illinois Press.

square. The black rectangles show apomorphic characteristics that are also synapomorphic, meaning they are shared across related species. For instance, species D uniquely has apomorphic trait 6; species C uniquely has apomorphic trait 5, but both C and D have apomorphic and synapomorphic trait 4. Therefore traits 4, 5, and 6 indicate speciation events from the most recent common ancestor of C and D. The open squares and rectangles in this diagram show “primitive” characteristics that are shared with the most recent common ancestor of A, B, C, and D.

One major conceptual difference between cladograms and their predecessors is the use of the “branches” themselves as informationally significant. Thus, the black bars and white squares signify derived and primitive characteristics, respectively. While time is still implied in the vertical axis, albeit not always labeled, cladograms don’t typically label known or hypothetical ancestors. Rather, these diagrams are generally labeled only across the top with known species or other monophyletic groups. Therefore, the emphasis is placed on the diversity of species and their relatedness to each other, whether they are close or distant. In addition, the emphasis on representing monophyletic groups produces relatively simple trees, with each node, as a point of evolutionary divergence, producing no more than two branches, a return to the form of dichotomous dialectic that prevailed in medieval logic trees. Furthermore, as Kevin Omland and colleagues point out, in cladograms the x-axis “has no meaning,” though there has been an unfortunate tendency to put more “primitive” species at the left and “higher” species at the right (2008, pp. 856, 862) and thus to read cladograms as progressive, a continuing holdover from the *scala naturae* (though with the axes reversed).²⁵

Early on, cladists relied on observable morphology to generate their trees, but later in the 20th century, various molecular methods were developed, including protein sequencing, DNA–DNA hybridization, and RNA sequencing (Pietsch, 2012, p. 274; Velasco, 2013, p. 341), all of which provided a literally material basis, on the

²⁵ Omland *et al.* emphasize that since cladograms represent only extant species, none can be ancestral to the others and since all have continued to evolve, none should be thought of as more primitive than others: “Improved tree thinking will not only help us better understand the evolution of the particular characters that we are studying, but will also improve our fundamental understanding of the process of evolution” (2008, p. 856).

level of molecules, for calculating genetic difference and constructing tree diagrams. An example from what Pietsch calls a “landmark paper” (2012, p. 275), shown in Figure 11, presents a classification of birds based on DNA samples from 1058 species (Sibley *et al.*, 1988, p. 410). This work followed Hennig’s precept that taxonomic categories should be based on the age of origin of each group. DNA–DNA hybridization is a way to determine the degree of difference (and thus the time since divergence, given assumptions about the rate of evolutionary change) by measuring the strength of chemical bonds between DNA strands from two organisms; we might consider this a molecular measure of “affinity.” Here the difference is shown by the delta T_{50H} number at each node; the number in parentheses is the number of DNA hybrids tested at that node (Sibley *et al.*, 1988, p. 410). This method of quantifying evolutionary relationships was somewhat controversial, and work by others using newer methods provided only “mixed” confirmation of these results (Archibald, 2014, pp. 176, 178).

Molecular approaches led to significant advances in evolutionary biology, demonstrating the value of the materialist approach to biological science. In 1987, Carl Richard Woese published a revolutionary version of the tree of life based on ribosomal RNA sequence data. Rather than dividing all living organisms into two kingdoms, the Eukaryotes and the Prokaryotes, this new tree, based on research published as early as 1977, proposed three kingdoms: the Eubacteria, the Eukaryotes (including plants, fungi, and animals), and the Archaeobacteria, or Archaea, previously unrecognized as a distinct kingdom. Since ribosomal RNA functions as an “evolutionary clock” (Woese, 1987, pp. 226-227), the RNA data enabled calculation of evolutionary distances, which are represented on the tree by proportional line lengths and order of branching.²⁶ And since time is shown only by the length of the lines and not by their orientation, this tree does not really have x- or y-axes and must be read differently from those that do. The original version of the figure showed no “root” because no universal common ancestor had been identified, but a later version does show the position of the root, based on a few genes that emerged before the three primary lineages appeared (Woese *et al.*, 1990, p. 4578, Fig. 1). Figure 12 is a public-domain version of the 1990 rooted diagram, which has been described as “the last of the great classical

²⁶ Although no numbers are shown directly on the diagram, extensive quantitative data are provided in the lengthy 1987 paper.

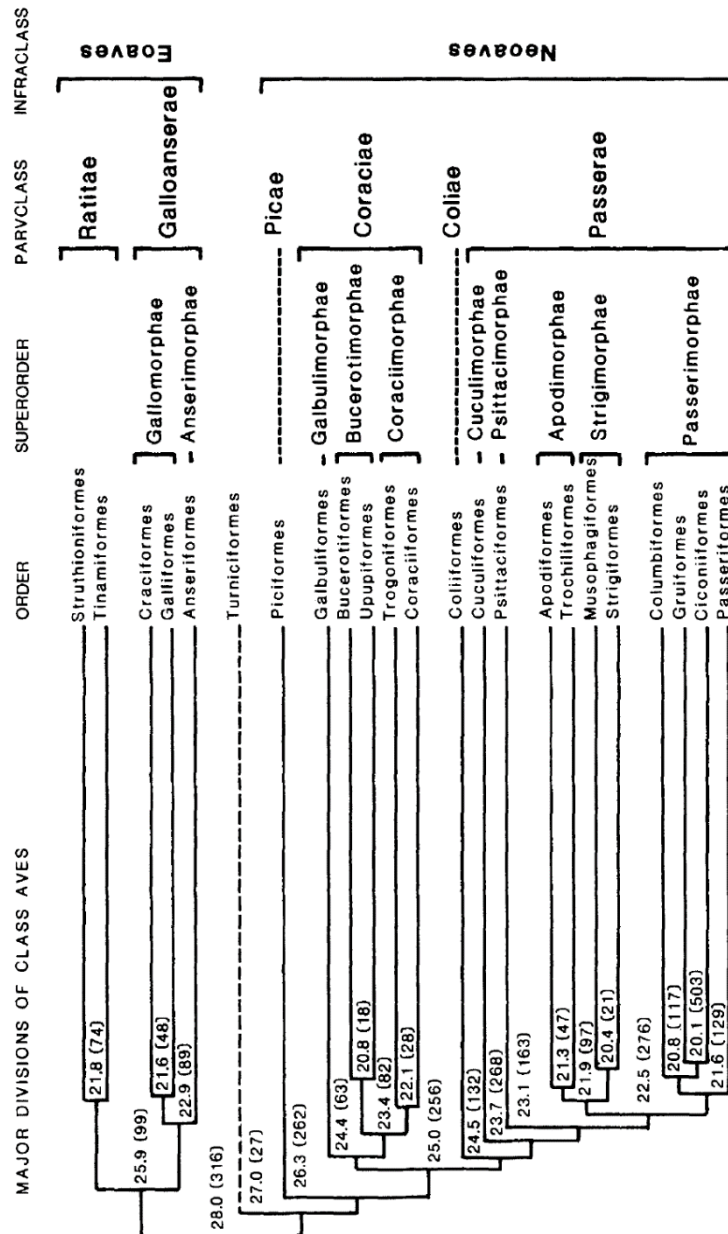


Figure 11. Major divisions of the class Aves. The numbers at the nodes represent a measure of genomic divergence based on DNA–DNA hybridization. Republished with permission of Oxford University Press, from “A Classification of the Living Birds of the World based on DNA–DNA Hybridization Studies,” by Charles G. Sibley, Jon E. Ahlquist, and Burt L. Monroe, in *The Auk*, 105 (3), 1988, Fig 1, p. 410; permission conveyed through Copyright Clearance Center, Inc.

trees, authoritative, profound, completely new to science” in the recent general-interest book on this topic by David Quammen (2018).

Phylogenetic Tree of Life

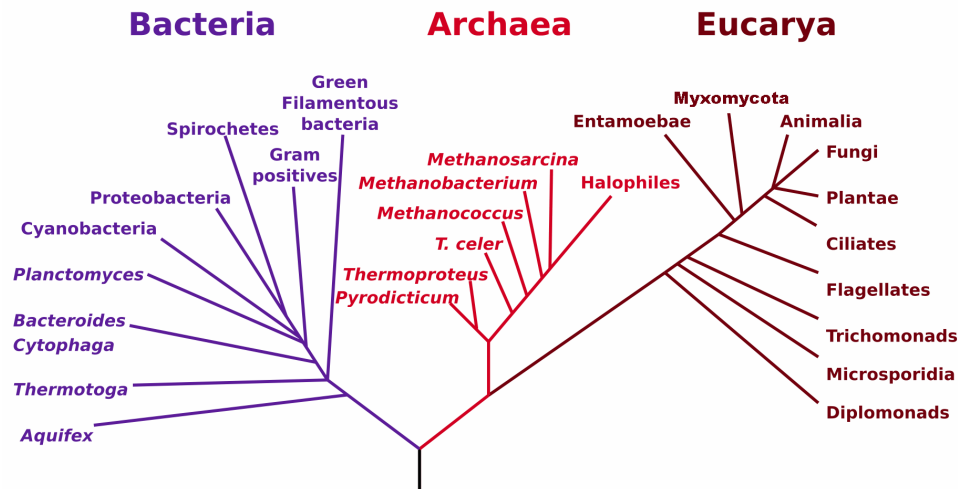


Figure 12. Universal phylogenetic tree in rooted form, originally from Woese *et al.* 1990 (p. 4578, Fig. 1). Wikimedia Commons (from NASA). Retrieved from <https://commons.wikimedia.org/wiki/File:PhylogeneticTree.png>.

Conceptually, Woese’s work opened an entire new domain of evolutionary biology. Since then, similar “universal” trees of life have shown that the majority of the earth’s diversity exists within the microbial kingdoms. Structurally, many of these diagrams are distinct in using a radial pattern instead of a vertical one, retaining the structure of a tree only in the logical sense of successive branching, but losing any visual resemblance to an actual tree. The radial pattern, used partly to save space, accomplishes a few things: it de-emphasizes the animal kingdom, which, as it turns out, makes up only a minute number of the total number of organisms on our planet, and it helps to minimize the erroneous implication of evolution as progress towards perfection, as there is no visually dominant end-point. However, like the more traditional upward- or sideways-branching tree structures, radial cladograms continue to carry the implication that diversity increases with time because they do not include extinct taxa; thus, if there is a narrative vector, it is one not of progress but of sheer proliferation. Figure 13 is an

example of a circular diagram, generated from completely sequenced genomes, where time is on the radial axis.²⁷

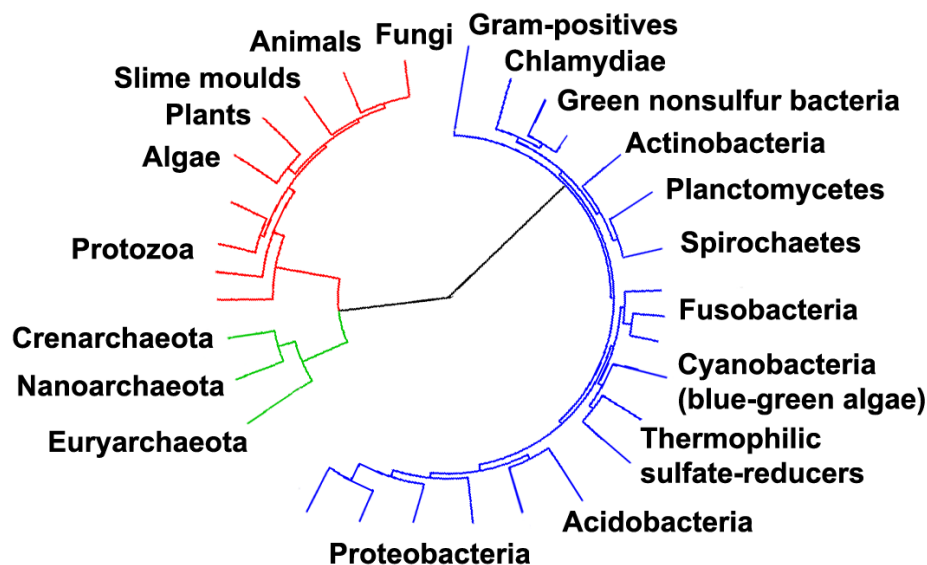


Figure 13. A circular “tree” of life, generated from the Interactive Tree of Life (ITOL), an online phylogenetic tree viewer. Eukaryotes are colored red, archaea green, and bacteria blue. By Tim Vickers, Wikimedia Commons. Retrieved from https://commons.wikimedia.org/wiki/File:Collapsed_tree_labels_simplified.png.

With the development of powerful computational algorithms, and fast, inexpensive DNA and RNA sequencing tools, cladistics became the most powerful form of phylogenetic analysis in the late 20th and early 21st centuries. The study of avian evolution discussed in our introduction used these powerful new methods. Jarvis *et al.* (2014) generated their tree using massive whole-genome analyses of a wide range of known avian species. That tree is a sideways cladogram fully within the materialist tradition of tree visualization, with an x-axis of time, a y-axis showing diversity, and bifurcations marked with numbers indicating a statistical measure of confidence based on resampling and replications. In another recent study, Hug *et al.* (2016) use similar whole genome methods based on ribosomal protein sequences to generate a new tree of life from

²⁷ A much more detailed version from the same dataset is available at https://commons.wikimedia.org/wiki/File:Tree_of_life_SVG.svg.

genomes in public databases and from over 1000 little studied organisms recovered from a variety of environments. The resulting tree shows an even greater diversity in the living world than was previously thought. Interestingly, the results are presented in two ways, both as an unrooted radial tree and as a sideways cladogram; both show a numerical scale for branch length based on the mean number of protein substitutions per site, which provide a physical basis for the visualizations. Both versions make it visually obvious that the diversity of the Prokaryotes far exceeds that of the Eukaryotes and in fact make the familiar plants and animals look like a minor evolutionary result. This project was ranked as one of Altmetric's top 100 papers of 2016.²⁸

The recent discoveries about the immense diversity of Prokaryotes and Archaea were accompanied by an increased understanding that microbial life in these kingdoms involves biological processes that differ significantly from those of the Eukaryotes, the plants and animals that dominated the tree diagrams of the nineteenth century and earlier, and these processes call into question the value of the tree diagram itself. Most significant perhaps is the process of lateral (or horizontal) gene transfer, that is, the movement of genetic material from one organism to another by means other than sexual or asexual reproduction.²⁹ Such movement of genetic material disrupts the pattern of vertical descent in successive generations and complicates the determination of phylogenetic relationships (Olendzenski & Gogarten, 2009). Other complicating processes include hybridization and endosymbiosis, or the fact that Eukaryotes at some early stage seem to have incorporated other organisms into their cellular machinery, such as mitochondria and chloroplasts (Velasco, 2013, p. 343). As J. David Archibald comments, "molecular methods . . . began to cast considerable doubt on the very idea that life's phylogeny might resemble a stately tree. Rather, life's history seemed more to suggest a tangled web" (2014, p. 178), and many have begun to question the ongoing utility and accuracy of the tree diagram in evolutionary biology. W. Ford Doolittle, for example, argues that the tree of life "should never have been imported without due consideration for its relevance into

²⁸ <https://www.altmetric.com/top100/2016/#journal=Nature+Microbiology>

²⁹ For example, genetic material can be transferred between bacteria by virus-like particles called "gene-transfer agents." See Quammen (2018).

microbiology” (2009, p. 2227); for Darwin, he claims, the tree of life “was a hypothesis, which lateral gene transfer in prokaryotes now shows to be false” (2009, p. 2221). Some have begun to doubt that the differences between phenetic (morphological) and cladistic (genealogical) approaches to classification can ever be resolved: “The enduring beauty of Darwin’s TOL [tree of life] hypothesis is that it promises to align the outcome of these two classificatory practices,” but lateral gene transfer “disrupts” this “workable alignment of phenetics and cladistic practices” (Doolittle, 2009, p. 2226; see also Velasco, 2013).

Doolittle proposes “pattern pluralism” to relieve the tree of life “of its responsibilities as the sole proper representation of the history of living things,” suggesting that scientists need to be alert to multiple mechanisms and patterns of relationship that may be obscured by over-reliance on tree-thinking (2009, p. 2227). Velasco mentions a number of other patterns that have been suggested “to play the ‘represent everything’ role”: the forest of life, the web or network of life, the coral of life, among others, suggesting that if any of these is correct, then Darwin’s tree hypothesis must be wrong (2013; see also Arnold & Fogarty, 2009; Ragan, 2009; 2013, p. 345).³⁰ If the “tree of life” hasn’t yet come to the end of the line scientifically, many believe it must be used in much more careful and constricted ways than it has been and that it should no longer claim the immense power over the biological imagination that it has held for so long. In rhetorical terms, it should no longer serve as a default warrant for enthymemes.

Nevertheless, there have been attempts to “save the tree,” in part by rethinking the diagram to include rhizomatic tangles or networked branching, such as in Doolittle’s widely reproduced and elaborated “reticulated tree” (1999, pp. 2127, Fig. 2123), which has become the source of the developing field of reticulate evolution

³⁰ In this regard, biologists are replicating the philosophical move made by Deleuze and Guattari in their advocacy of the rhizome as a better metaphor than the tree for Western thought: “We’re tired of trees. We should stop believing in trees, roots, and radicles. They’ve made us suffer too much. All of arborescent culture is founded on them, from biology to linguistics” (1987, p. 15). They characterize arborescent systems as “hierarchical . . . with centers of significance and subjectification” (1987, p. 16) and the rhizome as “an antigenealogy” (1987, p. 21). However, we doubt that biology can do without either hierarchy, which is central to classification, or genealogy, central to evolution.

(see Gontier, 2015) and a new type of diagram known as “reticulograms” (see Figure 14).

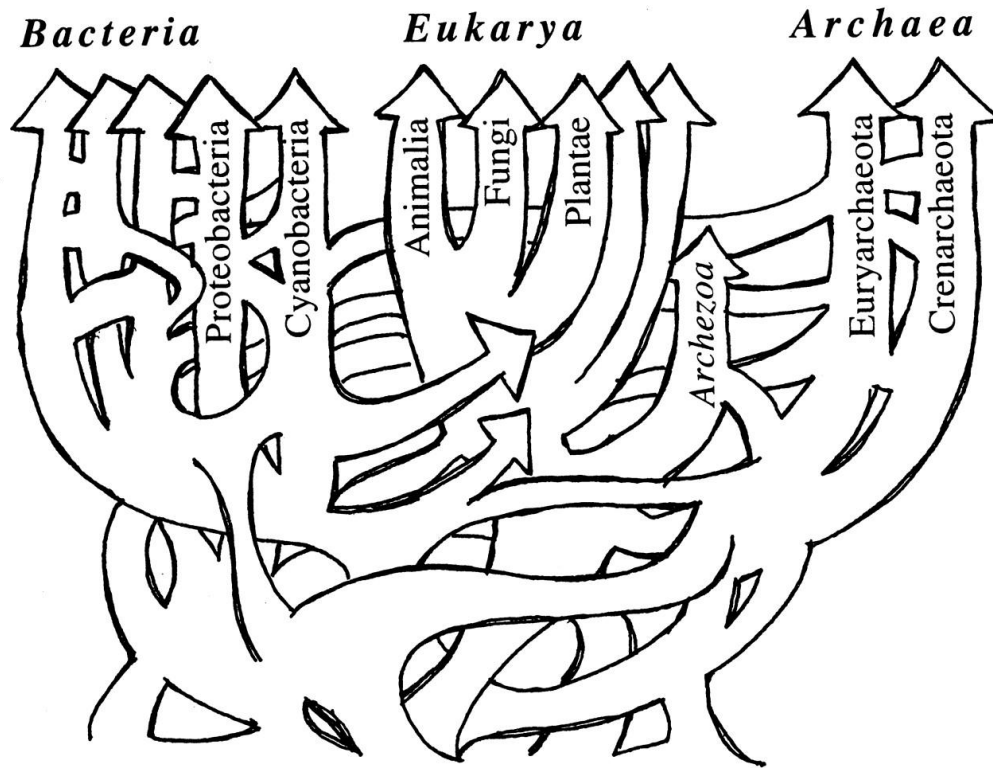


Figure 14. Doolittle’s “reticulated tree,” representing lateral gene transfer. Republished with permission of American Association for the Advancement of Science, from “Phylogenetic Classification and the Universal Tree,” by W. Ford Doolittle, in *Science* 284 (5423), 1999, Fig. 3, p. 2127, <https://science-sciencemag-org.prox.lib.ncsu.edu/content/284/5423/2124>; permission conveyed through Copyright Clearance Center, Inc.

The conventional tree image itself still dominates many ongoing projects, such as the online Tree of Life, a crowd-sourced effort whose “goal is to contain a page with pictures, text, and other information for every species and for each group of organisms, living or extinct,” displayed in a way that “visitors can browse the hierarchy of life and learn about phylogeny and evolution as well as the characteristics of individual groups.”³¹ Each page, at every level of classification, includes a cladogram showing the clades or classes

³¹ <http://tolweb.org/tree/>

included there with links to higher-level clades as well as to the specific classes covered. Other examples include the Interactive Tree of Life (ITOL), a more technical online tool, which allows scientists to contribute datasets and annotate, edit, and export high-resolution tree diagrams,³² and T-Rex, a web tool that maps lateral gene transfer and produces both traditional tree diagrams and reticulograms.³³

To summarize, what we find in tree diagrams based in a materialist tradition of visualization are several features of note. First, as noted earlier, most such diagrams have axes that can be labeled precisely with some unit of measure that provides a physical or statistical basis for the shape of the diagram and often serves as a proxy for time. Second, these diagrams retain the ambivalence we noted at the beginning: they show both states and processes (in Kress and van Leeuwen's terms, they are both conceptual and narrative), though in varying degrees. For example, in Figures 8 and 9, it is both the overall pattern of relations that is of interest but also the specific order and sequence of branching, particularly in Figure 9, where there is a quantitative basis for it. Third, orientation comes to be less significant, when the narrative vector is reduced, so we have sideways cladograms and radial trees, as well as upright rooted trees. Fourth, one axis often remains similar to earlier types of diagrams, representing variety or numerousness, but here the representation is less speculative and more precise, as with the species of bees on the x-axis in Figure 9 or the orders of birds on the y-axis in the cladogram of Figure 11. The other axis represents a measure of evolutionary divergence, or genetic diversity, or a proxy measurement for time, determined by the increasingly sophisticated molecular methods available. The exceptions in the examples we have used are the last three, Figures 12, 13, and 14, which are more abstract than empirical, but even these have been made possible by the quantitative methods of many prior studies, which they summarize. And finally, it is the material methods of genomics and molecular biology that have made it possible to challenge the hegemony of the tree of life as a visualization of evolutionary history.

³² <http://itol.embl.de/>

³³ <http://www.trex.uqam.ca/>; see also (Boc *et al.*, 2012).

Conclusion

We have called these visual representations of the tree of life “diagrams,” and it’s worth asking what the rhetorical qualities of a diagram are, in contrast to other types of visualizations. It seems generally agreed that a diagram is a visual representation that aims less at pictorial realism than at underlying structures or relationships; that they represent abstractions or concepts rather than objects; that what they represent is not otherwise available to ordinary vision (Bender & Marrinan, 2010, p. 33; Freedberg, 2003, p. 397; Gross & Harmon, 2014, ch. 2); in one formulation, “a diagram is a picture, in which one is intended to perform inference about the thing pictured, by mentally following around the parts of the diagram” (Franklin, 2000, p. 55). In some respects, to call the earliest visualizations of the tree of life “diagrams” is anachronistic, for the early cosmological and genealogical images do aim at picturing the order of creation or the genealogy of Jesus, for example, making it seem available to ordinary vision by being realistic, engaging, and memorable. Haeckel’s “great oak” is perhaps the most recent such image, and its audience is a broad one similar to the audiences for medieval religious iconography such as stained-glass windows. Later tree visualizations with more specialized scientific audiences are less decorative and more abstract, closer to what we now think of as a scientific diagram. And yet, as we have tried to demonstrate here, what we might think of as the diagrammatic qualities of these images do not depend on the presence or absence of pictorial detail but rather on the use of horizontal and vertical space to represent relationships of space or time, similarity or difference, inclusion or descent; the use of branches and nodes to represent entities and their relationships; the invocation of either stasis or directionality. The tree-form persists over time, even as the interpretive frameworks that we have called visual traditions change and with them the questions that these diagrams address, the inferences they invite, and the meanings they convey.

Fahnestock has called for “more specifically rhetorical histories of scientific discourse” that trace “the rise, change, and occasional fall of argumentative practices, devices, methods, techniques, or of the commonplaces” (2013, p. 13). Our visual rhetorical history of the tree of life demonstrates how one type of visual image can help explain how current practices in scientific visualization have developed and where some of the continuing disagreements in evolutionary biology come from. The relative stability of the tree

form in the changing contexts in which it has been used suggest that it functions as a “boundary object,” as characterized by Susan Star and James Greisemer: “Boundary objects are objects which are both plastic enough to adapt to local needs and constraints of the several parties employing them, yet robust enough to maintain a common identity across sites. . . . They have different meanings in different social worlds but their structure is common enough to more than one world to make them recognizable, a means of translation” (1989, p. 393). The robust qualities of boundary objects, then, can facilitate comprehension across boundaries even as their plastic qualities, while meeting the rhetorical needs of specialized rhetors, can obscure failures of cross-boundary comprehension. In our case, the relatively robust tree form has different meanings across the various traditions of visualization we have discussed. The meanings rely on different evidence to support them, from religious scripture, to logical dichotomies, to fossils, to mitochondrial DNA, and so on; in addition, the meanings are grounded in different interpretive traditions, from cosmology to logic to genealogy and scientific materialism.

If, as we have been suggesting, visual traditions serve as rhetorical contexts that provide backing, or “objects of agreement,” for enthymematic interpretation of tree diagrams, this may explain how boundary objects work rhetorically. They become polysemic warrants for arguments in different fields. We may think they mean the same thing in these different fields, but their polysemic plasticity is deceptive, and the “sameness” is illusory. So the tree of life may have the same general form in Darwin as it does in Haeckel or in a medieval treatise on logic or a modern biology textbook, but each makes a quite different argument in its own context: it “means” differently. The boundary object provides an enthymematic warrant for different kinds of inquiries and different kinds of arguments derived from different traditions of visualization. And the case of the tree of life illustrates the value of rhetoric in understanding scientific visualization; we offer the case in response to Gross’s claims about the poverty of rhetoric in this regard.

Over a century and a half after the publication of Darwin’s *Origin*, scientists are still working to construct a universal tree of life. The sheer size and complexity of mapping all the world’s species and their relationships have made the integration of data into one coherent and agreed-upon tree difficult, to say the least. To combat some of these complex issues, scientists have explicitly called for

“powerful visualization tools—tools that will enable visualization of ‘dark areas’ (poorly known or missing groups), identification of strongly supported vs. weakly supported areas of the tree, integration with all associated metadata . . . , and navigation tools to traverse branches of the tree and processes occurring within the lineages” (Collins, Kearney, & Maddison, 2013, § “NSF’s Assembling”). As a central visualization tool in evolutionary biology, the tree of life remains important, functioning as a tool for invention—literally showing “places” where our knowledge is missing or unsettled, providing evidence for new claims, and relying on backing and assumptions that draw from multiple traditions of tree visualization. Tree diagrams provide not just ways of seeing but ways of thinking and arguing, and these remain required skills for evolutionary biologists, even as the meaning and adequacy of the “tree of life” remains in contention.

Acknowledgments

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