The Roots of Phylogeny: How Did Haeckel Build His Trees?

BENOÎT DAYRAT

Department of Invertebrate Zoology and Geology, California Academy of Sciences, Golden Gate Park, San Francisco, California 94118, USA; E-mail: bdayrat@calacademy.org

Abstract.—Haeckel created much of our current vocabulary in evolutionary biology, such as the term phylogeny, which is currently used to designate trees. Assuming that Haeckel gave the same meaning to this term, one often reproduces Haeckel’s trees as the first illustrations of phylogenetic trees. A detailed analysis of Haeckel’s own evolutionary vocabulary and theory revealed that Haeckel’s trees were genealogical trees and that Haeckel’s phylogeny was a morphological concept. However, phylogeny was actually the core of Haeckel’s tree reconstruction, and understanding the exact meaning Haeckel gave to phylogeny is crucial to understanding the information Haeckel wanted to convey in his famous trees. Haeckel's phylogeny was a linear series of main morphological stages along the line of descent of a given species. The phylogeny of a single species would provide a trunk around which lateral branches were added as mere ornament; the phylogeny selected for drawing a tree of a given group was considered the most complete line of progress from lower to higher forms of this group, such as the phylogeny of Man for the genealogical tree of Vertebrates. Haeckel’s phylogeny was mainly inspired by the idea of the scala naturae, or scale of being. Therefore, Haeckel’s genealogical trees, which were only branched on the surface, mainly represented the old idea of scale of being. Even though Haeckel decided to draw genealogical trees after reading On the Origin of Species and was called the German Darwin, he did not draw Darwinian branching diagrams. Although Haeckel always saw Lamarck, Goethe, and Darwin as the three fathers of the theory of evolution, he was mainly influenced by Lamarck and Goethe in his approach to tree reconstruction. [Evolution; ontogeny; phylogenetics; recapitulation; scale of being; systematics.]

The meaning of scientific words can evolve. For example, the word evolution meant embryological development until the 19th century, when Lyell (1832) used it to designate Lamarck’s transformist theory. Less well known is the case of phylogeny, a word which the German biologist Ernst Haeckel (1834–1919) coined in 1866 in his Generelle Morphologie der Organismen. Today, we use the term phylogeny for designating phylogenetic trees, which are cladograms for the most part. Giving credit to Haeckel, his famous Monophylitischer Stammbaum der Organismen (1866, II: plate I) (Fig. 1) is traditionally cited as the first illustration of a phylogeny (e.g., Mayr, 1969; Hillis and Moritz, 1990) or phylogenetic tree (e.g., Wiley, 1981; Nielsen, 1995) of all organisms. The problem is that the original German title Monophylitischer Stammbaum der Organismen means monophyletic genealogical tree of organisms (e.g., Ax, 1987; Papavero and Llorente-Bousquets, 1996). Haeckel never called any of his hundreds of trees a phylogeny or a phylogenetic tree. Haeckel’s trees were genealogical and were distinct from what he called a phylogeny. Actually, he would build a genealogical tree by using a particular phylogeny. To understand the information Haeckel intended to provide in his trees, it is necessary to understand how he built each of those genealogical trees from what he called a phylogeny.

Haeckel took from Darwin (1859) the idea that the “natural system” should be represented as a genealogical tree. Because Darwin admitted that, unfortunately, we did not know the true genealogical tree of life, Haeckel’s main goal became finding a way to reconstruct such a tree. His efforts yielded the monumental Generelle Morphologie der Organismen (Haeckel, 1866), which provided what he interpreted as major improvements in the theory of descent: (1) a large vocabulary of neologisms, some of which became successful, such as phylogeny, monophyletic, polyphyletic, ecology, metamerism, and even Metazoa; (2) the biogenetic law, ontogeny recapitulates phylogeny, used to establish series of ancestral morphological stages; (3) pedigrees built from those series; and (4) the basis of his monistic philosophy, which over time became both his main interest and his new religion. However, the Generelle Morphologie der Organismen was not much of a success, even among scientists: “The Generelle Morphologie found but few readers, for which the voluminous and unpopular style of treatment, and its too extensive Greek terminology, may be chiefly to blame” (Haeckel, 1876b, I:xiii). Haeckel quickly found a more appropriate style, and the books he wrote after the Generelle Morphologie were successful to such an extent that he became one of the most famous biologists of the second half of the 19th century.

My main goal here is to show that even though Haeckel was called the German Darwin and found the idea of illustrating the natural system by genealogical trees in Darwin’s On the Origin of Species, his genealogical trees were not Darwinian. In constructing his trees, Haeckel was mainly influenced by the German Romantic writer and scientist Johann Wolfgang von Goethe (1749–1832) and by the French naturalist Jean-Baptiste de Lamarck (1744–1829), who were along with Darwin the three “fathers of the theory of descent,” according to Haeckel.

Sources and Methods

To determine in what context Haeckel proposed his evolutionary theory and his neologisms, his most important contributions were taken into account, biological treatises (Haeckel, 1862, 1866, 1868, 1870, 1874, 1876a, 1876b, 1894b, 1895, 1896, 1905a, 1905b) and philosophical
Haeckel's (1866, II: plate I) Monophyletischer Stammbaum der Organismen, i.e., monophyletic genealogical tree of organisms. The tree is monophyletic because it begins with a single common root, i.e., a single act of spontaneous generation. The rectangles (pmnq, pxyq, and pstq) illustrate the increasing number of lineages (Stämme in German) through time. The German word Stamm (from the Greek phylon), used by Haeckel at the bottom of the plate, has several meanings. The single Stamm refers to the root of the tree, its origin, which is also the exact meaning of phylon in the words monophyletic and polyphyletic. The three Stämme refer to the three first main branches of the monophyletic genealogical tree, i.e., the three kingdoms (Plantae, Protista, Animalia). The large majority of the 19 Stämme refer to Haeckel's phyla, or tribes.
essays (Haeckel, 1892, 1894a, 1899, 1900, 1904, 1905c, 1914). German and English editions of the same books were checked and compared. Citations were extracted from the first English editions when translations were available. Various Haeckelian studies were also consulted (e.g., Bolsche, 1906; Slosson, 1914; Keitel-Holz, 1984; Krausse, 1984–1987; Tort, 1996; Ziche, 2000).

It was also necessary to read the authors who inspired Haeckel. On the one hand, Haeckel stated that Darwin (1859, 1871), Goethe (e.g., 1883, 1888), and Lamarck (1809) were the three authors who inspired him a great deal, to such an extent that he called them the three fathers of evolution and their names were in the complete title of several of his books, such as The history of creation, or the development of the earth and its inhabitants by the action of natural causes, a popular exposition of the doctrine of evolution in general, and of that of Darwin, Goethe, and Lamarck in particular (Haeckel, 1868, 1876b). On the other hand, Haeckel never clearly said in which proportion each of these three authors inspired him. The goal here is to answer this question, at least for Haeckel’s reconstruction of trees.

ON HAECKEL’S EVOLUTIONARY VOCABULARY AND NEOLIGIMS

Understanding Haeckel’s tree reconstruction mainly depends upon understanding his evolutionary theory, which itself depends upon the terms he used and coined to talk about evolution. Haeckel’s neologisms are a crucial part of his work, even though many of them, such as promorphologie, antimerologie, or tectologie, were not successful. Therefore, it is necessary to give the exact meaning Haeckel would give to the terms he coined. Among all the Greek roots he used, three are absolutely crucial: phylon, genea, and genesis, from which he coined terms such as phylum, phylogenie, phylogenesis, ontogenie, biogenie, monophyletischer, and polyphyletischer. Haeckel carefully explained the Greek roots he used at the end of his Anthropogenie (Haeckel, 1874, 1876a).

Phylon as a Stem

The Greek phylon, translated as Stamm in German, means “tribe,” “branch,” “stem,” or even “race.” Haeckel gave three different meanings to the word phylon. In the two words “monophyletic” and “polyphyletic,” it clearly refers to the concept of stem. Haeckel coined monophyletic and polyphyletic to discuss this question: “Is the whole organic world of a common origin, or does it owe its origin to several acts of spontaneous generation?” (Haeckel, 1876b, II:42, emphasis in the original). He proposed two solutions (Haeckel, 1876b, II:45, emphasis in the original).

The unitary, or monophyletic, hypothesis of descent will endeavour to trace the first origin of all individual groups of organisms, as well as their totality, to a single common species of Monera which originated by spontaneous generation. The multiple, or polyphyletic, hypothesis of descent, on the other hand, will assume that several different species of Monera have arisen by spontaneous generation, and that these gave rise to several different main classes (tribes, or phyla). Haeckel never rejected the polyphyletic hypothesis (1876b, II:46, emphasis in the original).

Without here expressing our opinion in favour of either the one or the other conception, we must, nevertheless, remark that in general the monophyletic hypothesis of descent deserves to be preferred to the polyphyletic hypothesis of descent . . . . We may safely assume this simple original root, that is, the monophyletic origin, in the case of all the more highly developed groups of the animal and vegetable kingdoms. But it is very possible that the more complete Theory of Descent of the future will involve the polyphyletic origin of very many of the low and imperfect groups of the two organic kingdoms.

This statement explains why, in addition to monophyletic genealogical trees, Haeckel also drew three polyphyletic genealogical trees: (1) a Polyphylitischer Stammbaum der Organismen (Haeckel, 1868:347, 1876b:75) (Fig. 2) illustrating nine independent spontaneous generations for all organisms (one root for animals, one root for plants, and seven roots for protists) and many other
roots for extinct lineages of monerans (the term Monera was coined by Haeckel [e.g., 1870] to designate the simplest forms of life); (2) a Polyphyletisches Stamm zu den Pflanzenreichen, i.e., polyphyletic genealogical tree of the vegetable kingdom (Haeckel, 1868:382), illustrating six independent spontaneous generations for the plant kingdom and many other roots for extinct lineages of vegetable monerans; and (3) a Polyphyletisches Stammbum des Thierreichen, i.e., polyphyletic genealogical tree of the animal kingdom (Haeckel, 1868:392), illustrating nine independent acts of spontaneous generation for the animal kingdom and many other roots for extinct lineages of animal monerans.

Haeckel used the terms monophyletic or polyphyletic for trees of all organisms or trees of the three kingdoms (animals, plants, and protists). The trees of the other groups were just called Stammbaum, without specifying that they were monophylectic, such as for Coelenterates (e.g., 1866: plate III), Articulata (e.g., 1866: plate V), Arthropods (e.g., 1868: plate V), Molluscs (e.g., 1868: plate VI), or Mammals (e.g., 1866: plate VIII, 1868: plate VII). However, Haeckel would exceptionally add the term monophyletic, such as for the “monophyletic genealogical tree of vertebrates” (Haeckel, 1868: plate VI). According to Haeckel, the most important groups of the classification were not the kingdoms but the phyla, or tribes. That is the second meaning of the Greek phylon in Haeckel’s work.

**Phylon as a Branching Tribe**

The phylum was the highest category of the Haeckelian taxonomic hierarchy. Only phyla were called Stämme (i.e., tribes) by Haeckel; groups of lower ranks were designated as Gruppen (i.e., groups). The concept of phylum referred to a typological concept: Organismen-Stämme oder Phylten (Typen) (1866, I:50), Stamten (Typus) (1894a:29). The idea that organisms could share a common typical organization had been discussed starting from the end of the 18th century and was well accepted among systematists in the 1860s (e.g., Breidbach, 2002). Haeckel wrote that his phyla were mainly inherited from Cuvier’s (1817) embranchements based on comparative anatomy and from Von Baer’s (1828) “animal types” based on embryological studies. Goethe’s (1898) idea of typus, according to which one can define the anatomy of a common typus from which, for example, the anatomy of all vertebrates could be derived, also influenced Haeckel (1876a, I:83): “this idea . . . was one of the greatest advances in comparative anatomy.” Phyla are today what one commonly calls body plans. In practice, Haeckel recognized three phyla for the vegetable kingdom and six for the animal kingdom. However, Haeckel’s taxonomy was not stable with respect to categorized ranks. A phylum could sometimes be referred to as a cladem, which was the second category of the Haeckelian taxonomic ranks, and a cladem could sometimes be referred to as a phylum.

In the notes at the end of his Anthropogenie, Haeckel (1874, 1876a, II:460) wrote that “the phylon includes all organisms connected from a common typical parent-form.” In this sentence, the key word is “typical.” Haeckel really meant all the descendants of a “common typical parent-form,” and not “all” the descendants of a common parent form. The difference between these two expressions (with versus without “typical”) is crucial for understanding Haeckel’s idea of phylum. Not taking into account the word “typical” would suggest that a tribe could have a strict genealogical meaning (i.e., exclusively all the descendants of a parent form), which is actually absent in Haeckel’s sentence. Several of Haeckel’s phyla did not include exclusively all the descendants of a typical parent form but rather all the descendants sharing the typical organization of this common ancestor. For example, from the three tribes of Metaphyta, only Anthophyta (flowering plants, including Gymnospermae and Angiospermae) included all the descendants of the common typical ancestor; Thallophyta (including algae, mycetes, and lichens) and Diophyta (including Bryophyta and Pteridophyta) were two successive stages along the linear progress leading to Angiospermae (Haeckel, 1894a:90, 1894a:257) (Fig. 3). If Haeckel had used the word “all” in an exclusive way, his phylum Diophyta would have also included Anthrophyta. According to Haeckel, the concept of phylum was more typological than genealogical: every phylum would first of all correspond to a body plan.

**Phylon as a Linear Tribe**

My main goal here is to demonstrate that even though Haeckel accepted theoretically the idea that genealogical trees were branching diagrams, he drew them by using a linear view of evolution. For that reason, he also used a definition of tribe that was linear (1876a, I:309): “by tribe I mean the ancestors which form the chain of progenitors of [an] individual [of a given species].” As we will see, this last meaning of phylon as a linear chain of ancestors (Almenkette in German) of a given species is the key for understanding Haeckel’s entire work. The problem I attempt to solve here concerns the contradiction between phylon as a branched concept and phylon as a linear concept, which led Haeckel to come up with two distinct definitions of phylogeny.

**Genea and Genesis**

The Greek genea means “race,” “stock,” or even “offspring.” However, Haeckel gave to genea another meaning because he needed a word that would help him distinguish two concepts, evolution (Entwickelung in German) and history of evolution (Entwickelungsgeschichte in German) (Haeckel, 1876a, II:459):

Anthropogeny (Greek) = History of the evolution of Man; from Anthropos = Man, and genea = Evolution history. There is no especial Greek word for “the history of evolution;” in its place is used either genea (= descent), or genea (= generation). If genea is preferred to genea, the word must be written Anthropogony. The word “Anthropogony,” used by Josephus, means, however, only “the generation of man.” Genesis means “origination, or evolution;” therefore Anthropogony = “the evolution of man.”
According to Haeckel, there were three tribes of metaphytes: Thallophyta, Diaphyta, and Anthophyta. Only Anthophyta included exclusively all the descendants of a common typical parent form. Diaphyta, for example, included all the descendants sharing the typical morphology of the common typical ancestor but did not include exclusively all its descendants (i.e., Diaphyta and Anthophyta). Thus, Haeckel's concept of phylum, or tribe, was above all typological. Haeckel called a "tree" a diagram that was mainly reduced to a single line. Thus, the information conveyed in Haeckel's trees was entirely contained in the trunk of the tree.

The Haeckelian evolutionary vocabulary then clearly distinguished evolution, or genea, from history of evolution, or genesis (Fig. 4). Haeckel's idea of evolution can only be understood in the context of his monistic philosophy, according to which there is an eternal movement or eternal development in nature; this is above all the idea of evolution as an eternal motion that Haeckel wants to express by the term genesis. History of evolution, or genea, is a series of morphological stages that have been passed through during a given evolutionary path. In practice, Haeckel sometimes confused genea and genesis. For example, the title of his Anthropogenie (Haeckel, 1874) was
translated as The Evolution of Man (Haeckel, 1876a) instead of History of the Evolution of Man. That may explain why the unabridged Oxford English Dictionary assumes that phylogeny and phylogenesis can both mean “evolution of a tribe,” although phylogeny means, according to Haeckel, “history of evolution of tribes.”

The contrast made by Haeckel between phylogenesis and phylogeny is not contrast between “process” and “pattern” of evolution, as it is sometimes said to be (e.g., Farris, 1990). This interpretation reflects current opinions instead of Haeckel’s own ideas, which should be analyzed in their own context and with Haeckel’s own vocabulary. The terms process and pattern, which were introduced in systematics in the late 1970s because of the emergence of cladistics and the use of cladograms (e.g., Cracraft, 1979; Platnick, 1979), were not used by Haeckel and might therefore not be adequate for discussing his ideas.

Besides evolution and history of evolution, one of Haeckel’s major concerns was the notion of causes of evolution, i.e., the reasons why evolution is possible. Within the monistic context, causes are mechanical: phylogenesis is the cause of ontogenesis, heredity and adaptation are the causes of phylogenesis, and natural selection explains heredity and adaptation. The Haeckelian idea of causes of evolution would then be the closest thing that one could find to our modern concept of process. As a matter of fact, Cracraft (1979) defined the evolutionary processes as the causes of the historical pattern.

**FIGURE 4.** Haeckel’s evolution and history of evolution. (a) According to Haeckel, evolution, *genesis* in Greek, means development, which could be embryological or paleontological. Evolution as development (arrows) is fully in agreement with Haeckel’s monistic philosophy according to which there would be an eternal movement in nature. The paleontological evolution of a given species, or phylogenesis, is the movement that would go along the “chain of progenitors” of this species. This chain of progenitors is the genealogical line of descent, i.e., the actual series of ancestors of this species (dotted line). (b) History of evolution, or *genea*, is a series of main morphological stages passed through during evolution. For example, the history of evolution of a given species, or phylogeny, is the series of main morphological stages (rectangles) passed through along the line of descent of this species. Each stage would correspond to a period of time during which the ancestors of this given species would be assumed to share a similar morphology.

**TWO DEFINITIONS FOR PHYLOGENY**

Because Haeckel used *phylon* for “tribe” and *genea* for “history of evolution,” he would commonly use the expression “tribal history” (*Stammesgeschichte* in German) for phylogeny. However, according to Haeckel, a tribe could be constituted by a single line of descent or by many lines of descent. Haeckel was fully aware of this contradiction. He wrote only a few sentences about it (1876b, I:314, emphasis in the original):

*Ontogeny, or the history of the individual development of every organism (embryology and metamorphology), presents us with a simple unbranching or graduated chain of forms; and so it is with that portion of phylogeny which comprises the palaeontological history of the development of the direct ancestors only of an individual organism. But the whole of phylogeny—which meets us in the natural system of every organic tribe or phylum, and which is concerned with the investigation of the palaeontological development of all the branches of this tribe—forms a branching or tree-shaped developmental series, a veritable pedigree.*

A “portion of phylogeny” refers to a tribe as a single line of descent. A “whole of phylogeny” refers to a tribe as a complete branch of a tree. In practice, Haeckel never tried to reach the “whole of phylogeny.” He would actually only consider single portions of phylogeny, i.e., one portion of phylogeny per tree.

Haeckel would also use the word phylogeny for the history of evolution of organs instead of tribes. Phylogeny was still linear in this case. According to Haeckel (1889:38–39), the phylogeny of eight different main organs (nerves, muscles, coelom, genital organs, etc.) would support exactly the same linear succession in Metazoa: Gastraeades, Spongiae, Cnidaria, Platodes, Helminthes, Mollusca, Articulata, Echindodermata, Tunicata, Vertebrata. The use of the term phylogeny to address the successive stages in form of particular organs demonstrates that, according to Haeckel, phylogeny referred to morphological changes and not to genealogical lineages themselves (Fig. 4). In one of his later books, *The Riddle of the Universe*, Haeckel (1899, 1900) even provided an entire chapter on “the phylogeny of the soul.”

**FROM ON THE ORIGIN OF SPECIES TO THE GENERELLE MORPHOLOGIE DER ORGANISMEN**

Reading the first German translation of *On the Origin of Species* during the summer of 1860 was a crucial step in Haeckel’s scientific development. In a letter dated 9 July 1864, he sincerely professed to Darwin (Burkhardt and Smith, 2000:482), “Of all the books I have ever read, not a single one has come even close to making such an overpowering and lasting impression on me, as your theory of the evolution of species . . . Since then your theory—I can say without exaggerating—has occupied my mind every day.” According to Haeckel (e.g., 1866, 1868, 1874, 1876a, 1876b), Darwin’s theory consisted of two ideas: (1) natural selection is the cause of descent with modification through generations, and (2) the “natural system is genealogical in its arrangement, like a pedigree,” (Darwin, 1859:422) as shown in Darwin’s branching diagram. Darwin (1859:425) admitted that in practice “we
have no written pedigree” and thought that it would not be possible to reconstruct lines of descent with fossils because of the “imperfection of the geological record” (title of chapter IX of On the Origin of Species). That is the reason why Haeckel’s main goal was to find a method that would allow him to draw genealogical trees.

His first attempt at illustrating genealogical relationships appeared in his first imposing work, the Monographie der Radiolarien, in which he gave a Genealogische Verwandtschaftstabelle der Familien, Subfamilien undGattungen der Radiolarien, i.e., a “Table of genealogical relationships of families, subfamilies and genera of Radiolarians” (Haeckel, 1862:234). Nevertheless, this table was not a tree. Haeckel wanted to go a step further: drawing genealogical trees for all major groups of living organisms was one of the main goals of the Generelle Morphologie der Organismen (Haeckel, 1866). His method of tree reconstruction was mainly based on the biogenetic law: ontogeny recapitulates phylogeny. Even though Haeckel (1864) first proclaimed his biogenetic law at the 38th meeting of the German Naturalists and Physicians in 1863, he fully developed it in the Generelle Morphologie.

THE BIOGENETIC LAW

All the versions of the biogenetic law are more or less equivalent, except that the versions published in the Generelle Morphologie are usually a little bit longer and more complete. The version selected here was taken by Haeckel himself from the Generelle Morphologie to summarize his ideas about biogeny in the beginning of his Anthropogenie (1876a, I:1):

The History of the Evolution of Organisms consists of two kindred and closely connected parts: Ontogeny, which is the history of the evolution of individual organisms, and Phylogeny, which is the history of the evolution of organic tribes. Ontogeny is a brief and rapid recapitulation of Phylogeny, dependent on the physiological functions of Heredity (reproduction) and Adaptation (nutrition). The individual organism reproduces in the rapid and short course of its own evolution the most important of the changes in form through which its ancestors, according to laws of Heredity and Adaptation, have passed in the slow and long course of their palaeontological evolution.

Within the context of the biogenetic law, phylogeny is revealed through ontogeny. Haeckel also used other sources of evidence to support phylogeny, such as systematics, which he considered equal to comparative anatomy, and paleontology, i.e., the occurrence of a given typical organization in the fossil record. Systematics, paleontology, and embryology constitute what he called a three-fold parallelism (1876b, I:313, emphasis in the original). “The laws of inheritance and adaptation known to us are completely sufficient to explain this exceedingly important and interesting phenomenon, which may be briefly designated as the parallelism of individual, palaeontological and of systematic development.” However, within the context of the biogenetic law, ontogeny plays the most crucial role to reach phylogeny. Thus, it is important to determine Haeckel’s definition of ontogeny.

According to Haeckel, ontogeny is epigenetic. Mainly elaborated by Wolff (1759) and Von Baer (1828–1837), epigenesis contradicted the theory of preformation according to which all the structures of an adult would already be preformed in the earliest stages of development (Haeckel, 1876a, I:44): “The germ, or embryo which develops from the egg, shows in the various phases of its evolution an internal structure and an external form totally different from those of the developed organism. In none of these phases do we find any pre-formed parts.” According to Haeckel, the history of the development of an organism is, from the egg to the adult, a linear series of increasingly complex phases. The ontogeny of an organism is a series of changes in form through which it passes during its own development. The recapitulation of phylogeny by ontogeny implies that phylogeny is the series of morphological stages through which the ancestors of this organism have passed during their palaeontological evolution. Recapitulation is a partial repetition. For that reason, in practice, one can expect to obtain only the most important of the morphological changes.

Phylogeny as a linear series of morphological stages is in full agreement with the linear definition of tribe as “the chain of progenitors of the individual concerned” (Haeckel, 1876b, I:309). Phylogeny is thus the history of evolution of a “chain of progenitors” (Ahnenkette in German). Note that phylogeny is not the chain of progenitors, i.e., the actual chain of individual organisms but rather the series of the most important morphological stages passed through along this chain (Fig. 4). Phylogeny cannot be the chain of ancestors itself simply because Haeckel used two different words for two different things he wanted to distinguish clearly: (1) tribe or phylon, i.e., the chain of ancestors of a given species, and (2) the history of evolution of this tribe, or phylogenie. The chain of ancestors is a genealogical lineage constituted by actual organisms, whereas phylogeny refers to a series of morphological stages.

This distinction allows us to understand the expression “palaeontological history of evolution,” often used by Haeckel as a synonym for phylogeny. This expression needs much attention because it could be easily misinterpreted. The term “palaeontological” does not indicate that phylogeny is a series of actual ancestral organisms or species but rather that phylogeny refers to a succession of morphotypes in geological time. The biogenetic law does not reveal the actual series of ancestors but rather the main stages of their morphology. That is also why phylogeny (as a whole of lines of descent) and phylogeny cannot be the same things and were therefore designated by Haeckel by two different words: the Stammsgeschichte oder Phylogenie des Menschen, i.e., tribal history or phylogeny of man (Haeckel, 1874: plate IV), is the succession of main morphological changes along the line of descent of humans; the Stammbaum des Menschen, or “pedigree of man” (Haeckel, 1874: plate XV, 1876b, II: plate XV) (Fig. 5) is a tree illustrating genealogical lineages. This tree shows clearly how Haeckel built a genealogical tree from a single linear phylogeny, in this particular case the phylogeny of humans.
HAECKEL’S MONISM: UNITY AND DEVELOPMENT

Haeckel developed his monistic ideas in more depth in his last books (e.g., Haeckel, 1892, 1894a, 1899, 1900, 1904, 1905c), even though they were present and fundamental in his early contributions. Monism is a theory of unity and is opposed to dualism (Haeckel, 1900:20):

All the different philosophical tendencies may, from the point of view of modern science, be ranged in two antagonistic groups; they represent either a dualistic or a monistic interpretation of the cosmos. The former is usually bound up with teleological and idealistic dogmas, the latter with mechanical and realistic theories. Dualism, in the widest sense, breaks up the universe into two entirely distinct substances—the material world and an immaterial God, who is represented to be its creator, sustainer and ruler. Monism, on the contrary (likewise taken in its widest sense), recognises one sole substance in the universe, which is at once God and Nature; body and spirit (or matter and energy) it holds to be inseparable.

Haeckel owed his friend August Schleicher, one of the first comparative philologists (e.g., Schleicher, 1863), the first proposition of the monistic doctrine. Haeckel (1900:239) cited precursors in monistic cosmogony (e.g.,
Laplace, 1796), monistic geogeny (e.g., Lyell, 1830–1832), monistic biogeny (e.g., Lamarck, 1809; Darwin, 1859), and even monistic anthropogeny (e.g., Huxley, 1863; Darwin, 1871). Nevertheless, Goethe was by far his deepest inspiration for monism. Haeckel, who was anticlerical from an early age, found a new God in Goethe’s work, a God of unity, a synonym for nature and universe, which is why he cited extracts from Goethe’s Faust, Prometheus, or God and the World at the beginning and end of all his books. God and the World is a cycle in which Goethe (1983) at the end of his life decided to group some of his philosophical poems on natural history, such as his “Metamorphosis of Animals,” “Metamorphosis of Plants,” or “One and All.” The second volume of the Generelle Morphologie (Haeckel, 1866) begins with a short poem titled Epirrhema taken from the cycle God and the World, which expresses clearly that nature equals a God omnipresent (Goethe, 1983:159):

You must, when contemplating nature,
Attend to this, in each and every feature;
There’s nought outside and nought within,
For she is inside out and outside in.
Thus will you grasp, with no delay,
The holy secret, clear as day.

Besides unity, another crucial part of Haeckel’s monism is that nothing is stable in nature: there is an “eternal movement, or genetic energy, which reveals itself in the uninterrupted evolution of substance, in the perpetuum mobile of the universe” (Haeckel, 1900:245). Haeckel gave several examples of development: the development of an embryo, which does not take place in geological time, and Lamarck’s and Darwin’s theory of descent, which does take place in geological time. Haeckel also cited Goethe’s theory of metamorphosis as one of his major sources of inspiration. Indeed, the idea of uninterrupted motion in nature is clear in Goethe’s theory of metamorphosis, as expressed the “Metamorphosis of Plants” (Goethe, 1983:155):

Growing consider the plant and see how by gradual phases,
Slowly evolved, it forms, rises to blossom and fruit.
From the seed it develops as soon as the quietly fertile,
Womb of earth sends it out,
Sweetly released into life,
And to the prompting of light, the holy, for ever in motion,
Like the burgeoning leaves’ tenderest build, hands it on.

Goethe’s ideas on metamorphosis were influenced by the Bildungstrieb, i.e., formative force, developed in the context of the early Romantic period (Richards, 2002) by several authors such as Immanuel Kant and Frederich Blumenbach, both cited by Haeckel.

According to Haeckel, the causes of the “uninterrupted evolution” are mechanical and not final. Haeckel considered two mechanical causes that, according to him, had been discovered by Lamarck (1876b, I:1): “Heredity and Adaptation are the two formative functions, or the two mechanical causes of evolution.” Heredity and adaptation were explained through natural selection that “placed in our hands the means of tracing the causes of the Evolution of Forms” (Haeckel, 1876a, I:71). In Haeckel’s mind, natural selection was a sort of primary mechanical cause of evolution. As we have seen above, heredity and adaptation are crucial elements of the biogenetic law, which they actually connect to monistic philosophy.

FROM A PHYLLOGENY TO A TREE

The imposing trunk of the “pedigree of man” (Haeckel, 1876a, II: plate XV) (Fig. 5) corresponds, at least theoretically, to the “chain of progenitors” of Man, i.e., the line of descent that goes from the oldest ancestor up to humans. However, this trunk was obtained from the phylogeny of humans, which is why in practice it illustrates this phylogeny of humans instead of the detailed series of the ancestors of humans. The exact relationship between the line of descent of human and the phylogeny of humans reveals the core of Haeckel’s method of reconstructing genealogical trees. Each stage of the phylogeny of Man would correspond to a particular period of time in the line of descent of humans. During those stages, Haeckel would assume that the ancestors of Man had a similar morphology. To draw his “pedigree of man,” Haeckel merely added some lateral branches to the trunk (Fig. 6).
Haeckel (1895) later used the expression *stem groups* *(Stammmgruppe* in German) to designate the portions of a linear series of ancestors that could give rise to lateral branches. Haeckel assumed that the organisms of a given lateral branch would share the same general morphology as the stem group from which it would originate.

In the “Systematic Survey of the Most Important Stages in the Animal Ancestral Line of Man” (Haeckel, 1876a, II:44) and the “Systematic Survey of the Periods in the Tribal History [i.e., phylogeny] of the Human Race” (Haeckel, 1876a, II:184), Haeckel divided the phylogeny of humans in 4 main periods and 22 most important changes in form. In his last books, Haeckel (1895, 1905a, 1905b) considered a series of 30 stages, including some reptilian stages, instead of 22.

Because the genealogical tree of life, like all history, is unique, the pedigree of humans is the same as the pedigree of vertebrates. The phylogeny of humans with which Haeckel built his “pedigree of man” (Haeckel, 1876a: plate XV) (Fig. 5) was also the phylogeny from which he drew all his genealogical trees of vertebrates (e.g., 1866: plate VII; 1868: plate VI, 1895: 19, 1905b: plate I). The crucial importance of the particular line of descent of Man in Haeckel’s reconstruction of genealogical trees of vertebrates is graphically obvious in the “pedigree of man” of The Evolution of Man (1876a: plate XV). This is the only one of Haeckel’s trees in which the line of descent used as a trunk (in the present case, descent of Man) was illustrated as a very thick trunk.

The crucial importance of the linear series of morphological stages in Haeckel’s method of tree reconstruction is even more obvious in trees reduced to a single line (e.g., Haeckel, 1868:382; 1894b:257) (Fig. 3). Such trees, as far as they can be called that because they are not branched, show that according to Haeckel the information conveyed by trees was entirely contained in the trunk of the tree and not in the lateral branches. For the plant kingdom, the trunk used by Haeckel was the line of descent leading to the “bell-flowers,” such as composites, primroses, or honeysuckles. The phylogeny of composites is a series of a few main stages (Algae, Muscinae, Filicinae, Gymnospermae, Angiospermae, Monocotyledones, Dicotyledones, Gamopetalae, etc.) along this single lineage (e.g., Haeckel, 1866: plate II, 1868:382, 1876a: plate V, 1894b: 257) (Fig. 3).

Because the information conveyed in Haeckel’s trees was the success of main stages along the trunk, the number of lateral branches for a given group could vary from one tree to another. For example, the Bryophytes could be illustrated as one (Haeckel, 1866: plate II) or two (Haeckel, 1876b: plate V) branches originating from the trunk, and the Gymnosperms could be illustrated as one (Haeckel, 1866: plate II) or three (Haeckel, 1876b: plate V) branches originating from the trunk. Position and number of lateral branches had no real meaning in Haeckel’s trees. Only the successive main morphological stages along the trunk were important, i.e., in this case the succession of bryophytes, pteridophytes, gymnosperms, and angiosperms. Sometimes, Haeckel would draw trees in which he intended to convey another kind of information. For example, he would indicate the first appearance of groups in the fossil record by adding a geological time scale, such as for echinoderms (Haeckel, 1866: plate IV) or vertebrates (Haeckel, 1866: plate VII). However, the reconstruction of those trees would still mainly depend upon the linear phylogeny that had been chosen for the trunk. Moreover, the geological time scale was used to show that the succession of the first appearance of groups in the fossil record would follow the succession of the morphological stages along the trunk. For example, in Vertebrates, Haeckel would illustrate a succession of fishes, dipneusts, amphibians, reptiles, birds, and mammals.

When Haeckel wrote that phylogeny was the history of evolution of tribes, he basically meant that phylogeny was the history of evolution of phyla, i.e., groups that refer to body plans and have a special meaning in the classification of living organisms. One of Haeckel’s main goals was to build genealogical trees of all phyla. He also drew genealogical trees for groups that were not phyla (e.g., Haeckel, 1894b, 1895, 1896). Nevertheless, for each tree he drew, he always selected a single species whose phylogeny would provide a trunk. How did Haeckel make such a choice?

A Trunk for a Tree

According to Haeckel, two principles were obvious consequences of natural selection: differentiation, which is the multiplication of species (also called divergence), and progress, also called perfecting. The notion of progress is the key of Haeckel’s evolutionary theory: “The law of progress or of perfecting establishes the exceedingly important fact, on the ground of paleontological experience, that in successive periods of this earth’s history, a continual increase in perfection of organic formations has taken place” (1876b, I:276). Vertebrates were Haeckel’s favorite illustration of progress: “The fishes, dipneusts, amphibians, reptiles, monotremes, marsupials, placentals, lemur, apes, anthropoid apes, and apecmen (pithecanthropi) are inseparable links of a long ancestral chain, of which the last and most perfect link is man” (1905b:97). According to Haeckel, the phylogeny of humans is the most complete of all the phylogenies of vertebrates; only the phylogeny of humans would give a complete series of all the stages that the vertebrates passed through during their paleontological development.

Haeckel also applied his views to humans. Even if humans are the “highest result of the development of the Mammalian line, the crown of Creation” (Haeckel, 1876a, II:139), all humans are not at the same position at the top of the chain (1876b, II:332):

The various branches of the Indo-Germanic race have deviated furthest from the common primary form of ape-like men. During classic antiquity and the middle-ages, the Romanic branch (the Graeco-Italic group), one of the two main branches of the Indo-Germanic species, outstripped all other branches in the career of civilization, but at present the same position is occupied by the
phylogeny is clear. In his along a scale of living beings and Haeckel's concept of the Darwinian and Haeckelian evolutionary theories. The definition of progress constitutes a major difference between one line (Lamarck) or a few lines (Haeckel). This defining to Lamarck, Goethe, and Haeckel, progress concering to the lineage of the genealogical Tree of Life, whereas according to Darwin, progress could happen in any linear series, from lower to higher forms. Haeckel faithfully followed Lamarck instead of Darwin, who had expressed scepticism about the idea of a single main line of progress from lower to higher forms (e.g., Ghiselin, 1969). Darwin did not reject the idea of progress itself: “And as natural selection works solely by and for the good of each being, all corporeal and mental endowments will tend to progress towards perfection” (Darwin, 1859:489). However, according to Darwin, progress could happen in any lineage of the genealogical Tree of Life, whereas according to Lamarck, Goethe, and Haeckel, progress concerned one line (Lamarck) or a few lines (Haeckel). This definition of progress constitutes a major difference between the Darwinian and Haeckelian evolutionary theories.

The direct relation between Lamarck’s idea of progress along a scale of living beings and Haeckel’s concept of phylogeny is clear. In his Philosophie Zoologique, Lamarck (1809, I:275, my translation) classified the animals in a linear series of 14 classes distributed in six main stages or steps:

To make it easier to understand the principles that I followed in the exposition of the order of animals, and to make the gradation that we observe in the complexity [composition in French] of their organization clearer, from the most imperfect that are at the beginning of the series, up to the most perfect ones, that are at the end of it, I divided into six distinct stages all the modes of organization that we recognized over the large range of the animal scale. . . . In this way, it will be easy to study and to follow the steps of Nature through all its productions; and to distinguish, over the large range of the animal scale, the progress in the complexity of organization.

Lamarck’s arrangement of the animal kingdom was thus a linear scale of perfection. Each stage of this scale constituted one class of animals and was also called a mass (the French masse means a large group of objects): “this scale, that we aim to discover by classifying objects together by their natural relationships, only gives perceptible steps [degrés in French] in the masses of the general series, and not in the species or in the genera as well” (Lamarck, 1809:107, emphasis in the original, my translation). According to Lamarck, transformation through time happened from a given mass to the successive one.

Lamarck’s animal scale is clearly inherited from the scala naturae or scale of being that was broadly discussed during the 18th century, especially by Bonnet (1768). The scala naturae is a linear series of stages in organization; each stage is less perfect than the following one and more perfect than the previous one (e.g., Lovejoy, 1936). Nevertheless, there are two differences between Lamarck’s and Bonnet’s scales. First, Lamarck considered two distinct scales of progress, one for animals and another for plants, whereas Bonnet accepted only one single scale of being in which ‘zoophytes’ (e.g., sponges, corals) were the link between plants and animals. Second, Lamarck’s scales were series of transformations through time, whereas Bonnet’s scale of being was creationist.

Even though they are very closely related, Lamarck’s idea of scale of progress and Haeckel’s phylogeny are not the same. The main difference is the number of scales that each considered. Lamarck only considered two scales of progress, one for plants and one for animals, whereas Haeckel considered several scales. Haeckel would normally consider a single scale of progress per phylum, except for the phyla that would follow each other along a scale of progress, such as in Metaphyta (Fig. 3). Thus, his trees including several phyla, such as his trees of all organisms, would then be built by using several trunks, which is more obvious in his polyphyletic trees (e.g., Haeckel, 1866, II: plate I, 1868:347) (Figs. 1, 2). Even though most of his trees were built by using a single scale as a trunk, Haeckel could consider exceptionally more than one scale of progress for some particular groups. The trees of those groups would then be built around more than one trunk, such as for the “pedigree of mushrooms” (Haeckel, 1894b:317), which shows one trunk for the Ascomycetes and another for the Basidiomycetes.

When Haeckel confessed that “Lamarck had already pointed out the way to [phylogeny] in 1809” (1900:275), he clearly meant that phylogeny was a linear series of stages along a scale of perfection. As De Beer rightly observed (1954:29), phylogeny sensu Haeckel was “the scale of being rehabilitated as a result of the theory of evolution.” This definition of phylogeny may seem unusual to the modern reader but is fully Haeckelian. Although Haeckel wrote many pages on the history of natural history, he never mentioned the scala naturae. He surely wanted to preserve his reputation as the German Darwin.

CONCLUSION

Haeckel’s original meaning of phylogeny is very different from our current use of this term, i.e., as a cladogram illustrating sister-taxon relationships. Haeckel’s...
phylogeny was of course not a cladogram nor was it a genealogical tree. Haeckel’s own vocabulary is very clear about this point. Haeckel actually had different words for the different things he wanted to designate, and he never used “phylogeny” in any of the trees he drew. All Haeckel’s trees were called Stammbaum, which means “genealogical tree” or “pedigree.” For example, Haeckel’s Stammbaum des Menschen was the “pedigree of man” illustrating genealogical lineages of humans and other vertebrates. Haeckel’s Phyllogenie des Menschen, or “phylogeny of man,” was a completely different thing: it was the succession of the main morphological stages along the line of descent of humans. Haeckel’s phylogeny designated a series of morphological stages and not genealogical lineages. That point is particularly clear when Haeckel divided the phylogeny of humans into phylogenies of different organs (tegument, muscles, reproductive organs, nervous system, and even the soul).

The concept of phylogeny is key in Haeckel’s work because it is the core of his method of tree reconstruction. For every genealogical tree, Haeckel selected the species he considered the most perfect. From the biogenetic law, he obtained the phylogeny of this species, i.e., the linear succession of the main morphological stages of its ancestors (and not the series of ancestors itself). By choosing the supposedly highest species of a group, Haeckel was convinced of obtaining the most complete phylogeny of the entire group. In theory, he admitted the idea that there was a “whole of phylogeny” as the history of development along all the lines of descent of a given group. However, in practice, Haeckel only used the “portion of phylogeny” along the line of descent of a single species to reconstruct the genealogical tree of this group. For example, Haeckel never tried to reach the “whole of phylogeny” of vertebrates to reconstruct the genealogical tree of vertebrates but exclusively used the phylogeny of humans. Reconstructing a genealogical tree from the phylogeny of a single species was then quite easy. It simply required adding some lateral branches to the trunk obtained from this linear phylogeny. As a result of this method, Haeckel’s genealogical trees did not illustrate the actual series of ancestors, such as in Darwin’s branching diagram, but rather the series of main morphological steps in the evolutionary history of one species.

Haeckel’s method of tree reconstruction was entirely based on the idea that organisms are ordered along a scale of progress from lower to higher organisms. This conception, clearly inherited from the old idea of the scala naturae, was mainly transmitted to Haeckel by Lamarck and Goethe, who were both seen by Haeckel as fathers of the theory of descent, along with Darwin. The only difference between the old scala naturae and Haeckel’s ideas is the number of scales: naturalists of the 18th century admitted one single scale of progress leading to humans, whereas Haeckel admitted a few scales for all the living beings.

Haeckel built his complex view of the universe and his evolutionary theory by mixing many distinct and sometimes contradictory ideas. Even though he wanted to reconstruct Darwinian branching diagrams to illustrate the genealogical relationships of all organisms, his method of tree reconstruction was based on the acceptance of a re-visited scala naturae. Consequently, Haeckel’s trees were not branching diagrams but rather reflected an ancient hierarchical idea of nature according to which organisms were ordered from lower to higher forms. Haeckel’s trees were branched only on the surface. However, one of Haeckel’s most impressive skills was his ability to coin new and very successful terms. Even though the meaning of phylogeny evolved from its first Haeckelian sense, the word became commonly used starting from the end of the 19th century to designate evolutionary trees.

**ACKNOWLEDGMENTS**

This work has been discussed among two circles of systematists. I am grateful to all members of the systematics discussion group of the California Academy of Sciences and of the meetings of the Bay Area Biosystematists (San Francisco Bay Area, CA) for their comments. I am grateful to Marilyn Eversole, Mónica Medina, Amanda Grimes, Claude Dupuis, Michael Ghiselin, Kenneth Angielczyk, Rasmus Winther, Kevin Padian, Thomas Bach, and Simon Tillier for their help with the manuscript and their valuable suggestions. I am specifically grateful to Claude Dupuis and Michael Ghiselin, with whom I had many exciting discussions. Associate Editor Peter Linder and two anonymous reviewers provided suggestions that really improved the manuscript. This work was completed with support from the National Science Foundation (PEET DEB-9978155 and PEET DEB-9521930), the Woods Hole Oceanographic Institution, and the California Academy of Sciences.

**REFERENCES**

Haeckel, E. 1876b. The history of creation [E. Haeckel, R. Lankester, tr. from 2nd or 3rd German edition of Natürliche Schöpfungsgeschichte]. Appleton, New York.
Huxley, T. 1863. Evidence as to man’s place in nature. Appelton, New York.

First submitted 17 September 2002; reviews returned 26 January 2003; final acceptance 24 March 2003

Associate Editor: Peter Linder