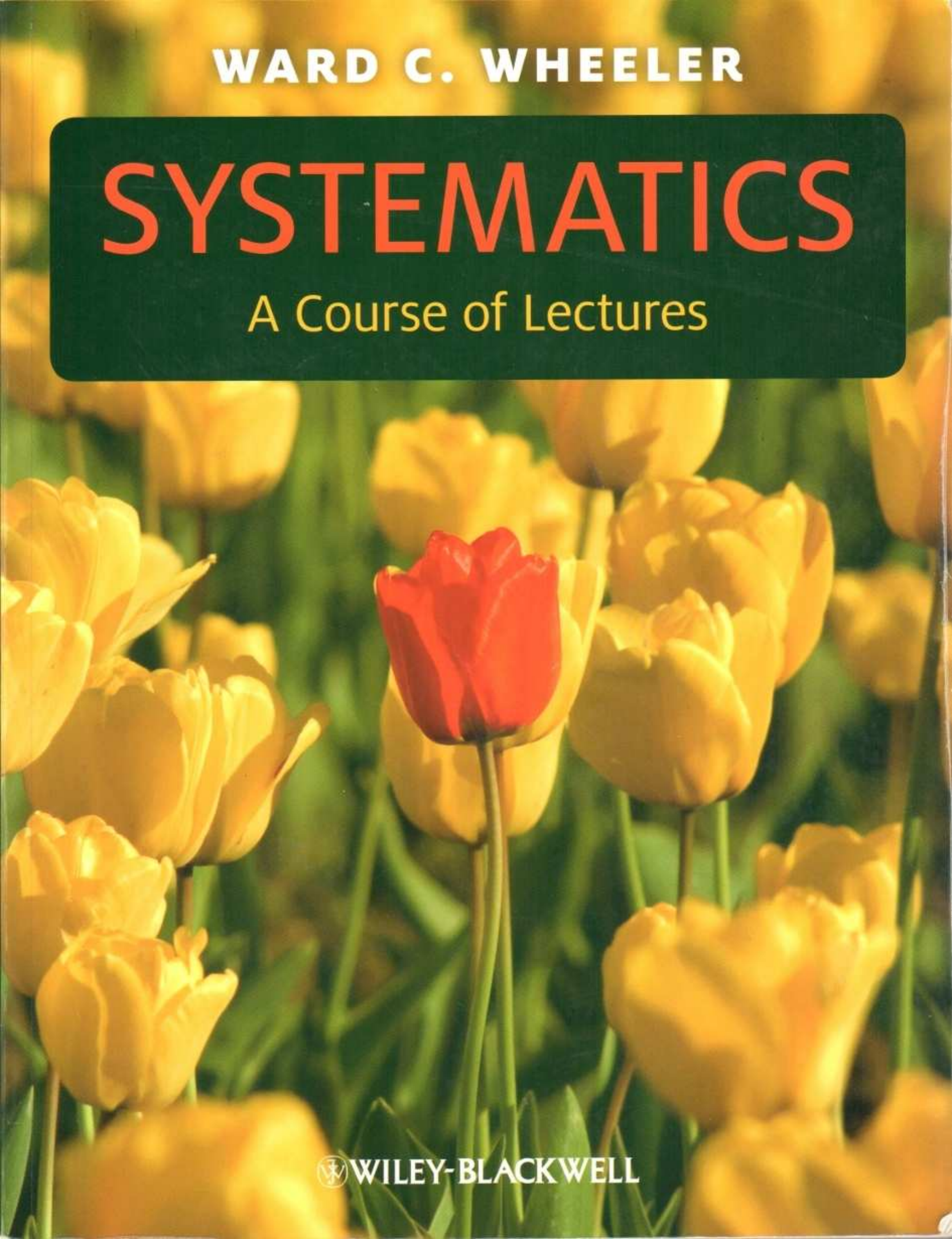
WARD C. WHEELER

SYSTEMATICS

A Course of Lectures



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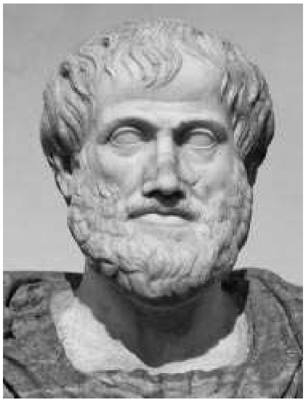
Chapter 1

History



Roman bust of Aristotle
(384–322 BCE)

Ibn Rushd (Averroes)
(1126–1198)

Systematics has its origins in two threads of biological science: classification and evolution. The organization of natural variation into sets, groups, and hierarchies traces its roots to Aristotle and evolution to Darwin. Put simply, systematization of nature can and has progressed in absence of causative theories relying on ideas of "plan of nature," divine or otherwise. Evolutionists (Darwin, Wallace, and others) proposed a rationale for these patterns. This mixture is the foundation of modern systematics.

Originally, systematics was natural history. Today we think of systematics as being a more inclusive term, encompassing field collection, empirical comparative biology, and theory. To begin with, however, taxonomy, now known as the process of naming species and higher taxa in a coherent, hypothesis-based, and regular way, and systematics were equivalent.

1.1 Aristotle

Systematics as classification (or taxonomy) draws its Western origins from Aristotle[1]. A student of Plato at the Academy and reputed teacher of Alexander the Great, Aristotle founded the Lyceum in Athens, writing on a broad variety of topics including what we now call biology. To Aristotle, living things (*species*) came from nature as did other physical classes (*e.g.* gold or lead). Today, we refer to his classification of living things (Aristotle, 350 BCE) that show similarities with the sorts of classifications we create now. In short, there are three features of his methodology that we recognize immediately: it was functional, binary, and empirical.

Aristotle's classification divided animals (his work on plants is lost) using functional features as opposed to those of habitat or anatomical differences: "Of land animals some are furnished with wings, such as birds and bees." Although he recognized these features as different in aspect, they are identical in use.

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[1] Largely through translation and commentary by Ibn Rushd (Averroes).

Systematics: A Course of Lectures, First Edition. Ward C. Wheeler.

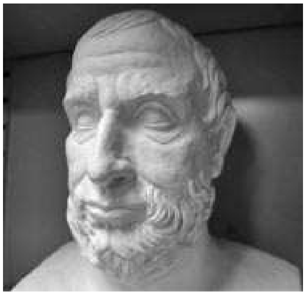
Features were also described in binary terms: "Some are nocturnal, as the owl and the bat; others live in the daylight." These included egg- or live-bearing, blooded or non-blooded, and wet or dry respiration.

An additional feature of Aristotle's work was its empirical content. Aspects of creatures were based on observation rather than ideal forms. In this, he recognized that some creatures did not fit into his binary classification scheme: "The above-mentioned organs, then, are the most indispensable parts of animals; and with some of them all animals without exception, and with others animals for the most part, must needs be provided." Sober (1980) argued that these departures from Aristotle's expectations (Natural State Model) were brought about (in Aristotle's mind) by errors due to some perturbations (hybridization, developmental trauma) resulting in "terata" or monsters. These forms could be novel and helped to explain natural variation within his scheme.

- Blooded Animals
    - Live-bearing animals
        - humans
        - other mammals
    - Egg-laying animals
        - birds
        - fish
- Non-Blooded Animals
    - Hard-shelled sea animals: Testacea
    - Soft-shelled sea animals: Crustacea
    - Non-shelled sea animals: Cephalopods
    - Insects
    - Bees
- Dualizing species (potential "terata," errors in nature)
    - Whales, seals and porpoises—in water, but bear live young
    - Bats—have wings and can walk
    - Sponges—like plants and like animals.

Aristotle clearly had notions of biological progression (*scala naturae*) from lower (plant) to higher (animals through humans) forms that others later seized upon as being evolutionary and we reject today. Aristotle's classification of animals was neither comprehensive nor entirely consistent, but was hierarchical, predictive (in some sense), and formed the beginning of modern classification.

1.2 Theophrastus


Theophrastus
(*c*.371–*c*.287 BCE)

Theophrastus succeeded Aristotle and is best known in biology for his *Enquiry into Plants* and *On the Causes of Plants*. As a study of classification, his work

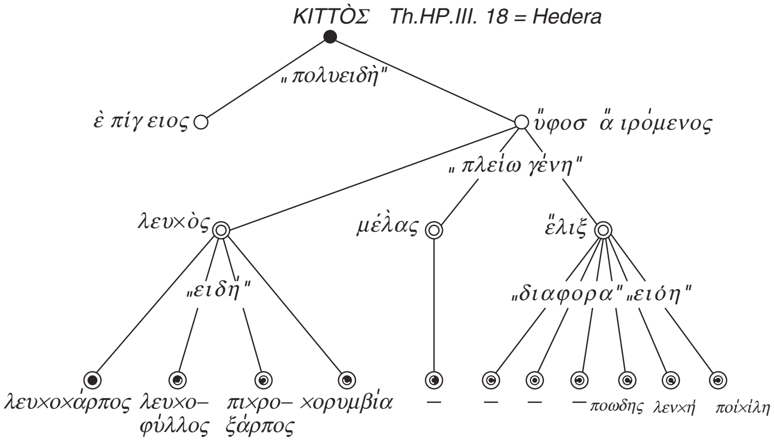


Figure 1.1: Branching diagram after Theophrastus (Vácsy, 1971).

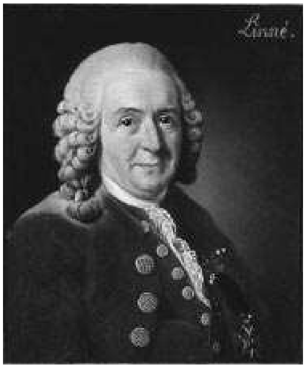
on ivy (*κιττός*) discussed extensively by Nelson and Platnick (1981), has been held to be a foundational work in taxonomy based (in part at least) on dichotomous distinctions (*e.g.* growing on ground versus upright) of a few essential features.

Theophrastus distinguished ivies based on growth form and color of leaves and fruit. Although he never presented a branching diagram, later workers (including Nelson and Platnick) have summarized these observations in a variety of branching diagrams (Vácsy, 1971) (Fig. 1.1).

Pierre Belon
(1517–1564)

1.3 Pierre Belon

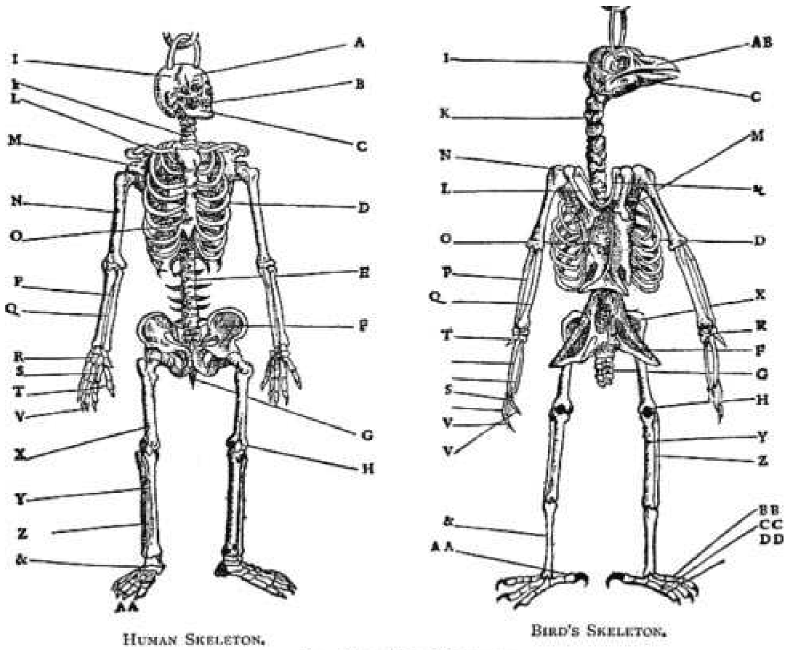
Trained as a physician, Pierre Belon, studied botany and traveled widely in southern Europe and the Middle East. He published a number of works based on these travels and is best known for his comparative anatomical representation of the skeletons of humans and birds (Belon, 1555) (Fig. 1.2).



Carl von Linné
(1707–1778)

1.4 Carolus Linnaeus

Carolus Linnaeus (Carl von Linné) built on Aristotle and created a classification system that has been the basis for biological nomenclature and communication for over 250 years. Through its descendants, the current codes of zoological, botanical, and other nomenclature, his influence is still felt today. Linnaeus was interested in both classification and identification (animal, plant, and mineral species), hence his system included descriptions and diagnoses for the creatures he included. He formalized the custom of binomial nomenclature, genus and species we use today.



From Belon's *Book of Birds*, 1555.

Figure 1.2: Belon's funky chicken (Belon, 1555).

Linnaeus was known, somewhat scandalously in his day, for his sexual system of classification (Fig. 1.3). This was most extensively applied to plants, but was also employed in the classification of minerals and fossils. Flowers were described using such terms as visible (public marriage) or clandestine, and single or multiple husbands or wives (stamens and pistils). Floral parts were even analogized to the foreskin and labia.

Nomenclature for many fungal, plant, and other eukaryote groups[2] is founded on the *Species Plantarum* (Linnaeus, 1753), and that for animals the 10th Edition of *Systema Naturae* (Linnaeus, 1758). The system is hierarchical with seven levels reflecting order in nature (as opposed to the views of Georges Louis Leclerc, 1778 [Buffon], who believed the construct arbitrary and natural variation a result of the combinatorics of components).

- Imperium (Empire)—everything
- Regnum (Kingdom)—animal, vegetable, or mineral
- Classis (Class)—in the animal kingdom there were six (mammals, birds, amphibians, fish, insects, and worms)
- Ordo (Order)—subdivisions of Class
- Genus—subdivisions of Order

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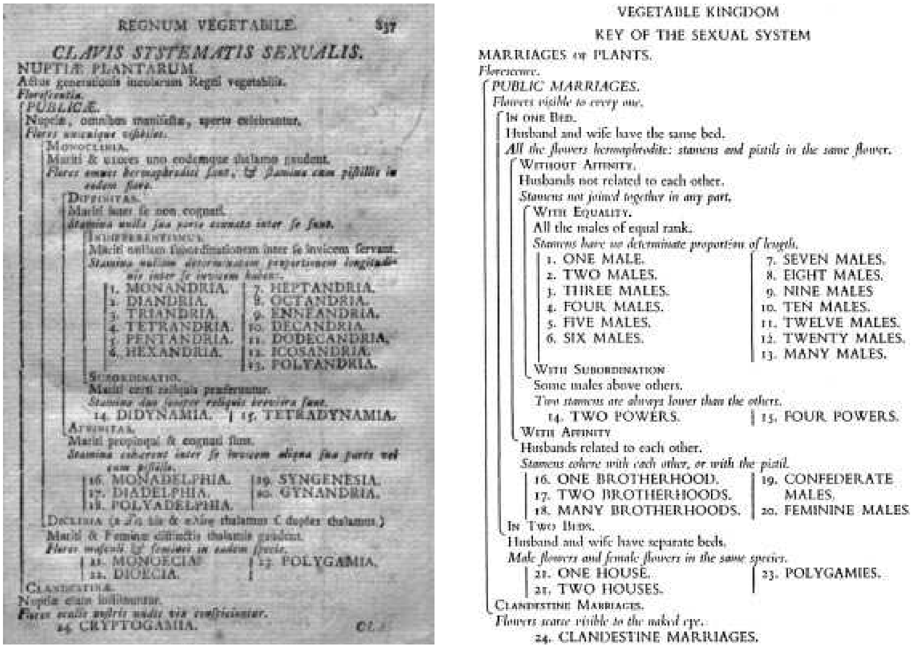
[2] For the current code of botanical nomenclature see `http://ibot.sav.sk/icbn/main.htm`.

- Species—subdivisions of Genus
- Varietas (Variety)—species varieties or "sub-species."



REGNUM VEGETABILE. 837

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.
2. DIANDRIA.
3. TRIANDRIA.
4. TETRANDRIA.
5. PENTANDRIA.
6. HEXANDRIA.
7. HEPTANDRIA.
8. OCTANDRIA.
9. ENNEANDRIA.
10. DECANDRIA.
11. DODECANDRIA.
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 cohærent inter ſe invicem aliqua ſua parte vel cum piſtillo.
16. MONADELPHIA.
17. DIADELPHIA.
18. POLYADELPHIA.
19. SYNGENESIA.
20. GYNANDRIA.
DICLINIA (a δὶς bis & κλίνη thalamus l. duplex thalamus.)
Mariti & Feminæ diſtinctis thalamis gaudent.
Flores maſculi & feminei in eadem ſpecie.
21. MONOECIA.
22. DIOECIA.
23. POLYGAMIA.
CLANDESTINA.
Nuptiæ clam inſtituuntur.
Flores oculis noſtris nudis vix conſpiciuntur.
24. CRYPTOGAMIA.
CLA

VEGETABLE KINGDOM
KEY OF THE SEXUAL SYSTEM

MARRIAGES OF PLANTS.
Florescence.
PUBLIC MARRIAGES.
Flowers visible to every one.
IN ONE BED.
Husband and wife have the same bed.
All the flowers hermaphrodite: stamens and pistils in the same flower.
WITHOUT AFFINITY.
Husbands not related to each other.
Stamens not joined together in any part.
WITH EQUALITY.
All the males of equal rank.
Stamens have no determinate proportion of length.
1. ONE MALE.
2. TWO MALES.
3. THREE MALES.
4. FOUR MALES.
5. FIVE MALES.
6. SIX MALES.
7. SEVEN MALES.
8. EIGHT MALES.
9. NINE MALES
10. TEN MALES.
11. TWELVE MALES.
12. TWENTY MALES.
13. MANY MALES.
WITH SUBORDINATION
Some males above others.
Two stamens are always lower than the others.
14. TWO POWERS. | 15. FOUR POWERS.
WITH AFFINITY
Husbands related to each other.
Stamens cohere with each other, or with the pistil.
16. ONE BROTHERHOOD.
17. TWO BROTHERHOODS.
18. MANY BROTHERHOODS.
19. CONFEDERATE MALES.
20. FEMININE MALES
IN TWO BEDS.
Husband and wife have separate beds.
Male flowers and female flowers in the same species.
21. ONE HOUSE.
21. TWO HOUSES.
23. POLYGAMIES.
CLANDESTINE MARRIAGES.
Flowers scarce visible to the naked eye.
24. CLANDESTINE MARRIAGES.

(a) Sexual system for plants (Linnaeus, 1758). (b) English translation.

Figure 1.3: Linnaeus' sexual system for classification (a) with English translation (b) (Linnaeus, 1758).

Georges Louis Leclerc, Comte de Buffon
(1707–1788)

The contemporary standard hierarchy includes seven levels: Kingdom, Phylum, Class, Order, Family, Genus, and Species, although other levels are often created as needed to describe diversity conveniently (*e.g.* McKenna and Bell, 1997).

1.5 Georges Louis Leclerc, Comte de Buffon

Georges Louis Leclerc, Comte de Buffon, began his scientific career in mathematics and probability theory[3]. He was appointed director of the *Jardin du Roi* (later *Jardin des Plantes*), making it into a research center.

Buffon is best known for the encyclopedic and massive *Histoire naturelle, générale et particulière* (1749–1788). He was an ardent anti-Linnean, believing taxa arbitrary, hence there could be no preferred classification. He later thought, however, that species were real (due to the *moule intérieur*—a concept at the

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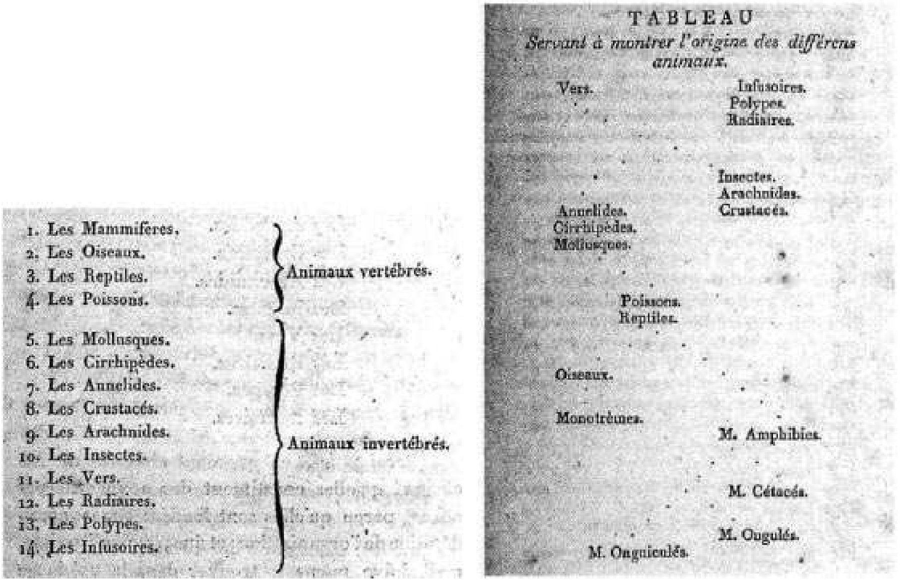
[3] Buffon's Needle: Given a needle of length l dropped on a plane with a series of parallel lines d apart, what is the probability that the needle will cross a line? The solution, $\frac{2l}{d\pi}$ can be used to estimate π.

foundation of comparative biology). Furthermore, Buffon believed that species could "improve" or "degenerate" into others, (*e.g.* humans to apes) changing in response to their environment. Some (*e.g.* Mayr, 1982) have argued that Buffon was among the first evolutionary thinkers with mutable species. His observation that the mammalian species of tropical old and new world, though living in similar environments, share not one taxon, went completely against then-current thought and is seen as the foundation of biogeography as a discipline (Nelson and Platnick, 1981).

Jean-Baptiste Lamarck (1744–1829)

1.6 Jean-Baptiste Lamarck

Jean-Baptiste Lamarck (who coined the word "Biologie" in 1802) believed that classifications were entirely artificial, but still useful (especially if dichotomous). His notion of classification is closer to our modern keys (Nelson and Platnick, 1981). An example of this comes from his *Philosophie zoologique* (Lamarck, 1809), with the division of animal life into vertebrates and invertebrates on the presence or absence of "blood" (Fig. 1.4(a)).



1. Les Mammifères.
2. Les Oiseaux.
3. Les Reptiles.
4. Les Poissons.

Animaux vertébrés.

5. Les Mollusques.
6. Les Cirrhipèdes.
7. Les Annelides.
8. Les Crustacés.
9. Les Arachnides.
10. Les Insectes.
11. Les Vers.
12. Les Radiaires.
13. Les Polypes.
14. Les Infusoires.

Animaux invertébrés.

(a) Lamarck's classification of animals. (b) Lamarck's transmutational tree.

Figure 1.4: Lamarck's division of animal life (a) and transmutational tree (b) (Lamarck, 1809).

Lamarck is best known for his theory of Transmutation (Fig. 1.4(b))—where species are immutable, but creatures may move through one species to another based on a motivating force to perfection and complexity, as well as the familiar "use and dis-use." Not only are new species created in this manner, but species can "re-evolve" in different places or times as environment and innate drive allow.

Georges Cuvier
(1769–1832)

1.7 Georges Cuvier

The hugely influential Léopold Chrétien Frédéric Dagobert "Georges" Cuvier divided animal life not into the *Scala Naturae* of Aristotle, or two-class Vertebrate/ Invertebrate divide of Lamarck, but into four "embranchements": Vertebrata, Articulata, Mollusca, and Radiata (Cuvier, 1812). These branches were representative of basic body plans or "archetypes" derived (in Cuvier's view) from functional requirements as opposed to common genealogical origin of structure. Based on his comparative anatomical work with living and fossil taxa, Cuvier believed that species were immutable but could go extinct, ("catastrophism") leaving an unfillable hole. New species, then, only appeared to be new, and were really migrants not seen before. Cuvier established the process of extinction as fact, a revolutionary idea in its day.

Étienne Geoffroy Saint-Hilaire
(1772–1844)

1.8 Étienne Geoffroy Saint-Hilaire

Although (like Lamarck), the comparative anatomist Étienne Geoffroy Saint-Hilaire is remembered for his later evolutionary views[4], Geoffroy believed that there were ideal types in nature and that species might transform among these immutable forms. Unlike Lamarck, who believed that the actions of creatures motivated transmutation, Geoffroy believed environmental conditions motivated change. This environmental effect was mediated during the development of the organism. He also believed in a fundamental unity of form for all animals (both living and extinct), with homologous structures performing similar tasks. In this, he disagreed sharply with Cuvier and his four archetypes (embranchements), not with the existence of archetypes, but with their number.

Johann Wolfgang von Goethe
(1749–1832)

1.9 Johann Wolfgang von Goethe

With Oken and Owen, Goethe was one of the foremost "ideal morphologists" of the 19th century in that he saw universal patterns underlying the forms of organisms. He coined the term "Morphology" to signify the entirety of an organism's form through development to adult as opposed to "gestalt" (or type—which was inadequate in his view). This is similar to Hennig's concept of the "semaphoront" to represent the totality of characters expressed by an organism over its entire life cycle.

Goethe applied these ideas to the comparative morphology and development of plants (von Goethe, 1790)[5] as Geoffroy did to animals, creating morphological ideals to which all plants ascribed. He claimed, based on observation, that

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[4] "The external world is all-powerful in alteration of the form of organized bodies... these are inherited, and they influence all the rest of the organization of the animal, because if these modifications lead to injurious effects, the animals which exhibit them perish and are replaced by others of a somewhat different form, a form changed so as to be adapted to the new environment" (Saint-Hilaire, 1833).

[5] In his spare time, he wrote a book called *Faust*.

archetypes contained the inherent nature of a taxon, such as "bird-ness" or "mammal-ness." This ideal was not thought to be ancestral or primitive in any way, but embodied the morphological relationships of the members of the group.

1.10 Lorenz Oken


Lorenz Oken
(1779–1851)

Oken was a leader in the "Naturphilosophie" (Oken, 1802) and an ideal morphologist. In this, he sought general laws to describe the diversity in nature through the identification of ideal forms. One of the central tenets of the *Naturphilosophie* was that there were aspects of natural law and organization that would be perceived by all observers. He applied this to his classification of animal life, and created five groups based on his perception of sense organs.

1. Dermatazoa—invertebrates
2. Glossozoa—fish (with tongue)
3. Rhinozoa—reptiles (with nose opening)
4. Otozoa—birds (with external ear)
5. Ophthalmozoa—mammals (nose, ears, and eyes).

Oken is also known for his attempts to serially homologize vertebral elements with the vertebrate skull, suggesting fusion of separate elements as the main developmental mechanism. Although falsified for vertebrates, the idea found ground in discussions of the development of the arthropod head.

1.11 Richard Owen


Richard Owen
(1804–1892)

Richard Owen was a vertebrate comparative anatomist known for his role in founding the British Museum (Natural History), the definitions of homology and analogy, and his opposition (after initial favor) to Darwinian evolution. Owen (1847) defined a homologue as "The same organ in different animals under every variety of form and function." Analogy was, in his view, based on function, "A part or organ in one animal which has the same function as another part or organ in a different animal."

Owen derived the general archetype for vertebrates based (as in Oken) on the serial homology of vertebral elements (Fig. 1.5).

Owen's notion of homology and archetype was tightly connected with the component parts that made up the archetype—the homologues.

A system based on concentric groupings of creatures in sets of five, "Quinarianism" (Macleay, 1819), was briefly popular in early 19th century Britain.

1.12 Charles Darwin

To Aristotle, biological "species" were a component of nature in the same way that rocks, sky, and the moon were. Linnaeus held that the order of natural variation was evidence of divine plan. Darwin (1859b) brought the causative theory

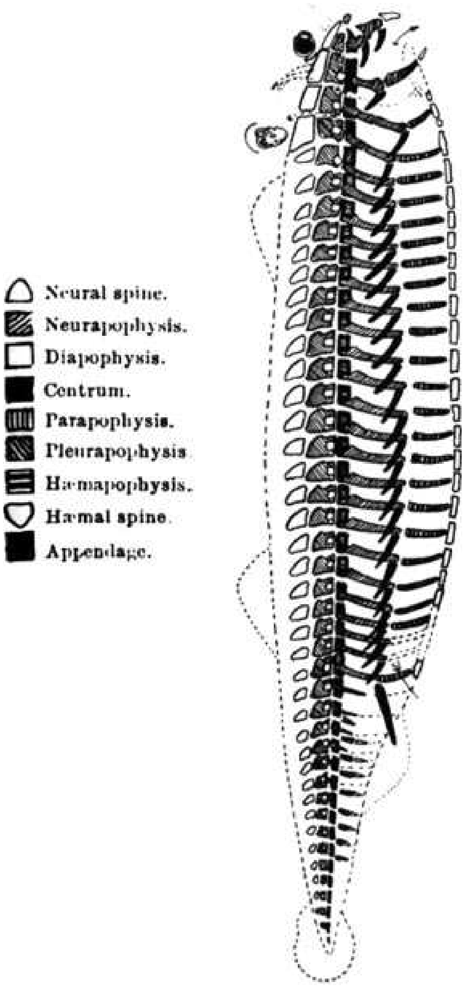
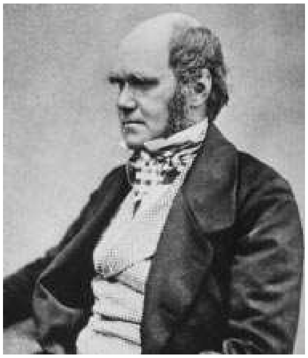


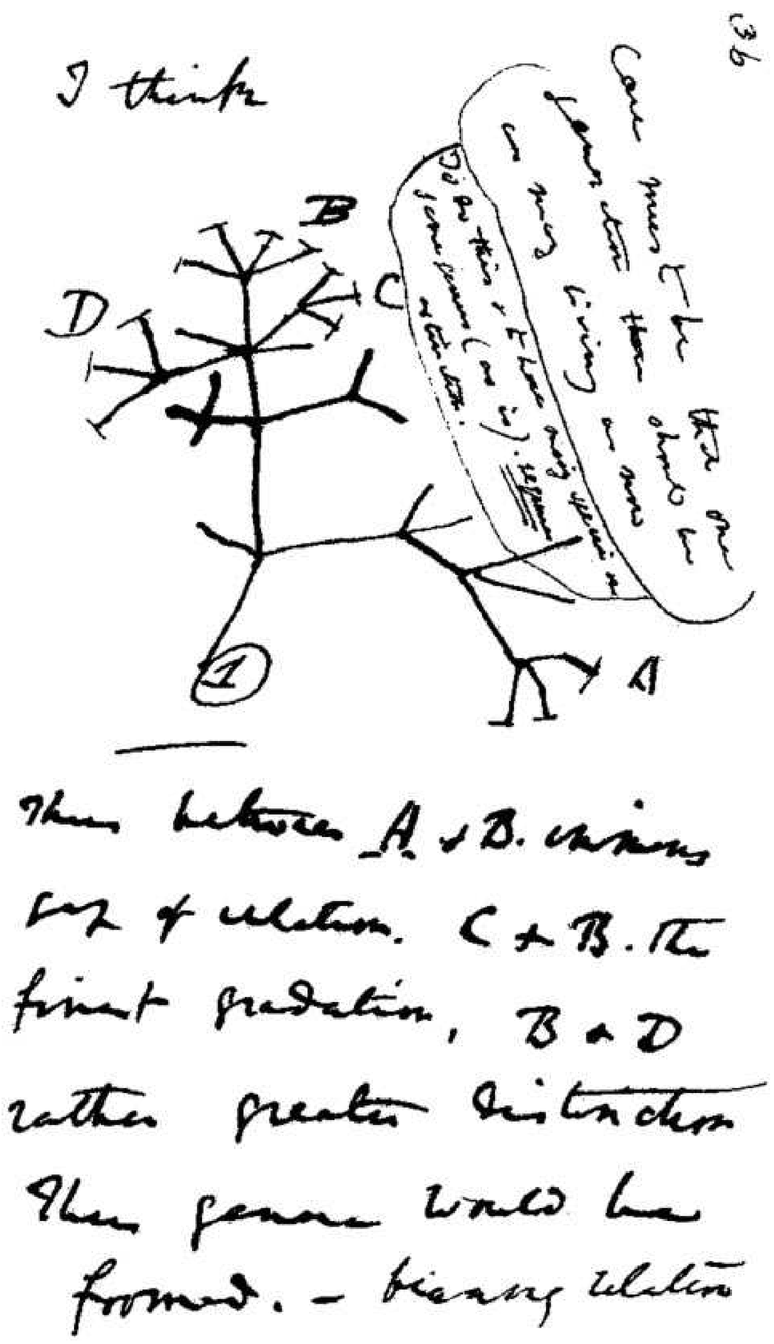
Figure 1.5: Owen's vertebrate archetype showing his model of a series of unmodified vertebral elements (Russell, 1916; after Owen, 1847).



Charles Darwin
(1809–1882)

of evolution to generate and explain the hierarchical distribution of biological variation. This had a huge intellectual impact in justifying classification as a reflection of genealogy for the first time, and bringing intellectual order (however reluctantly) to a variety of conflicting, if reasonable, classificatory schemes.

The genealogical implications of Darwin's work led him to think in terms of evolutionary "trees," (Fig. 1.6), the ubiquitous metaphor we use today. The relationship between classification and evolutionary genealogy, however, was not particularly clarified (Hull, 1988). Although the similarities between genealogy and classification were ineluctable, Darwin was concerned (as were many who followed) with representing both degree of genealogical relationship and degree of evolutionary modification in a single object. He felt quite clearly that



I think

Case must be that one generation then should be as many living as now. To do this & to have many species in same genus (as is) requires extinction.

Thus between A & B immens gap of relation. C & B the finest gradation, B & D rather greater distinction. Thus genera would be formed. — bearing relation

Figure 1.6: Darwin's famous "I think..." tree depiction.

classifications were more than evolutionary trees, writing that "genealogy by itself does not give classification" (Darwin, 1859a).

How to classify even a hypothetical case of genealogy (Fig. 1.7)? Darwin's Figure presents many issues—ancestral species, extinction, different "degrees of modification," different ages of taxa. As discussed by Hull (1988), Darwin gave no clear answer. He provided an intellectual framework, but no guide to actually determining phylogenetic relationships or constructing classifications based on this knowledge.

Darwin transformed Owen's archetype into an ancestor. Cladistics further transformed the ancestor into a median.

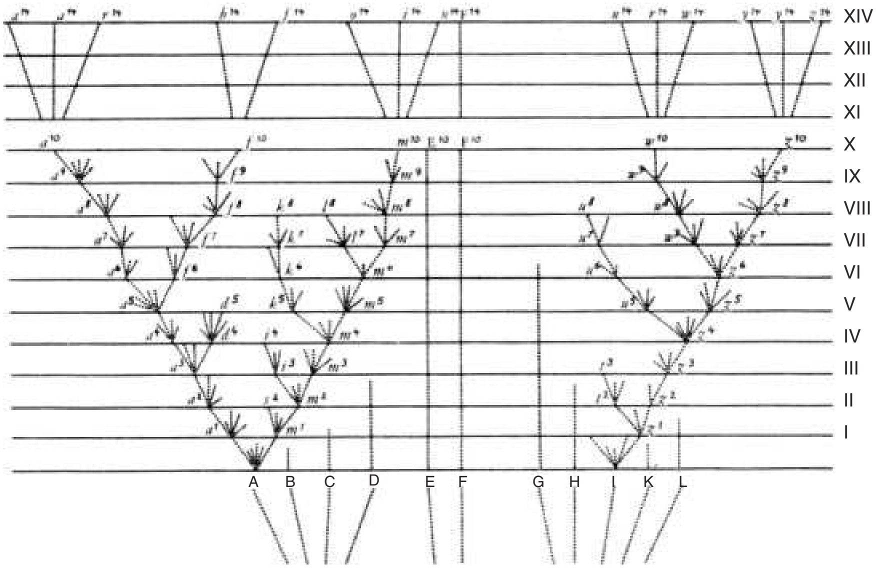


Figure 1.7: Darwin's hypothetical phylogeny from the *Origin*.

1.13 Stammbäume

Haeckel (1866) presented the situation in a graphical form (Fig. 1.8), including both genealogical relationships (as branches), degrees of modification (distance from root), and even Aristotle's *Scala Naturae* beginning with Monera at the root and progressing through worms, mollusks, echinoderms, tetrapods, mammals, and primates before crowning with humans. In his 1863 lecture, Haeckel divided the scientific community into Darwinians (progressives) and traditionalists (conservatives): "Development and progress!" ("Entwicklung und Fortschritt!") versus "Creation and species!" ("Schöpfung und Species!"). He even coined the word "Phylogeny" (Haeckel, 1866) to describe the scheme of genealogical relationships[6]. Haeckel felt that paleontology and development were the primary

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[6] And the term "First World War" in 1914.

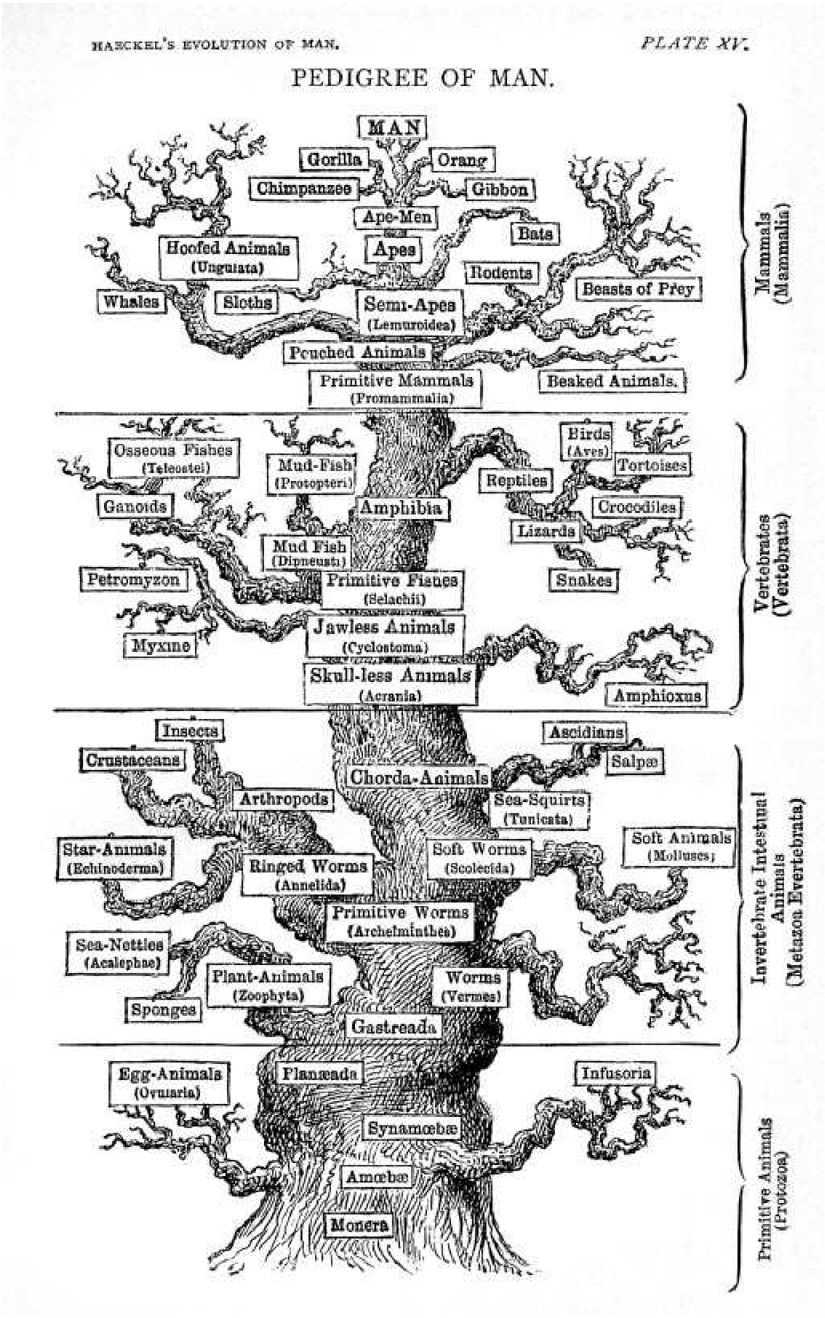

Figure 1.8: Ernst Haeckel and the first phylogenetic “tree” representation (Haeckel, 1866).

ways to discover phylogeny (Haeckel, 1876). Morphology was a third leg, but of lesser importance. Bronn (1858, 1861) also had a tree like representation and was the translator of Darwin into the German version that Haeckel read (Richards, 2005). Bronn found Darwin's ideas untested, while Haeckel did not.

August Schleicher constructed linguistic trees as Darwin had biological. A friend of Haeckel, Schleicher "tested" Darwin with language (Schleicher, 1869). Interestingly, he thought there were better linguistic fossils than biological, and hence they could form a strong test of Darwin's ideas.

Ernst Mayr
(1904–2005)

George Gaylord Simpson
(1902–1984)

1.14 Evolutionary Taxonomy

After publication of the *Origin*, evolution, genetics, and paleontology went their own ways. In the middle of the 20th century, these were brought together in what became known as the "New Synthesis." Among many, Dobzhansky (1937), Mayr (1942), Simpson (1944)[7], and Wright (1931) were most prominent. The New Synthesis brought together these strands of biology creating a satisfyingly complete (to them) Darwinian theory encompassing these formerly disparate fields (Provine, 1986; Hull, 1988). The New Synthesis begat the "New Systematics" (Huxley, 1940), which grew to become known as Evolutionary Taxonomy. Evolutionary Taxonomy competed with Phenetics (sometimes referred to as Numerical Taxonomy) and Phylogenetic Systematics (Cladistics) in the Cladistics Wars of the 1970s and 1980s, transforming systematics and classification and forming the basis for contemporary systematic research.

Here, we are limited to a brief precis of the scientific positions and differences among these three schools of systematics. Hull (1988) recounts, in great detail, the progress of the debate beginning in the late 1960s. They were amazing and frequently bitter times. As Hull writes, "Perhaps the seminar rooms of the American Museum of Natural History are not as perilous as Wallace's upper Amazon, but they come close."

Evolutionary Taxonomy as promulgated by Simpson (1961) and Mayr (1969) reached its apex in the late 1960s. This branch of systematics seized on the problem Darwin had seen in classification in that he felt that genealogy alone was not sufficient to create a classification—that systematics needed to include information on ancestors, processes, and degrees of evolutionary difference (similarity) as well as strict genealogy of taxa. There was also a great emphasis on species concepts that will be discussed later (Chapter 3).

At its heart (and the cause of its eventual downfall), Evolutionary Taxonomy was imprecise, authoritarian, and unable to articulate a specific goal other than ill-defined "naturalness." The only rule, *per se*, was that all the members of a taxonomic group should be descended from a single common ancestor. These groups were called "monophyletic" in a sense attributed to Haeckel (1866). This is in contrast to the Hennigian (Hennig, 1950, 1966) notion of monophyly that required a monophyletic group to contain *all* descendants of a common ancestor. Hennig would have called some of the "monophyletic" groups of Evolutionary

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[7] Whose AMNH office I occupy.

Taxonomy paraphyletic (*e.g.* "Reptilia"), while Hennig's monophyly was referred to as "holophyly" by Mayr (Fig. 1.9). We now follow Hennig's concepts and their strict definitions (Farris, 1974). According to Simpson (1961), even the "monophyly" rule could be relaxed in order to maintain cherished group definitions (*e.g.* Simpson's Mammalia).

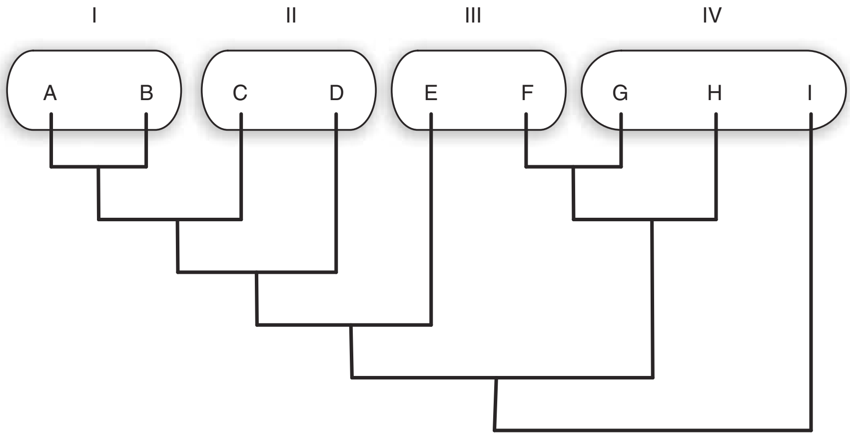


Figure 1.9: Alternate valid groups. Evolutionary Taxonomy would allow groups I, II, and IV; Hennigian Phylogenetic Systematics only I; Phenetics would allow III (as well as the others depending on degree of similarity).

In applying this rule, there were no specific criteria. Since Evolutionary Taxonomy strove to include evolutionary level (grade) information, individual investigators had to judge the relative importance of different features themselves. This weighting of information relied on the expert or authority status of the proponents of a given scenario. Great weight was given to the identification of fossil ancestors and their inclusion in systematic discussions because they were links in the Darwinian chain.

Furthermore, given that genealogy was only one element of a classification, a single genealogy could yield multiple, contradictory classifications. As stated by Mayr (1969), "Even if we had perfect understanding of phylogeny, it would be possible to convert it into many different classifications."

The lack of rules, authoritarian basis for interpretation of evidence, and inherent imprecision in the meaning of classifications produced doomed Evolutionary Taxonomy. Little remains today that is recognizably derived from this research program other than, ironically enough, the term "Cladistics."

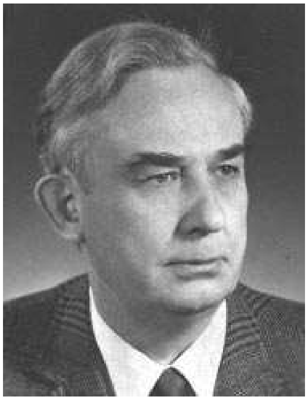
1.15 Phenetics

Phenetics, or as it was once referred to, Numerical Taxonomy (as with Cladistics, Mayr, 1965, was the origin of the name), arose through criticisms of Evolutionary

Robert Sokal

Taxonomy. As articulated by Charles Michener, Robert Sokal, Peter Sneath, and others (Michener and Sokal, 1957; Sokal and Sneath, 1963; Sneath and Sokal, 1973), Phenetics had many features lacking in Evolutionary Taxonomy, and was free of some of its more obvious problems. Phenetic classification was based on overall similarity and required an explicit matrix of features, equally weighted. The idea was that the observations of creatures should be explicit and open to objective criticisms by other workers. The equal weighting was specified to avoid the authoritarian arguments about the relative importance of features and to produce generally useful classifications. Similarity was expressed in a phenogram, a branching tree diagram representing levels of similarity among taxa.

The method was explicit, rules-based, and objective. It also made no reference to, and had no necessary relationship with, genealogy or evolutionary trees at all. In fact, phenetic classifications could include groups of genealogically unrelated, but similar, taxa in groups termed "polyphyletic" by both Evolutionary Taxonomy and Cladistics (Fig. 1.9). This was an unavoidable consequence of lumping all similarity in the same basket, a fault found as well (if to a lesser extent) in Evolutionary Taxonomy (see Schuh and Brower, 2009, for more discussion). The specifics of phenetic (and distance methods in general) tree building are discussed later (Chapter 9).



Willi Hennig
(1913–1976)

There are few advocates of phenetic classification in contemporary science. Several contributions, however, remain. The ideas of objectivity and explicitness of evidence, specificity of rule-based tree construction, and liberation from authoritarianism all helped systematics move from art to science. Phenetics was mistaken in several major aspects, but its influence can be seen in modern, computational systematic analysis.

1.16 Phylogenetic Systematics

Phylogenetic Systematics, or as it is more commonly known, Cladistics, has its foundation in the work of Hennig (1950)[8]. Although known and read by German speakers (*e.g.* Mayr and Sokal), Hennig's work did not become widely known until later publications (Hennig, 1965, 1966). The presentation of the work (in German as well as in English) was regarded as difficult, even though the concepts were few, simple, and clear. As promulgated by Nelson (1972) and Brundin (1966), Hennig's ideas became more broadly known following the path of Nelson from Stockholm to London to New York (Schuh and Brower, 2009).

1.16.1 Hennig's Three Questions

English uses the term "sister-group" because *Gruppe* is feminine in German. Those systematists in romance-language speaking countries use "brother" group.

Hennig proposed three questions: "what is a phylogenetic relationship, how is it established, and how is knowledge of it expressed so that misunderstandings are

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[8] The concept of what constitutes phylogenetic relationship and has come to be known as the "sister-group" was discussed both by Rosa (1918) and more prominently by Zimmermann (1931). Hennig (1950) cited Zimmerman as important to the development of his ideas (Nelson and Platnick, 1981; Donoghue and Kadereit, 1992; Williams and Ebach, 2008).

A. Myriapoda
B. Insecta
B.1 Entognatha
B.1 a Diplura
B.1 b Ellipura
B.1 ba Protura
B.1 bb Collembola
B.2 Ectognatha

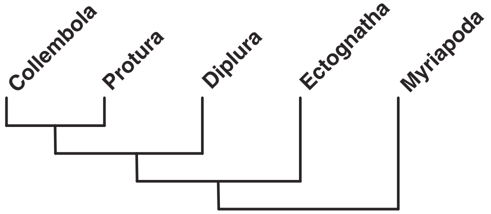

Figure 1.10: Isomorphism between Hennigian classification (left) and genealogy (right).

excluded" (Hennig, 1965). His answers were equally precise. Phylogenetic relationship meant genealogical relationship, expressed as a series of nested sister-group relationships where two taxa are more closely related (in terms of recency of common ancestry) to each other than they are to a third[9]. These sister-group relationships are established by "special" similarity or synapomorphy—a derived (= advanced) feature present in the sister taxa and absent in others. The expression of these relationships is presented in a branching diagram summarizing the sister-group relationships termed a "cladogram" (Fig. 1.10). In Hennig's sense, a cladogram was not an evolutionary tree since it did not contain ancestor–descendant relationships, but was built on sister-group statements only.

Although Hennig had a view of species very close to that of Mayr and the evolutionary taxonomists (and the pheneticists as well), the answers to Hennig's three questions set his framework apart. In the first place, he defined phylogenetic relationship strictly in terms of recency of common ancestry. His emphasis was entirely on the "clade" as opposed to the "grade" (terms coined by Huxley, 1959) as Mayr (1965) would say. This was a definition that removed the uncertainties that existed in nearly all (phenetics aside) classification schemes.

The rules of evidence he proposed also set him apart from others in that he limited evidence of relationship to aspects that were shared and derived

Plato (360 BCE) was also the originator of $\log n$ binary search—"To separate off at once the subject of investigation, is a most excellent plan, if only the separation be rightly made... But you should not chip off too small a piece, my friend; the safer way is to cut through the middle; which is also the more likely way of finding classes. Attention to this principle makes all the difference in a process of enquiry."

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[9] As Platnick (1989) has pointed out, the distinction between those groups that positively share features and those that are united only by their absence was known to the ancient Greeks. Plato (360 BCE): "The error was just as if some one who wanted to divide the human race, were to divide them after the fashion which prevails in this part of the world; here they cut off the Hellenes as one species, and all the other species of mankind, which are innumerable, and have no ties or common language, they include under the single name of 'barbarians,' and because they have one name they are supposed to be of one species also. Or suppose that in dividing numbers you were to cut off ten thousand from all the rest, and make of it one species, comprehending the first under another separate name, you might say that here too was a single class, because you had given it a single name. Whereas you would make a much better and more equal and logical classification of numbers, if you divided them into odd and even; or of the human species, if you divided them into male and female; and only separated off Lydians or Phrygians, or any other tribe, and arrayed them against the rest of the world, when you could no longer make a division into parts which were also classes."

AMNH *circa* 1910

(synapomorphy). Phenetics made no distinction between similarity that was primitive or general (symplesiomorphy), and that which was restricted or derived (synapomorphy). Furthermore, unique features of a lineage or group played no role in their placement. An evolutionary taxonomist might place a group as distinct from its relatives purely on the basis of how different its features were from other creatures (autapomorphy) such as Mayr's rejection of Archosauria (Aves + Crocodilia). The patristic (amount of change) distinctions were irrelevant to their cladistic relationships. [These terms will be discussed in later sections.] This would all have been fine if all evidence agreed, but that is not the case. Alternate statements of synapomorphy or homoplasy (convergence or parallelism) confused this issue.

Hennig annoyed many in that his cladograms made no reference to ancestors. His methodology required that ancestral species went extinct as splitting (cladogenetic) events occurred. Species only existed between splitting events, hence ancestors were difficult if not impossible to recognize (Chapter 3). This seemed anti-evolutionary, even heretical and won no friends among paleontologists. Extinct taxa could be accorded no special status—they were to be treated as any extant taxon (Chapter 2).

1.17 Molecules and Morphology

The 1980s saw tremendous technological improvement in molecular data gathering techniques. By the end of the decade, DNA sequence data were becoming available in sufficient quantity to play a role in supporting and challenging phylogenetic hypotheses, an activity that had previously been the sole province of anatomical (including developmental) data. Many meeting symposia and papers were produced agonizing over the issue (*e.g.* Patterson, 1987). In the intervening years, the topic has become something of a non-issue. Molecular sequence data are ubiquitous and easily garnered (for living taxa), forming a component of nearly all modern analyses. Anatomical information is a direct link to the world in which creatures live and is the only route to analysis of extinct taxa. Data are data and all are qualified to participate in systematic hypothesis testing.

A current descendant of this argument is that over the analysis of combined or partitioned data sets. This plays out in the debates over "Total Evidence" (Chapter 2) and, to some extent, over supertree consensus techniques (Chapter 16).

1.18 We are all Cladists

Today we struggle with different criteria to distinguish between competing and disagreeing evidence. In contemporary systematics, several methods are used to make these judgements based on Ockham's razor (parsimony) or stochastic evolutionary models (likelihood and Bayesian techniques). Although they differ in their criteria, they all agree that groups must be monophyletic in the

Hennigian sense, that classifications must match genealogy exactly, and that evidence must rely on special similarity (if differently weighted). All systematists today, whether they like it or not, are Hennigian cladists.

1.19 Exercises

1. Were the pre-Darwinians Cladists?
2. What remains of Phenetics?
3. Do we read what we want into the older literature?
4. What about the "original intent" of terms (*e.g.* monophyly)? Does it matter? Can we know? Is definitional consistency important?
5. What are the relationships among the following terms: archetype, bauplan, semaphoront, ancestor, and hypothetical ancestor?
6. What constitutes "reality" and "natural-ness" in a taxon?