
CAPTURING THE ORDER IN NATURE AND DARWIN'S TREE OF LIFE

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ABSTRACT. Following the publication in 1859 of *On the Origin of Species*, perception of natural affinities began to change from a 'creation plan', known for similarities and differences among species, to that of 'kinship', known for genealogical relationships. The achievement of a diagram to represent affinities through evolutionary relationships became a major enterprise for many naturalists. Although Darwin posed the challenge to depict the common descent and evolutionary relationships for living beings in the form of a 'Tree of Life', he was not the first to employ the tree metaphor in the life sciences, as he stated at the beginning of his famous arboreal metaphor: "the affinities of all the beings of the same class have sometimes been represented by a great tree." Who were those authors that represented affinities of beings in the form of trees and when these trees appeared? Were there other metaphors to represent the order found in nature?

KEY WORDS. Natural system, Charles Darwin, Tree of Life, branching diagrams, natural affinities, common descent, genealogical relationships.

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Charles Darwin, 1859.

The authors' intention in this paper is to present a synthesis in order to situate Darwin's theoretical achievements in context. As a synthesis, the following text takes into account the historical research produced in the past, thus celebrating some scholars who have done fascinating studies in this particular theme.

INTRODUCTION

In 1837, Charles Darwin started experimenting with diagrams to capture his ideas on the origin and transformation of species. These diagrams (unpublished in Darwin's time and some of them until very recently (see

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Voss, 2010)), were variations of the same metaphor: branching and re-branching to represent the appearance, divergence and extinction of species. Later, in 1859 he publicly christened his metaphor the great 'Tree of Life.'

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

A few years after Darwin published *On the Origin of Species*, the idea that the startling diversity of living beings was the outcome of the evolutionary process was so widespread that the theory and its author found their place into caricatures, musical comedies, spirit labels, jingles, and the like. In fact, few other scientific theories have become so much a part of modern culture as the one on evolution (Browne, 2001).

Darwin's only diagram as well as the beautiful and eloquent metaphor at the end of chapter 4—which established that the core of the theory were the relationships among species through genealogy—have received much scholar attention since their first appearance.

After 1859, the perception of natural affinities began to change from a 'creation plan,' known for similarities and differences among species, to that of 'kinship,' known for genealogical relationships. The achievement of a diagram to represent affinities through evolutionary relationships became a major enterprise for many naturalists. Such diagram involved a single story of organisms, so if they could decipher that story, they would understand the natural way for grouping organisms. Therefore, the research of evolutionary relatedness among groups of living beings became a practice that dominated much of the inquiry on the organic world around the last decades of nineteenth century, allowing the disciplines of systematics and biogeography to flourish.

Although Darwin posed the challenge to find the way to capture common descent and evolutionary relationships for living beings in the form of a 'Tree of Life', he was not the first to employ the metaphor of a tree in the life sciences, as he stated at the beginning of his famous arboreal metaphor: "the affinities of all the beings of the same class have sometimes been represented by a great tree."

Who were those authors that represented affinities of beings in the form of trees and when these trees appeared? Were there other metaphors to represent the order found in nature?

DARWIN'S FIRST DIAGRAMS

When Charles Darwin returned to his native England on October 2, 1836, after traveling around the world aboard the HMS *Beagle*, he had gathered 15 notebooks, 368 pages with zoological observations, almost 200 pages on marine invertebrates and various notes on geological topics (Stott 2003, p. 65). He had also collected 5 436 plant and animal specimens (including fossils), 1 529 of them preserved in alcohol (Fagan 2007).

In addition to Darwin's personal interest in collecting, his work as an editor led him to work closely with the specialists responsible for the classification of these specimens (Richard Owen, John Gould, Thomas Bell, George R. Waterhouse and Leonard Jenyns). This resulted in several significant discoveries that marked the course of his ideas, two of which have a special relevance for the further development of his concept of the 'Tree of Life.'

First, John Gould pointed out, among other things, that the finches Darwin had collected in the Galapagos archipelago were from thirteen separate species, not merely different varieties of the same. Richard Owen in turn, noted the relationship between some of the giant animal fossils with living species in South America, such as armadillos and sloths.

Second, as Julia Voss (2010) has shown, Darwin became aware of the problems in the field of classification at that time, as he experienced firsthand the conflicts between scholars to classify the animal collections. Darwin recorded in his diary that "zoologists seem to perceive as a nuisance the many creatures never before described" (Darwin, 1836), and he was never able to get help to fully classify his marine invertebrate collection (Keynes, 2000). The reason was that Europe, and particularly England, was experiencing a taxonomic crisis. On the one hand, unclassified species needed to be identified and named; on the other, they needed a place in the natural system. There was no consensus whatsoever about the nature of the relationship between organisms; although the concern to find the 'natural order or system' have increased since the eighteenth century¹, when the amount of known organisms began to expand significantly as a result of the great expeditions.

Even though scientists could not find a way to establish a uniform criteria to classify organisms, there was a general agreement that the natural system should be presented using charts (O'Hara, 1988, 1991, 1996; Papavero & Llorente, 1993-2004; Voss, 2010). Therefore, various representations such as circles, stars and maps proliferated in the early nineteenth century, adding to the already abundant imagery, specially networks and affinity trees, that had sprang to search for the natural affinities amongst living beings since the seventeenth century.

Since his time aboard the *Beagle*, Darwin had thought about the nature of species. But until Owen and Gould introduced him, respectively, to the

classification of fossils and birds, he understood their evolutionary significance and abandoned the belief in the constancy and immutability of species. In a letter to Ernst Haeckel in 1864, Darwin wrote:

In South America three classes of facts were brought strongly before my mind: 1stly the manner in which closely allied species replace species in going Southward. 2ndly the close affinity of the species inhabiting the Islands near to S. America to those proper to the Continent. This struck me profoundly, especially the difference of the species in the adjoining islets in the Galapagos Archipelago. 3rdly the relation of the living Edentata & Rodentia to the extinct species. I shall never forget my astonishment when I dug out a gigantic piece of armour like that of the living Armadillo (Darwin, 1864).

With all the information he had acquired by 1837, Darwin began to increasingly believe that the explanation for biogeographic and paleontological phenomena was that species had to arise from the evolution of preexisting ones. This also allowed him to consider the problem of the nature of species and their classification.

In the summer of that year, Darwin drew his first sketches of 'trees' in page 26 (Fig. 1) of his *Notebook B*, which would be the first in a series of four devoted to the subject of the transmutation of species (B, C, D and E). Previously he had mentioned that "*Organized beings represent a tree irregularly branched, some branches far more branched—hence Genera. As many terminal buds dying as new ones generated.*"

According to Voss (2010), the first drawing illustrated his thought on evolutionary adaptations, according to the division of the natural system into three elements proposed by British entomologist William Sharp MacLeay: air, land and water. With the second diagram, Darwin played with his observations on the long gaps in the fossil record.

Next, Darwin begins page 36 with the words 'I think' and focuses on another branching diagram to consider extinction: "I think case must be that one generation then should have as many living as now. To do this and to have many species in same genus (as is), requires extinction." As a result, Darwin also took into account many other features of species transformation, thus he managed to materialize the branched system of descent with modification—although he had not yet a plausible explanation for the branching and rebranching of his figure (Fig. 2).

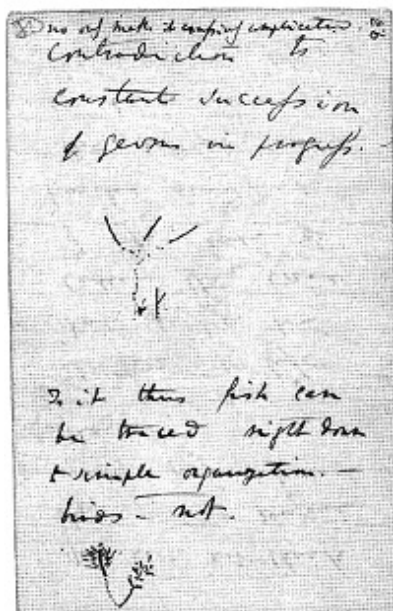


FIGURE 1.
Two models of irregularly branching trees. Darwin, *Notebook B*, 1837, p. 26.



FIGURE 2.
Tree diagram on *Notebook B* (page 36).

The diagrams in his *Notebook B* would become an essential tool for the development of his theory. With them, Darwin managed to visualize the fundamental aspects of evolution. Especially with the last sketch, he was able to explain the relationship between different species of the same class or family, and to present the main ingredients for a satisfactory explanation of the natural world order. It posits a common origin represented by the tree's base; the emergence of new species symbolized by angles; their further divergence in time represented by lines; the living species by perpendicular bars, and extinct species by lines that stop. Therefore, though the diagram depicts the relationships between living and extinct species of South America (Eldredge, 2005), it is the record itself of the emergence of his idea of a common descent. "...an image can stimulate us to think in a new, unanticipated direction ...this is what happened to Darwin when he devised his theory of evolution: he was guided by an image" (Maderspacher, 2006).

The ideas woven into this diagram—which would eventually provide the key that would begin to solve the heated debate on the natural system by proposing genealogy as the underlying link between organisms—did not materialize until twenty two years later, in *On the Origin of Species*. During that time, Darwin worked on his theory—the cause of the branching and constant adaptation of species—and continued drawing trees which incorporated new thoughts, focused on understanding the laws that cause similarities and differences between species and their amazing adaptations.

Darwin was not the first to rely on an image to give meaning to his ideas—since he was immersed in natural history's long-predominating visual tradition. Neither was he the first to represent the relationship between organisms by means of a tree, nor was he the only one to resort to metaphors and analogies to explain his theories. At that time, the display of ideas in figurative language was of great value (Alter, 1999). Though it was Hugh Strickland in 1841 that established that images should be the means to discover the natural system², the use of diagrams to represent it was already a widespread practice. The pictorial metaphor of Darwin's evolutionary tree is born from a long tradition of relationship diagrams—of animals and plants, families and languages—and of an allegorical use of language to help understanding the studied phenomena.

Exploring the pre-Darwinian use of diagrams and metaphors to represent the classification of species allows to illuminate further the importance and meaning of the later contributions made by Darwin.

THE NATURAL SYSTEM'S VISUAL TRADITION:
CHAINS, LADDERS, NETWORKS, CIRCLES, MAPS AND STARS

During Darwin's time, naturalists were engaged in the problem of achieving natural classifications of living beings, to assign their place within the order of life. This "search for the natural order" can be traced back to ancient times and in most cultures. In Europe, naturalists soon found the natural world to be more complex than previously thought, and especially since the sixteenth century, an astonishing imagery sprung around this enterprise, which reflects the depth of attention naturalists gave to it. Not just trees, but different 'objects' or concepts served as metaphors to order the world, which can appropriately cohere into three main ontological categories: series, trees and networks (Barsanti, 1992; Ragan, 2009; Rieppel, 2010), each reflecting a particular conception of species and of the theories underlying the foundation of each natural system (kinds of affinities) (Torrens, 2013).

A key feature of the natural system is that it is actually a diagram, with the ontological and epistemological possibilities and limitations this entails. From the Middle Ages until the mid eighteenth century, the accepted representation of the natural order was the *Scala naturae* (or Great Chain of Being), which mirrors the Divine Order or Creation Plan. Thus, series are the oldest metaphors for order in nature.

The idea of the series had its roots in Aristotle, who based his strategy for the recognition of natural groups seeking for the 'essence' of organisms, that is, their unchanging traits, ignoring as incidental those details that gave them diversity (Torres, 1995). That is why Aristotelian classifications are essentialist, moreover, they are teleological. Aristotle's teleological vision sustains that nature does nothing randomly or without a purpose; where the purpose lays in nature itself without being imposed by outside agents. This idea would later be important to differentiate Aristotle's from his medieval commentators.

Although Aristotle did not conduct any formal classification—or none has survived, two have been interpreted from his writings—in *Research on Animals*, Aristotle outlined a series of differences and dichotomies that enabled him to classify the animals being studied—*anaima*, 'bloodless animals' and *enaima*, 'blooded animals.' In the book *Generazione Animalium*, Aristotle featured a classification of animals according to their degree of perfection, which is known as the "natural scale of beings" or "real order." This classification (Fig. 3) combined the logical division by binary opposition (*diaeresis*) with a hierarchy of beings ranging from the higher and more complex to the simplest and most elementary (García-Gual, 1992).

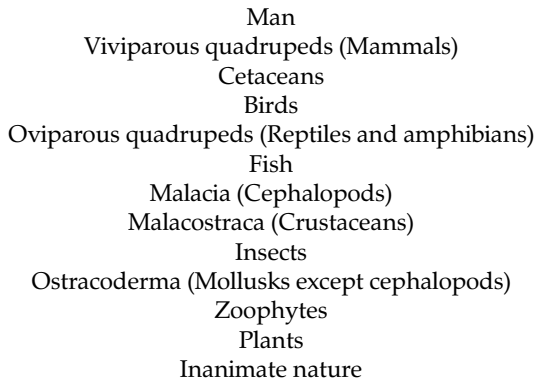


FIGURE 3. Linear array; animal groups according to Aristotle.

It is important to note that—although the question arises about which of the two classifications reflected the true natural order for Aristotle—dichotomous logical order does not contradict the natural scale’s linear order. These orders were subsequently differentiated so that the logical one served only to classify beings and the natural scale was their true order (see García-Gual, 1992).

THE *SCALA NATURAE* IN THE MIDDLE AGES

Aristotle’s legacy was basic in the Middle Ages. Both his essentialism and his principle of logical division pervaded classifications from that period until the eighteenth century. During the Middle Ages, Aristotle’s teleological essentialism became the key to identify the species substance according to its degree of resemblance to God (see Ridley, 1986). This theological concept stems from commentators such as Thomas Aquinas and Avicenna, who identified the Aristotelian *telos* or purpose with the reason why God created a particular species, i.e., a divine plan. On the other hand, Aristotle’s natural scale followed a fixed hierarchical order in the form of a ladder that climbs from inanimate nature, through a series of groups, culminating in humans, which can be thought as progression from simple to complex. This reflects his teleological thinking, as for Aristotle every inferior being was related to something superior and dominant (see Jaeger, 1997). This progression from simple to complex was the main reason the linear sequence diagrams became so deeply ingrained in later thinking. They were also called ‘natural scale’ or ‘chain of being’, since the idea of progression was consistent with the Christian outlook, which considered the natural order as an upward ladder with God at the top (see Guthrie, 1981).

Aristotle had said that *nature does nothing in vain* (IA 2, 704b12-17), to which Christians easily added: *neither does God*. Thus, teleology became one of the bases for the theological interpretation of things, linking teleological explanations with the existence of a supreme being, the maker of nature (Guthrie, 1981). Teleology became the validation of divine intention.

During the Middle Ages, the basic principle of the *Scala* was continuity in nature. This continuity could be appreciated in "the polyp that combines plant with animal. The squirrel that glides, linking bird to mammal. The monkey that touches mammal and human" (Bonnet, 1764, p. 29). Its graphical representation was a ladder that progressed hierarchically from the most simple to the most perfect, concluding in the human being, for, as Bacon stated, "if we look for final causes, man must be regarded as the center of the world; to the extent that if man were removed from it, the rest would seem to be a complete aberration with no end, no purpose..." (Bacon, 1609, p. 747).

Swiss naturalist and philosopher Charles Bonnet is perhaps the foremost representative of this way of thinking. His diagram is a clear indication that the natural scale was a powerful and convenient metaphor as it united all creation in a single continuous series of ever-increasing complexity and perfection (Fig. 4).

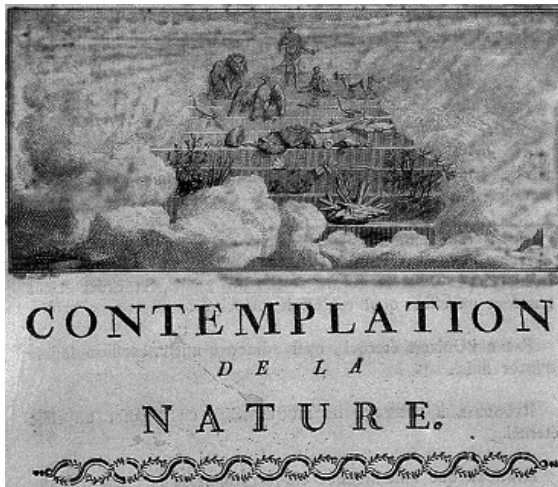


FIGURE 4. Charles Bonnet's Great Chain of Being, *Oeuvres d'histoire naturelle et de philosophie*, 1779: 83.

It was in the eighteenth century when the chain of being reached its widest dissemination, even if it was not easy to reconcile the facts of nature on a generalization of this kind. Bonnet agrees that some of the organisms' traits were difficult to place in a consistent gradation of forms and he wonders: "can the ladder of nature branch out in its ascent?... Can insects and mollusks form two side branches of a main branch?" (Bonnet, 1764, p. 29). Still, there has been no other period in history when there was so much talk of the chain of being and so much of its iconography developed. "Next to the word 'Nature', the 'Great Chain of Being' was the sacred phrase of the eighteenth century, playing a part somewhat analogous to that of the blessed word 'evolution' in the late nineteenth" (Lovejoy, 1964).

ALTERNATIVES TO THE NATURAL SYSTEM

By the late eighteenth century, the growing confusion that dominated the issue of the location of species in the natural system became evident. Due to the increasing knowledge on the diversity of animals, plants and microorganisms, the notion about the apparent continuity of life began to teeter. Were coral polyps or certain microscopic creatures plants or animals? What to do with the obvious varieties observed among species?

There are several examples of the naturalists' confusion when they tried to place their objects of study within a defined linear order. In his *Della storia naturale marina dell'Adriatico* of 1750, Vitaliano Donati argues that "when I look at Nature's productions, I do not see a single, simple progression or chain of beings, but a large number of uniform, perpetual and constant progressions that should be compared more to a network than to a chain..." (Donati, 1750). The renowned French naturalist Georges had abandoned the idea that animals could be organized in a series, and the famous French botanist Adrien de Jussieu mentioned in 1843 that "relations between groups must be definitely cross linked; it is impossible to form linear series because emphasizing a relationship in one direction necessarily involves breaking it in another" (de Jussieu, 1843).

Between the late eighteenth and early nineteenth century, efforts to find alternatives to the *Scala's* linear sequence resulted in the development of reticulated systems such as networks, webs, branching diagrams and tree-like figures. Networks were appropriate metaphors because they allowed a number of 'chains' to intertwine and accommodate anything that could threaten the continuity of a single series. The following two figures are examples of the use of networks to represent the natural system (Figs. 5 and 6).

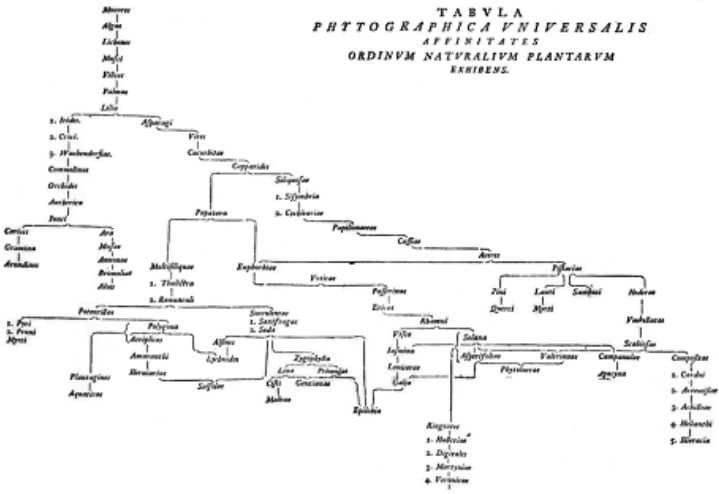


FIGURE 5.
Affinity networks of the natural order of plants, *Ordines naturales plantarum commentatio botanica*, Johann Röhling (1774).



FIGURE 6.
Affinity network of the plant kingdom, *Tabula affinitatum regni vegetabilis*, August Johann Georg Carl Batsch (1802).

Linnaeus expressed the network of affinities in the metaphor of a map-like structure with mutual affinities going in all directions (Müller-Wille, 2007: x).

The metaphor of a branching tree was born in this era. Peter Simon Pallas (1766), Georges Louis Leclerc de Buffon (1766), Augustin Augier (1801) and Nicholas Charles Seringe (1815) are some examples of scholars drawing or referring to the idea of a tree-like branching diagram. It is count Jean Baptiste de Lamarck who has a special relevance in this matter. According to Burkhardt (1995) and Gould (2000), when faced with the restrictions imposed by the linear order of forms, Lamarck managed to develop the idea of organism transformation, although it was not well received by the scientific community as it lacked a consistent mechanism.

In 1800, Lamarck was curator and zoology professor at the *Muséum d'Histoire Naturelle* of Paris, where he worked with invertebrates. As an outcome of his work, he realized it was impossible for the animal world to fit in single series, since he noticed organism variations within *phyla* represented by orders and species that did not fit into a linear sequence.

If the factor which is incessantly working towards complicating organization were the only one which had any influence on the shape and organs of animals, the growing complexity of organization would everywhere be very regular. But it is not; nature is forced to submit her works to the influence of their environment [...] This is the special factor which occasionally produces [...] the often curious deviations that may be observed in the progression (Lamarck, 1809: 69).

Lamarck started to work on his own classification of invertebrates. By 1809, he had proposed ten different groups, despite the fact that Linnaeus considered only two, insects and worms. Lamarck—like most naturalists concerned with the classification of the organic world—soon came across a fundamental problem. He did not know where to place worms. Given their bilateral symmetry and superiority in terms of mobility, they belonged above radiata (a collection of jellyfish, sea urchins and such). Yet, given their lack of nerve cords and circulatory system, they should be placed below. Thus the conflict for Lamarck—as for many others—was the distribution of characters.

It is due to this conflict that Lamarck proposed “the first branching diagram [with evolutionary implications] that has ever been published in the history of biology” (Gould, 2000), thereby demolishing the linear progression model (Fig. 7).

TABLEAU
 Servant à montrer l'origine des différents
 animaux.

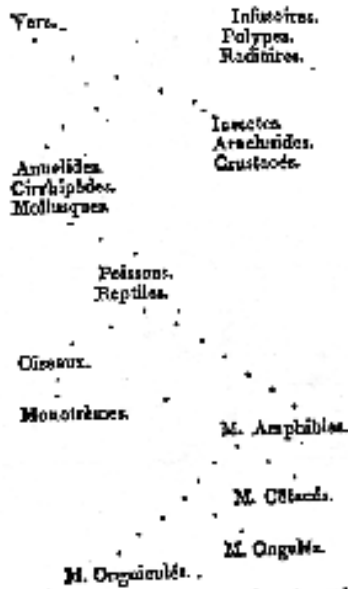


FIGURE 7.
 Tree diagram of life, *Filosofia zoológica*, 1809: 176.

Although many still consider Lamarck never fully embraced the completely branched tree model, with a single trunk to represent the common ancestor for all organisms, he sort of did—at least verbally. In his last book, *Analytical System of Positive Knowledge of Man*, published in 1820, Lamarck proposed a single ancestor for all animals called ‘monad.’ This monad represented the point of origin from where infusoria originated, followed by the polyp’s apparition in the same main stem. Then a branching occurred, which originated three lineages. Radiata, which did not keep evolving; worms, which continued to branch out in all segmented animal *phyla*—including annelids, insects, arachnids, crustaceans and barnacles, each by a separate division event—and tunicates, that split into multiple lineages of mollusks and vertebrates (Gould, 2000). With this description it becomes clear that, if Lamarck had drawn it, the idea would have been represented by a tree-like diagram with three main branches, some branching out more than others to give rise to all living beings.

It is important to remark that even though Lamarck used metaphorical the tree language—perhaps similar to Darwin’s—he never draw a dia-

gram reminiscent of a 'tree.' Besides, Lamarck assumed a perpetual creation of new species, yet he was never able to fully account for a mechanism that explained the transformations he considered to be occurring in the organic world.

BRITISH CREATIVITY IN THE SEARCH OF NATURAL DESCRIPTIONS

In England, the pursuit of a natural system was also fueled by the considerable effort and creativity on the part of Darwin's contemporaries. Two schools of thought can be identified. Those who assumed that natural relations reflected continuity, regularity and mathematical proportion, and those that advocated irregularity and disorder in the organic world (Voss, 2010).

The first is represented by the *Quinarian School*, whose chief advocate was entomologist William Sharp MacLeay. MacLeay argued that the natural system represented "God's plan to regulate Creation" (MacLeay, 1823: 46). He sought to illustrate this by identifying two types of fundamental relationships between organisms, affinities and analogies. Affinity identification—relationships based upon some kind of essential similarity—allowed to organize the animal kingdom in groups of five similar species, represented by circles or stars (Fig. 8). These groups were connected to each other through analogies or similarities between distant organisms (Nelson & Platnick, 1981, O'Hara, 1991), which meant that all animal families were related to each other in an idea of continuity. For 'Quinarians' there were no leaps in nature, so the apparent 'gaps' separating their groups were a result of extinctions or organisms yet undiscovered or created. Although not explicitly, according to Dov Ospovat (1981), the arrangement of organisms made by Lamarck in 1809 was a source of inspiration for MacLeay, as it allowed to express the natural world's continuity and complexity. "Nature appeared to me to have branched out in the animal kingdom in the most beautiful and regular though intricate manner, that might be compared to those zoophytes which ramify in every direction, but of which the extreme fibers form by their connection the most delicate circular reticulations" (Ospovat, 1981, p. 102). Though not a transformist, MacLeay thought that if branching were properly understood, it would become apparent that the natural system was perfect and regular.

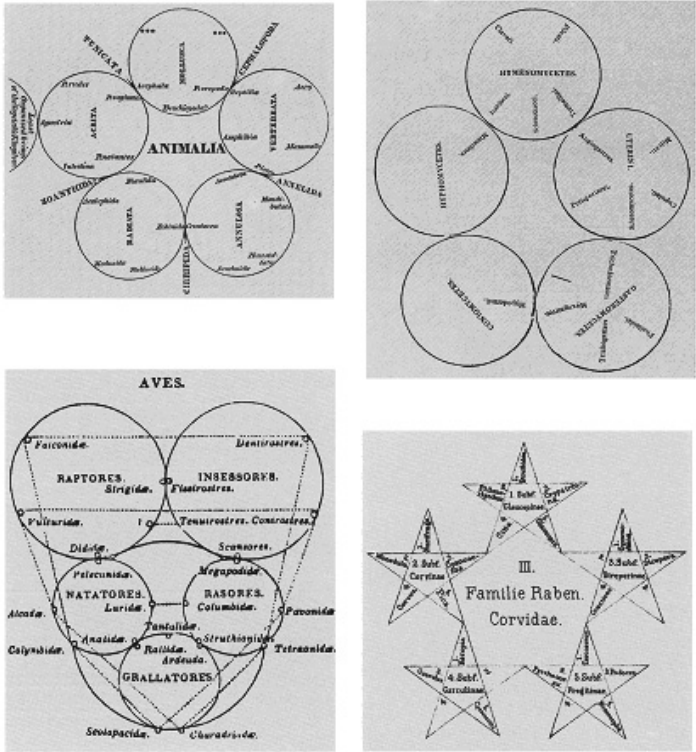


FIGURE 8. These charts—MacLeay, 1819-1821; Berkeley, 1838; Swainson, 1836, and Kaup, 1854 (left to right)—are a sample of the wide array of diagrams that appeared in England in the first half of the nineteenth century. All reflect order and use regular geometrical—especially quinary—forms.

The second school of thought is represented by Hugh Strickland and his followers, who depicted the natural system as an irregular and disorderly entity. They took into account only the affinities of living beings, not analogies, to build their 'affinity maps.' According to Strickland, "the natural system may, perhaps, be most truly compared to an irregularly branching tree, or rather to an assemblage of detached trees and shrubs of various sizes and modes of growth" (Strickland, 1841, p. 190) (Fig. 9).

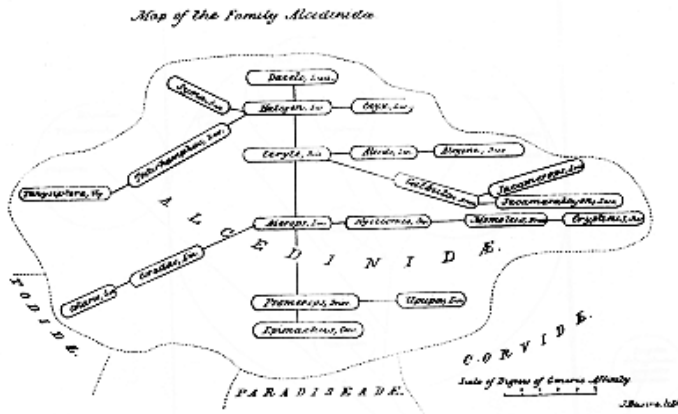


FIGURE 9. Map of the bird family Alcedinidae, Strickland, 1841.

In between these schools stood British zoologists, though by 1840 the majority had rejected the quinarian system. However, in 1837 Darwin mentioned MacLeay in more than eighty pages (Ospovat, 1981, p. 102) in his notebooks on transmutation. This shows the great influence of this school. In fact, the first sketch Darwin draw in page 26 of his *Notebook B* (Fig. 10), splits into three lines corresponding to the tripartite natural system proposed by MacLeay. Darwin pondered “would there not be a triple branching in the tree of life owing to three elements air, land & water” (Darwin, 1837:23), since in MacLeay’s natural system, animal species should be divided in accordance to such elements (Darwin, 1843).



FIGURE 10. Darwin’s first irregular branching tree. Darwin, *Notebook B*, p. 26.

Darwin soon noticed that MacLeay's natural system seem useless for describing the natural world's order (Ospovat, 1981). In a letter written to Robert Waterhouse in 1843, he mentioned that the use of circles did not represent a feature of nature; instead, it was a deceptive practice. "I believe infinite harm has been done by these circles, which catch the eye as of equal size, and inevitably lead the mind to suppose they are of equal value" (Darwin, 1843) Thus, Darwin dropped the quinary system to focus on his later trees, as a reflection of the irregularity and disorder he saw both in the Empire's collections and in nature itself. In this sense, it is possible that Strickland's—with whom he corresponded extensively between 1840 and 1842—affinity maps also represented a powerful source of inspiration for his diagrams (Voss, 2010, p. 90).

NOTES

- 1 It is important to differentiate between the classification issue that flourished from the sixteenth century and the identification of natural groups in the natural system. Both techniques for the identification of species belong to the realm of taxonomy, but the first tries to name species according to keys in an 'artificial system', while the second calls for the creation of a diagram that reflects the laws underlying the true order of nature.
- 2 Presentation of his article "On the true Method of discovering the Natural System in Zoology and Botany" at the annual meeting of the British Association for the Advancement of Science in 1841.

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