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How Phenograms and Cladograms became Molecular Phylogenetic Trees

Abstract

Tree diagrams are the prevailing form of visualization in biological classification and phylogenetics. Already during the time of the so called Systematist Wars from the mid-1960s until the 1980s most journal articles and textbooks published by systematists contained tree diagrams. Although this episode of systematics is well studied by historians and philosophers of biology, most analyses prioritize scientific theories over practices and tend to emphasize conflicting theoretical assumptions about biological units, speciation, and classification between the opposing parties. In this article, I offer an alternative perspective by viewing the conflict through the lens of representational practices by examining cladograms and phenograms, i.e. the diagrams used by cladists and pheneticists to represent the results of their studies.

Although both types of diagrams have a tree topology, they were used to represent different forms of knowledge. However, a practice-centered view also reveals essential similarities between the competing approaches such as the use of computers and mathematical algorithms. Promoted by interrelated processes of automation, molecularization, and mathematization molecular phylogenetics began to dominate systematics in the late 1980s, which obscured traditional debates. I argue, that the compatibility of phenetic and cladistic practices with the quantitative approach of molecular evolution as well as the shift of emphasis from classification to phylogenetic inference facilitated the integration of elements of cladistic and phenetic practices into molecular phylogenetics. Today, cladograms are still used and viewed as specific types of molecular phylogenetic trees. Phenograms eventually became molecular phylogenetic trees through reinterpretation while the construction methods did not undergo significant changes. Thus, phenograms and cladograms are now used to represent similar forms of knowledge.

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Introduction

During the time from the 1960s until the 1980s, systematics was characterized by heated and often emotional debates over different approaches to biological classification and taxonomic practices. This episode in the history of biology is often referred to as 'Systematist Wars' (Hull 1988, chapter 5). The three main contestants in the conflict were evolutionary systematists, numerical taxonomists, and cladists. The investigations of the conflict in theoretical biology as well as history and philosophy of biology usually prioritize scientific theories over practices and tend to emphasize conceptual differences between the opposing parties, e.g. about biological units, speciation, and classification. A prominent example is David Hull's (1988) account of the competing theories as independent historical lineages of ideas. More recent accounts, however, challenge this view of scientific theories as abstract conceptual systems and propose a practice-oriented approach to studying this episode in systematics (e.g. Sterner & Lidgard 2017).

Following this practice-oriented view of the Systematist Wars, I investigate Numerical Taxonomy and Cladistics as two different approaches of doing systematics by analyzing their representational practices. In the sciences, particularly in biology, visualization plays a pivotal role, at times to the extent that text illustrates images, not the other way around. Diagrams are used to graphically communicate scientific results and hypotheses to fellow scientists and to a broader public. Since research aims at producing knowledge of a certain type, often represented in specific formats, diagrams structure and guide scientific research. Thus, the analysis of representational practices shed light on central topics in philosophy of science such as processes of scientific change and continuity of practices.

Both pheneticists and cladists have used tree diagrams to visually represent their results. The "iconographic tradition" (Gould 1995: x) of using tree-shaped images and diagrams to represent relationships between individual organisms or groups of organisms started long before Darwin published his famous branching diagram in *The Origin of Species* in 1859 (Ragan 2009). Tree images and diagrams have developed into "canonical icons" in biology, particularly in evolutionary biology and phylogenetics (Gould 1995). The widespread use of phylogenetic trees in evolutionary biology and phylogenetics makes it difficult to imagine biological practice

without tree diagrams. Today, phylogenetic trees are essential tools for studies in evolutionary biology, but before the period of the Systematist Wars tree diagrams were first and foremost used for classification. My analysis focusses on the historical developments that gave rise to the field molecular phylogenetics to explain the transformation of phenograms and cladograms into molecular phylogenetic trees.

Systematists at War

By the time the Systematist Wars started, the established approach to biological classification was evolutionary taxonomy (evolutionary systematics), previously called 'New Systematics' (Sterner & Lidgard 2017). The most well-known proponents of evolutionary systematics are the zoologists Ernst Mayr and George Gaylord Simpson. Classification based on evolutionary taxonomy emphasizes the importance of evolution and speciation processes (Mayr 1969; Simpson 1961). According to Mayr's biological species concept, species are interbreeding populations that are reproductively isolated from other populations caused by a period of geographic isolation (Mayr 1942, 1996). To study the degree of divergence between groups of organisms, evolutionary systematists evaluated morphological characters across geographic ranges of populations. The construction of evolutionary trees as a basis for classification involved the weighting of characters and formation of groups based on previously established phylogenetic hypotheses. With the rise of Numerical Taxonomy and Cladistics, the established approach was challenged to its methodological foundations by proponents of these alternative approaches (Hull 1988; Suárez-Díaz & Anaya-Muñoz 2008).

Phenetic approaches to classification emerged in the late 1950s as an important part of a broader approach of implementing numerical methods in biological systematics called Numerical Taxonomy. Due to the influence of their book *Principles of Numerical Taxonomy* published in 1963, microbiologist Peter Sneath and statistician Robert Sokal are seen as the main advocates of phenetic classification. In phenetics statistical methods are applied to generate clusters of similar organisms based on overall similarity. To create a hierarchical classification, the clusters can be joined together and form higher level units. Thus, the phenetic approach to classification does not require phylogenetic analysis nor reference to speciation processes. They

treat classification and phylogenetic inference, the two main tasks of systematics, as separate and independent form each other. In fact, part of the broader program pursued by numerical taxonomist was to perform cladistics analysis by applying numerical methods (numerical cladistics) (Sneath & Sokal 1973, chapter 6.4). Sneath and Sokal (1973: 4) explicitly emphasize that numerical taxonomy "includes the drawing phylogenetic inferences from the data by statistical or other mathematical methods".

Evolutionary systematics and phenetics were challenged by cladistics (or phylogenetic systematics). The cladistic approach goes back to the entomologist Willi Hennig and is based on the recognition of monophyletic groups (or clades), defined as "a group of species descended from a single ('stem') species, and which includes all species descended from this stem species" (Hennig 1966: 73). Monophyletic groups can be identified by shared derived characters. Thus, according to Cladists, classifications should reflect phylogenetic relationships. My analysis of phenograms and cladograms in the following section shows the similarities and differences between cladistics and phenetic practices in more detail.

Representing results in phenetics and cladistics

To understand the differences and similarities between phenetics and cladistics I will examine two exemplary diagrams (a phenogram and a cladogram) by analyzing their components, graphic structures, meanings, and the context of their construction and use. As exemplars, these diagrams represent common features of most phenograms and cladograms that were used during the time period in question. The phenogram was published by Gary Schnell in *Systematic Zoology* in 1970 and the cladogram was published by Greg Spicer in the *Journal of Crustacean Biology* in 1985.

Already at a first glance, it becomes clear that both diagrams share basic components and have structural similarities. Both the cladogram and the phenogram are composed of vertical and horizontal lines that form a branching structure with a predominantly bifurcating pattern. However, the phenogram's root is on the left and the tips of the branches are on the right, whereas the cladogram's branches are

growing from bottom to top. This depiction of the phenogram on its side has a pragmatic reason:

> Although early practice tended to have the branches of a phenogram pointing upwards, convenience and the ever increasing size of studies have made authors place phenograms almost uniformly on their side with branches running horizontal across the page. (Sneath & Sokal 1973: 260)

Figure 1: Phenogram (Schnell 1970)   Figure 2: Cladogram (Spicer 1985)

This statement generally also holds true for cladograms, but since the number of species represented in this cladogram is relatively small, the branches run from bottom to top. In addition to the schematic tokens, both diagrams contain words and numbers. We can also observe a similar degree of pictorial abstraction. Both diagrams are highly schematized trees as opposed to more figurative tree diagrams like Haeckel's famous oak tree. Each diagram also has unique components. The cladogram has three different types of square-shaped symbols and a key that indicates the meaning of the symbols, the phenogram has a labelled x-axis. Although many alternative diagrammatic forms of representation exist in numerical taxonomy (e.g. ordination plots, contour diagrams; see Sneath & Sokal 1973: chapter 5.9), pheneticists often used tree diagrams to represent their results, because hierarchical classification systems could easily be derived from them: "The results of cluster analysis have been traditionally represented by dendrograms [tree diagrams], which have the advantage that they are readily interpretable as conventional taxonomic hierarchies" (Sneath & Sokal 1973: 260). Thus, tree diagrams were used due to mathematical conventions, but also preferred because of their purpose as classification tools. In cladistics, however, tree diagrams were the only form of diagrammatic representation.

As mentioned above, phenetics is an approach to taxonomy which classifies organisms based on resemblance and phenograms are used to represent the degree of similarity between groups of organisms, so called "phenetic relationship" (Sneath & Sokal 1973: 29; see Wiley 1981: 98). In this phenogram (figure 1) the numbers

represent extant OTUs (Operational Taxonomic Units), also referred to as 'phenons', and the words next to the numbers are species names and represent previously identified and named species. Pheneticists insist that although phenons can be equated with rank categories such as 'species', they are not fully synonymous with taxa:

> The groups established by numerical taxonomy may, if desired be equated with the usual rank categories such as genus, tribe, or family. However, these terms have evolutionary, nomenclatural, and other connotations one may wish to avoid. We therefore prefer new expressions. […] The term phenon is intended to be general, to cover the groups produced by any form of cluster analysis or from any form of similarity coefficients. (Sneath & Sokal 1973: 294)

This statement illustrates that it was very important to pheneticists to avoid the evolutionary connotations of established terms like 'taxa' or 'species' to emphasize the difference between their approach and competing approaches to classification. It is important to understand that phenograms had not been used to represent evolutionary relationships of any kind, only degrees of similarity indicated by the position of the nodes in the diagram. In this phenogram, for example, OTUs 26 and 27 share more similarities with each other than with OTU 1 (figure 1, top of the diagram).

Phenograms are constructed by means of numerical methods using phenotypic characters. "What one wishes to measure in phenetic taxonomy is the expression of the genome of the organism through its life history – its phenome, in fact" (Sneath & Sokal 1973: 96). Usually, a large number of characters is used to generate phenograms. In this case to construct the phenogram 51 skeletal measurements of gulls were analyzed applying UPGMA (Unweighted Pair Group Method with Arithmetic Mean) cluster analysis, a statistical method for evaluating relationships (Schnell 1970, see caption in figure 1). Since it is tedious to do phenetic clustering and other numerical methods by hand, the introduction of computers into systematics research in the 1960s simplified and accelerated the pheneticists' work enormously (Hagen 2001). However, by the time Schnell conducted his study cheap personal computers were not yet available, so that researchers had to rely on computation facilities. In his acknowledgements Schnell (1970: 301) explicitly expresses his

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gratitude for the "computer time was made available by the Computation Center at the University of Kansas".

During the times of the Systematist Wars there were controversial discussions focusing on what cladograms represent and in what respect they differ from phylogenetic trees. Until the mid-1970s cladograms were usually understood as phylogenetic trees justified by synapomorphic characters (Wiley 1981: 98). In the following years a debate flared up as a reaction to a widely circulated, but never published manuscript by Gareth Nelson, where he states that cladograms are not phylogenetic trees, but tree diagrams representing patterns of unique characters (Wiley 1981: 98; Eldredge & Cracraft 1980: 10). Following his understanding of cladograms, Eldredge and Cracraft (1980: 10) claim, that "a cladogram subsumes the logical structure of a set of trees. Phylogenetic trees, in specifying actual series of ancestral and descendant taxa, are more detailed and precise sorts of hypotheses than are cladograms". From this perspective, cladograms are tree diagrams without specified ancestors. The distinction of cladograms and phylogenetic trees resulted in the common opinion that a large array of phylogenetic trees exists for each cladogram (Platnick 1977; Harper 1976; Cracraft 1979; see Wiley 1981 for a counter opinion). Since cladograms are constructed from characters that are classified as evolutionary novelties and ancestors do not exhibit novelties unique to themselves, it is difficult to make justified claims about ancestors. This argument had led cladists to focus on identifying nested sets of unique characters depicted on branching diagrams (Eldredge & Cracraft 1980: 10). The interpretation of cladograms as diagrams exhibiting patterns of character distributions does not require additional hypotheses about speciation events or specific assumptions about evolutionary processes. Due to this interpretation, cladograms were considered a suitable basis for classification: "The procedure has the added advantage of being easily converted into classifications with a minimum of required conventions" (Eldredge & Cracraft 1980: 10). The emphasis on character distributions is obvious in the exemplary cladogram (figure 2) where the numbers 1-10 represent different characters and the different square symbols indicate whether the character in question is apomorphic or plesiomorphic in the respective species. As in the phenogram, the words at the tips of the branches are species names and represent extant species.

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Cladograms are diagrams used for representing patterns as results of evolutionary processes, not simply similarities. While phenograms represent similarities between organisms, cladograms represent kinship relationships. Cladists like Eldredge and Cracraft (1980: 10) understand cladograms "as diagrams of the history of taxa" which "can be interpreted in terms of relative recency of common ancestry". Wiley (1981: 97) defines a cladogram as "a branching diagram of entities where the branching is based on inferred historical connections between the entities as evidenced by synapomorphies". Thus, this diagram (figure 2) can be interpreted as follows. *S. moorei* is more closely related to *S. kargesi* than to the other species in this group. In other words, *S. moorei* is the sister group (or sister species) of *S. kargesi*. No information about actual or hypothetical common ancestors is given in the cladogram nor in Spicer's article. In fact, Spicer (1985: 171-172) discusses another study by Wiman who conducted hybridization experiments with some of the species in question and concluded that *S. mackini* is the common ancestor of the other North American species. Spicer (1985: 172) does not agree with Wiman, because he believes, that "it is theoretically and practically difficult to interpret unambiguously ancestor-descendent relationships, and therefore they are not considered objectively testable".

Both phenograms and cladograms are based on shared characters, which is why "phenetic similarity may be an indicator of cladistic relationship", but "it is not necessarily congruent with the latter" (Sneath & Sokal 1973: 29). This discrepancy between phenetic similarity and cladistic relationships is caused by the cladists' interpretation of characters as ancestral or derived, plesiomorphic or apomorphic. Plesiomorphic characters are ancestral characters that are homologous within a group, but not unique to members of that group (apomorphy) (A Dictionary of Biology 2004). In the cladogram shown in figure 2, *S. moorei* and *S. kargesi* both have a rounded frontal appendage (character 1), which is unique for this group (apomorphic) (Spicer 1985: 171). In the other 7 species represented in the diagram, the frontal appendage is bilobed, a character state not unique to this subgroup, because it was inherited from the ancestor they share with *S. moorei* and *S. kargesi* (ibid.). Thus, rounded frontal appendages are understood as an evolutionary novelty. Pheneticists, on the other hand, do not differentiate between different types of character states and base their analysis solely on *unweighted* similarity.

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Since it is not possible to gain direct knowledge of historical patterns, parsimony algorithms are used to infer evolutionary relationships (Eldredge & Cracraft 1980: 67). This means, that of all possible cladograms for the group in question, the cladogram that minimizes the total number of character state changes is to be preferred. The cladogram in figure 2 is a so called Wagner Tree and was constructed with the aid of a computer program called Wagner-78 which applies parsimony to cladistic analysis (Spicer 1985: 168; Farris 1970). Spicer (1985: 171) used 10 morphological characters of shrimp species (e.g. teeth, fingers, and spines) to construct his cladogram.

The analysis of the phenogram and the cladogram and the corresponding practices shows that pheneticists and cladists were committed to different ontologies. Pheneticists classified operational taxonomic units into groups of phenons, whereas cladists followed the Linnaean classificatory system which classifies groups of organisms into taxa such as species and genera. To pheneticists like Sneath it was important that "the 'natural' classification would contain the most information, be highly predictive and would have the most general purpose" (Vernon 1988: 149). To achieve this goal, pheneticists based their analysis on many unweighted characters, so that the classification system would reflect different degrees of overall similarity. From a cladist's point of view, on the other hand, a 'natural' classification systems should reflect evolutionary relationships. Thus, the controversy between cladists and pheneticists revolved around the question whether or not a classification should represent evolutionary relatedness. Despite these fundamental disagreements, phenetic and cladistic practices also show a number of similarities as illustrated by this case study. Both parties use tree diagrams as a basis for classification. Both diagrams are constructed by the use of computers based on mathematical algorithms and morphological characters. Both parties were striving for objective classifications by avoiding human intervention and judgement as far as possible, which suggests a shared ideal of scientific objectivity (see Suárez-Díaz & Anaya-Muñoz 2008). I suggest that the compatibility of these practices with practices in molecular evolution and the ideal of objectivity that evolved in systematics within the 20th century enabled the integration of elements from systematics into molecular phylogenetics. In the following two sections I will give an outline of the developments in systematics and molecular evolution that facilitated this integration.

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20th century taxonomy: evolutionization, mathematization, automation

In the late 19th/early 20th century suffered severe image problems to the extent that it was considered old-fashioned, out-of-date, and unscientific. Thus, it became increasingly unattractive not only to funding bodies, but also to other biologists and biology students (Vernon 1993). Taxonomy was considered an outdated discipline mainly because the methods and practices had not significantly changed with the acceptance of Darwin's theory of evolution and natural selection. Morphology-based classifications were simply (re)interpreted in evolutionary terms based on the assumption that established methods produced "natural" taxa which could readily be interpreted phylogenetically. Taxonomists were seen as museum men who sorted dead specimens according to morphological characters with the final goal of correctly naming them (Mayr 1942; Simpson 1945). Thus, in order to update the discipline and make it more explicitly scientific, new methods, data, technologies, and theories, in short, new ways of practicing taxonomy were introduced in the course of the 20th century (Vernon 1993; Vernon 1988; Hagen 2001).

One of the approaches of scientization in the early 20th century was Experimental Taxonomy which was mostly practiced by botanists (Vernon 1993). It was one of the early attempts to add evolutionary content to taxonomic practice. In order to replace the notion of 'old taxonomy' J. S. Huxley (1940) coined the term 'New Systematics' which was used to summarize the early attempts to revamp and evolutionize the discipline by including evidence from cytology, ecological data, and considering geographic variation and reproductive relations (Vernon 1993). In the 1940s and 1950s, Mayr and Simpson, two of the main architects of the evolutionary synthesis, initiated a new approach to practicing systematics by emphasizing the connections between taxonomic and evolutionary work. To make evolutionary aspects explicit and more central, they focused on speciation and reproductive behavior and introduced paleontological data, studies of populations in the field, breeding experiments, physiological evidence, and evidence from genetics and embryology to taxonomy. Their approach, today known as 'Evolutionary Systematics', contributed substantially to firmly rooting mainstream taxonomic practices in evolutionary theory (Vernon 1993). Although Mayr and Simpson subscribed to the same theoretical commitments

concerning biological classification, they did not share the same practices. While Mayr introduced a qualitative formalism based on expert judgement, Simpson supported quantitative approaches and pioneered the use of statistical methods in systematics, but he also saw the danger of applying them uncritically (Sterner & Lidgard 2014; Hagen 2001). Thus, Simpson also emphasized the artistic dimension of systematics he firmly believed in value of expert (tacit) knowledge, intuition, and experience (Hagen 2001, 2003).

In the late 1950s Numerical Taxonomy arose as a competing approach to the scientization of taxonomy. The main reason for developing new ideas was a general dissatisfaction with the current state of taxonomy, particularly with its evolutionary foundation which was seen as a source of speculation (Vernon 1988). The ideas that gave rise to the new school of practicing taxonomy were formulated independently by three different groups, namely Cain and Harrison, Sokal and Michener, and Sneath (Vernon 1988). Although there were great differences between the groups, they agreed on central features such as the separation of classification and phylogenetic reconstruction. They argued that classifications should not reflect phylogenetic relationships, instead they should only be based on phenetic similarity assessed through the use of many characters and numerical methods (Vernon 1988: 156). This quantitative approach slightly predated the introduction of computers into systematics. Although the origin of Numerical Taxonomy was not a consequence of technological advances, computers played an important role in the subsequent development of a quantitative formalism (Vernon 1988: 144; Sterner & Lidgard 2014). Although numerical taxonomists advocated a non-evolutionary classification system, they introduced numerical approaches to cladistic analysis of discrete morphological characters (Camin & Sokal 1965). This shows that numerical taxonomy was a broader program which was not limited to phenetic classification, however, to numerical taxonomists phylogenetic inference and classification were two separate activities.

While Mayr advocated a qualitative approach based on expert judgement, numerical taxonomists suggested a quantitative approach based on automated procedures (Sterner & Lidgard 2014). These two approaches are based on different ideals of scientific objectivity. Both Mayr and Simpson valued expert knowledge and experience, whereas Sneath and Sokal as proponents of numerical taxonomy tried

to avoid human judgement which, to them, was the source of subjectivity (Suárez-Díaz & Anaya-Muñoz 2008; Hagen 2001). They regarded computers and automated mathematical procedures as more reliable than trained judgement, because results produced by automated procedures are reproducible in the sense that different taxonomists would independently come to the same classification of the group in question (Hagen 2001). In the eyes of numerical taxonomists, the weighting of characters as practiced by evolutionary taxonomists and their idiosyncratic methods did not lead to subjective classifications (Suárez-Díaz & Anaya-Muñoz 2008). The establishment of mathematical-mechanical objectivity in systematics, a field traditionally based on qualitative approaches, lead to a further development of computers and computer programs (Hagen 2001).

In the mid-1960s cladistic approaches to practicing systematics emerged. Cladists argued that classifications should reflect evolutionary history which could be achieved through the identification of monophyletic groups (i.e. groups that consist of all descendants of a common ancestor). Cladists also introduced new practices to systematics, e.g. the inference of phylogenetic relationships by applying the parsimony principle. Hennig's work did not explicitly suggest a mathematical approach, but due to its emphasis on explicit rules and formal logic, cladistic analysis was suitable for computer programming. Hagen (2001: 308) argues, that parsimony was appealing to systematists because it could be explicitly defined in mathematical terms, even though the application of parsimony algorithms was questionable on biological and philosophical grounds. Already in the late 1960s numerical methods to phylogenetic inference based on Hennig's theory were developed (Kluge & Farris 1969; Farris et al. 1970).

Both cladists and numerical taxonomists had developed numerical methods for cladistic analysis and further analysis of phenetic and cladistic approaches to taxonomic practices revealed "shared elements in the computational workflows of phenetic and cladistic theories" (Sterner & Lidgard 2017). Sterner and Lidgard's (2017) analysis of workflows and methodologies in systematics suggests that phenetics and cladistics should not be understood as two distinct theories. It also shows that "systematists made methodological progress in ways that depended on positive sharing of ideas between otherwise polarized social groups" (Sterner & Lidgard 2017). Both cladists and numerical taxonomists promoted the interlinked

processes of mathematization and automation within their own theoretical frameworks and due to shared practices they were able to borrow ideas from each other. Eventually, the ongoing automation of systematics undermined the informal and inarticulate judgements of evolutionary taxonomy (Hagen 2001: 309).

This short overview shows that the attempts of scientization and formalization of taxonomy gave rise to different theoretical frameworks of doing systematics. However, it also reveals similarities between the opposing parties. Both evolutionary systematists and cladists argued that classifications should reflect phylogenetic relationships; cladists and numerical taxonomists both used numerical methods to infer phylogenetic relationships. These similarities are also expressed in the shared representational practices that I have discussed in the previous section. It also becomes clear that systematics underwent a shift of emphasis from classification and other related activities such as describing and naming of species to studies of evolutionary relationships. During the 20th century the interrelated processes of mathematization, automation and the process of evolutionization were initiated. I argue, that the further development of these processes set the stage for the introduction and eventual dominance of molecular characters in systematics. In section xx we will see that the similarities between phenetics, cladistics, and molecular phylogenetics eventually made the conversion of phenograms and cladograms into molecular phylogenetic trees possible. First, however, I will give an outline of some parallel, yet independent, developments in molecular evolution that gave rise to molecular phylogenetics.

The rise of molecular phylogenetics

The use of molecular data, broadly defined as including molecules and molecular reactions, to study relationships among species has a long history that started in the late 19th century (for a detailed account of the history of the use of molecular data in phylogenetic analysis see Suárez-Díaz 2014). Here I will, however, focus on developments in Molecular Evolution, a field that emerged in the 1960s at the interface of molecular biology, biochemistry, and evolutionary biology, biophysics, studies on the origin of life, and exobiology. This new field brought together

researchers from at least three different research traditions, namely experimental, theoretical, and comparative traditions (Suárez-Díaz 2009).

Since the time of its origination the field was characterized by on ongoing process of quantification and automation. However, in the 1960s sequencing a complete protein was a time-consuming and difficult procedure, so that protein sequences could not yet be used for quantitative analysis: "Protein sequences were so scarce that at the end of the 1960s they could only provide the basis for structural analyses in the study of phylogenetic relationships, but nothing more" (Suárez-Díaz 2014: 463). The first fully automated sequencing machine, called sequenator, was developed by Pehr Edman in the late 1960s (García-Sancho 2012). Since sequencing automation had started with proteins, it is not surprising that the first computer-generated phylogenetic trees were also based on protein structure (Hagen 2001; Suárez-Díaz 2014; Strasser 2010).

Molecular evolutionists who followed a comparative approach were interested in using molecular characters to study relationships among species and reconstruct phylogenies. Emile Zuckerkandl and Linus Pauling, who introduced the concept of the molecular clock at a conference in 1964, belonged to this group of researchers. Biochemists Emanuel Margoliash and Walter Fitch shared the comparative approach to studying evolutionary relationships. Mainly because of his important contribution to developing algorithms for the inference of molecular phylogenies, Fitch is considered as the founder of molecular phylogenetics (Atchley 2011). Fitch and Margoliash published their computer-generated molecular phylogenetic tree in 1967. However, the first computer-generated molecular phylogenetic tree was published by physical chemist Margaret Dayhoff and Mathematician Richard Eck in 1966. Two equally important pioneers in the field of molecular phylogenetics, population geneticist L. L. Cavalli-Sforza and statistician A. W. F. Edwards constructed the first computer-generated molecular phylogenetic tree for human populations which was also published in 1967. These researcher's primary interest was the study of molecular evolution and neither of them had been trained in taxonomy, so they were not particularly concerned with theories of biological classification. In the early days of molecular evolution, most of these researchers were not aware of the ongoing conflicts between proponents of Numerical Taxonomy, Evolutionary Taxonomy, and Cladistics. Thus, their computational approaches do not map neatly onto one of the

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different schools of systematics (Hagen 2001: 302-303). Cavalli-Sforza and Edwards (1967: 234; see also Edwards & Cavalli-Sforza 1964), however, explicitly discuss the relation of their work to taxonomy, particularly to Numerical Taxonomy:

> Although data suitable for our type of evolutionary study may seem to be largely taxonomic, it should be noted that the aim of this work is not the same as that of taxonomy, as the word is normally understood (see Edwards and Cavalli-Sforza, 1964); in particular, 'numerical taxonomy' (Sokal and Sneath, 1963) is not primarily concerned with phylogeny, and the fact that the techniques to be described here and those of numerical taxonomy both involve the treatment of 'taxonomic' data should not be allowed to mask the differences between them, either at the logical or methodological levels.

Although both numerical taxonomists and molecular evolutionists followed a quantitative approach, Cavalli-Sforza and Edwards clearly distanced themselves from the theoretical foundations of Numerical Taxonomy. Interestingly, but not surprisingly, Sneath and Sokal (1973: 323ff) embraced the new approaches from molecular evolution and presented them as if they were part of the broader program of numerical taxonomy. In their chapter "Numerical Approaches to Cladistic Analysis" the approaches by Edwards and Cavalli-Sforza, Camin and Sokal, Farris and his collaborators, Fitch and Margoliash, and Dayhoff are all mentioned in the first paragraph. This way of presenting their research, without making the underlying conceptual differences clear, leaves the reader with the impression that these are simply different methods of Numerical Taxonomy. It is true, that "[m]athematically, the computational approaches used by molecular evolutionists could be considered extensions of numerical taxonomy" (Hagen 2001: 303), but this depiction ignores the different disciplinary contexts of their origin.

The distinctions between systematics and molecular evolution became even more blurred when molecular data began to dominate phylogenetic analysis in the 1980s. In molecular evolution sequences started to dominate over experimental techniques due to technological advancements, particularly the automation of sequencing (Suárez-Díaz 2014). Only then it was possible to generate a sufficient amount of digitalized data for sophisticated statistical analysis. This brief history of molecular evolution shows that the field did not arise from systematics, but in the disciplinary context of molecular evolution. However, systematists rapidly adopted the

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computational approaches used by molecular evolutionists. Eventually, sequences also prevailed in systematics, because molecular data was considered cleaner and more direct evidence of evolution than morphological data. Furthermore, sequences are particularly suitable for quantitative analysis due to their discrete nature (Suárez-Díaz & Anaya-Muñoz 2008) and they can be used for comparative studies between all species including prokaryotes.

The seamless integration of molecular computational approaches into systematics was only possible because systematists and molecular evolutionists had overlapping interests (i.e. studying phylogenetic relationships) and because both fields were characterized by ongoing processes of mathematization, automation and quantification. Not only the introduction of computers played an important role for in the incorporation of molecular data into systematics, but also the establishment of data bases for molecular sequences, and improvement of automated sequencing (see Hagen 2001; Suárez-Díaz 2014) Today, molecular phylogenetics is situated at the intersection of molecular evolution and systematics. In the next section I will show how methods and representational practices that originated in systematics were integrated into molecular approaches to phylogenetic inference.

How phenograms and cladograms became molecular phylogenetic trees

Before the practice turn in philosophy of science, diagrams and other scientific representations like models or scientific theories were often analyzed in terms of their relationship with the world. Thus, philosophers evaluated if and how representations correspond to certain parts or aspects of the world (targets). After the practice turn, however, the focus has shifted to the relationships between scientific practice, i.e. the researchers' actions, and the targets. The turn to scientific practice generated new questions in philosophy of science. Instead of mainly being interested in the relationship between targets and representations, philosophers asked what scientists *do* to represent the world or how models are *used* to generate knowledge (e.g. Knuuttila 2011; Giere 2004). More recently, philosophers also got interested in the cognitive aspects of representing and started to investigate the relationship between representations and individual researchers or research groups (e.g. Vorms 2011; Nersessian 2012). However, the relationship between representations and entire

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scientific communities have been more or less neglected in philosophy of science. I believe, to properly understand scientific representations, it is necessary to address all of the relationships mentioned above. I have already discussed the practices of phenogram and cladogram construction and the question what the different components of respective diagrams represent (section 3). In this section, I will focus on the context and agent dependent aspects of diagram use and interpretation.

Marion Vorms (2011) builds on Goodman's notion of a symbol system to analyze the relationship between a model and its user. However, Goodman's notion of a symbol system and his distinction between syntactic and semantic properties are also applicable to other types of representational systems like diagrammatic symbol systems. Vorms' (2011: 259) refinement of Goodman's symbol system opens up "the possibility that one could account for the inferential differences between representations in terms of a set of syntactic and semantic rules relating a representation with its content". In order to extract information from a diagram, the user needs knowledge of the system's syntax and semantics (Vorms 2011: 260). Thus, before the user is able to make inferences from the diagram to features of its target, they have to know how to read the diagram. Particularly in scientific contexts, drawing information from a diagram can require a substantial amount of background knowledge (Vorms 2011: 261). "For a given graph, the system that defines it determines which of its features are syntactically relevant, and how they are to be interpreted, *within the graph.*" (Vorms 2011: 260, emphasis original). Following this line of argument, Vorms shows, that format and cognitive accessibility of models (or diagrams) are agent and context dependent. I will apply Vorms' approach to discuss the integration of cladograms and phenograms into the new context of molecular phylogenetics, which can be understood as a shift into a new representational system.

As tree diagrams the two diagrams presented in section 3 have the same basic format and are used in the same broad context of biological systematics. The components of the diagrams are very similar due to mathematical and inner-disciplinary conventions and they are used for a similar purpose, namely classification. Without the additional information that the tree diagram in figure 1 is a phenogram, it could easily be mistaken for an evolutionary tree. Only by carving out the agent and context dependency of diagram construction and interpretation

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(section 3), it becomes clear that phenograms and cladograms result from applying different methods, different reasoning processes and approaches to scientific practice in two distinct communities. Thus, diagrams not only represent aspects or components of the world, but also theories, interests, concepts, and beliefs of individual researchers or an entire scientific community. Already in the 1960s, Willi Hennig (1966: 76) pointed out, that using the same format to represent different forms of knowledge causes confusion:

> This equivocation of terms [morphological similarity, phylogenetic relationship] is connected with the fact that the hierarchic type of system is used for representing both phylogenetic kinship and the entirely different form relationship. Such ambiguity is dangerous because it greatly favors the logical error of metabasis in conclusions drawn from the structure of the classification on an animal group.

In molecular phylogenetics results are still represented in tree diagrams. Already at a first glance at the contents of (molecular) phylogenetics textbooks (e.g. Knoop & Müller 2009; Wiley & Lieberman 2011; Nei & Kumar 2000; Brohmann 2016), it becomes clear that UPGMA and parsimony are considered valid methods for phylogeny reconstruction. In the case of parsimony this might not seem particularly surprising, but one might ask how a phenetic clustering method ended up in phylogenetics textbooks. Usually, the different methods to phylogenetic inference are explained in separate sections on Maximum Parsimony, Maximum Likelihood, and Distance Methods such as UPGMA and Neighbor Joining.

During the Systematist Wars pheneticists and cladists agreed, that phenograms (constructed with clustering algorithms such as UPGMA) represent phenetic similarity, not evolutionary relationships. Nowadays, however, tree diagrams constructed with clustering algorithms are used to represent phylogenetic relationships: "[UPGMA] is probably the oldest and simplest method used for constructing phylogenetic trees from distance data" (Vandamme 2009: 26). This shows, the construction method and the representational format have not changed, only the interpretation of the diagram. This shift can only be explained with reference to the context of use. The following statement from a textbook by Nei and Kumar (2000: 87, emphasis added) illustrates the reinterpretation of phenograms as molecular phylogenetic trees.

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This method [UPGMA] is often attributed to Sokal and Michener (1958), but the method used by these authors is quite different from the currently used version. Its clear-cut algorithm appears in Sneath and Sokal's (1973) book. A tree constructed by this method is sometimes called a phenogram, because it was originally used to represent the extent of phenotypic similarity for a group of species in numerical taxonomy. However, **it can be used for constructing molecular phylogenies when the rate of gene substitution is more or less constant**.

Thus, phenograms are modified in accordance with evolutionary theory by adding the criterion of constant substitution rates which goes back to Zuckerkandl and Pauling's concept of the molecular clock (Van de Peer 2009: 144). This process of evolutionization took place within the context of a shift in emphasis from classification to phylogenetic inference in systematics. The transformation of phenograms into molecular phylogenetic trees was possible, because UPGMA as a statistical method fit well into the quantitative framework of molecular phylogenetics and morphological characters could easily be replaced with molecular characters without the need of changing the algorithm. As I have already mentioned in the previous section, the approaches of Numerical Taxonomy and Molecular Evolution were mathematically similar. Today, however, UPGMA-based tree diagrams are understood as phylogenetic trees. The context and agent dependency of interpreting the results of cluster analysis was already emphasized by Sneath and Sokal (1973: 323-324, emphasis added):

Most similarity coefficients and clustering algorithms employed in numerical cladistics are also employed in numerical phenetics. The important distinction between phenetic and cladistic analysis lies not in the similarity coefficients or clustering algorithms, therefore, **but in the assumptions underlying their use** in numerical cladistics **and in the conclusions drawn from the results of the study**.

Most authors, however, are aware of the limitations and problems that come with the use of distance methods for phylogenetic inference:

[Distance methods] tend to return an incorrect phylogeny under several common scenarios (for example when rates of molecular evolution vary between lineages […]). […] A distance tree is just a way of displaying information about similarities and differences. It may reflect evolutionary relationships, because descent with modification tends to leave a hierarchical pattern of differences. But just because we

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can draw a tree from a distance matrix does not mean we have uncovered evolutionary history. (Brohmann 2016: 347).

Another factor which probably facilitated the integration of phenograms into an evolutionary framework is the cultural-historical meaning and use of tree images. I argue, that trees have become a "cultural icon" (Heßler 2007, my own translation) for evolution. Cultural icons are symbols which were detached from their original context to represent certain concepts (Heßler 2007: 292). Long before Darwin, tree diagrams and images were used to represent kinship (e.g. medieval aristocratic family trees). In biology, trees were already established as representations of evolutionary relationships before the begin of the Systematist Wars in the 1960s. The tree is more than just a mathematical diagram, it became a "canonical icon" (Gould 1995) representing not only kinship among organisms, but the concept of evolution itself (Sommer?; Hellström?). Interestingly, German biologists even call phylogenetic trees 'Stammbäume' (i.e. family trees) (Knoop & Müller 2009). Graphic and verbal tree images such as the metaphor *Tree of Life* became the "unifying metanarrative" (Doolittle & Bapteste 2007: 2048) of evolutionary biology and phylogenetics. Trees also represent a certain "style of reasoning" (Hacking 2002) or "Denkstil" (Fleck 1980 [1935]), dubbed "tree thinking" (e.g. Velasco 2012; Baum & Offner 2008; Baum & Smith 2012; Gregory 2008; O'Hara 1998). From this perspective it is not surprising that molecular phylogeneticists were prone to reinterpret phenograms as phylogenetic trees and integrated them into an evolutionary framework.

While the term 'phenogram' is usually absent from the glossary of molecular phylogenetics textbooks, the term 'cladogram' was retained. Since cladograms had already been used to represent evolutionary relatedness, they could easily be transformed into molecular phylogenetic trees. In the context of molecular phylogenetics, cladograms are usually interpreted as phylogenetic trees without information on branch lengths (Knoop & Müller 2009: 60ff). Thus, cladograms can be used to determine monophyletic groups, but they do not provide information on the amount of evolutionary changes within a lineage. Lemey et al. (2009: 656, emphasis omitted) define a cladogram as

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a branching or tree diagram representing the estimated evolutionary relationships among a set of taxa. In contrast to a phylogram, branch lengths in a cladogram are not proportional to the amount of inferred evolutionary change.

The distinction between phylogenetic trees and cladograms as trees with and without specified ancestors, that had been emphasized by some cladists in the late 1970s and early 1980s, has become obsolete, because neither cladograms nor other types of molecular phylogenetic trees contain specified ancestors. In phylogenetic analysis all recent taxa within a group are treated as sister taxa that are represented by the external branches (Baum & Smith 2012). In this sense, molecular phylogenetics is still rooted in the cladistic approach advocated by Willi Hennig. The internal (and usually unnamed) nodes of phylogenetic trees can be interpreted as actual or hypothetical common ancestors, speciation events, and/or the emergence of unique derived characters (see Maddison & Maddison 2000: 37ff for different interpretations of phylogenetic trees). Although the debate of the difference between cladograms and phylogenetic trees has largely subsided, the biological meaning of tree diagrams used in systematics is still muddled (Martin et a. 2010).

Maximum parsimony as the central cladistic method to tree inference has also remained an important part of the molecular phylogenetics toolkit. Although parsimony algorithms originated in pre-molecular systematics and were originally developed to construct cladograms from morphological characters, they can also be applied to molecular data by estimating the minimum number of nucleotide substitutions (Nei & Kumar 2000: 115ff). With the integration of parsimony methods into a molecular framework and the shift of emphasis from classification to phylogenic analysis, the use of the term 'cladistics' had changed:

> Initially, cladistics was equated with Hennigian phylogenetic systematics. Later, the term 'cladistics' was used to refer to the application of parsimony algorithms in systematics (Williams et al. 2010: 174).

Today, parsimony-based approaches are often perceived as outdated and inferior to so-called model-based approaches such as Maximum Likelihood. Some researchers view Maximum Parsimony merely as "a useful 'fallback' method when model-based methods cannot be used due to computational limitations" (Swoffort & Sullivan 2009: 269). Many molecular phylogeneticists prefer Maximum Likelihood methods over

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parsimony, because they are based on an explicit model of evolution. However, the debate between proponents of likelihood and other model-based statistical approaches and those who favor parsimony approaches is still unsettled.

Who won the war?

According to Hull (1988), cladists have defeated their competitors, proponents of evolutionary systematics and phenetics (see also Mishler 2009). Others (e.g. Felsenstein 2004, Sneath 1995) admit that phenetics has lost the battle, but argue, that numerical taxonomy eventually won the war. However, both narratives neglect broader processes like mathematization, molecularization, and automation. My analysis of the integration of systematics and molecular evolution, which gave rise to the field Molecular Phylogenetics, shows that focusing on the conflicts between evolutionary systematists, numerical taxonomists, and cladists neglects the force of a broader transformation of biological research. Automatization, mathematization, evolutionization, and quantification have reshaped systematics profoundly and overshadowed the debate that revolved around theories and practices of classification. Technological advancements eventually led to the automation of sequencing and the introduction of cheap personal computers into systematics, which promoted the molecularization of phylogenetics and initiated a new era:

> The conflict between pheneticists and cladists properly belongs to the era of morphological systematics—an era that is now effectively at an end. The availability of molecular data has revolutionized the field and made many old controversies obsolete (Hughes 1999: 34).

My analysis shows that the construction of phylogenetic trees by using statistical methods was initiated independently in systematics and molecular evolution. These practices were integrated and further developed to eventually dominate Molecular Phylogenetics. Although the statistical methods used today could be interpreted as an extension of the methods applied by numerical taxonomists, it is misleading to portray this development as a triumph of Numerical Taxonomy over Cladistics and Evolutionary Systematics. However, it is true, that numerical taxonomists like Robert Sokal have played an important role in developing computational techniques for phylogenetic analysis, although most numerical taxonomists viewed phylogenetic

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inference as a highly speculative endeavor. The fact that nowadays phylogenetic analysis is the central activity in systematics and classifications are based on the inferred tree structures indicates that Numerical Taxonomy has not prevailed over competing approaches. It is equally mistaken to portray Cladists as victors of the Systematist Wars. While it is true that some elements of Hennigian theory have persisted and parsimony algorithms are still used for phylogenetic analysis, Molecular Phylogenetics is not a direct descendent of Cladistics. As shown in section xx, Molecular Phylogenetics emerged as a sub-field of Molecular Evolution independent of practices in systematics. The integration of practices from systematics with practices of Molecular Evolution was possible, because they fit into the prevailing quantitative framework. With the molecularization of systematics and the shift of emphasis from classification to phylogenetic analysis, cladistics and phenetics are no longer perceived as different theoretical frameworks, but rather as methods of studying molecular evolution:

> Thus, a contemporary solution might be to ignore the words *cladistics* and *phenetics*, and to assume they represent just alternative methodologies (among many), to be judged by certain parameters and applied to DNA as the sole source of data (Williams et al. 2010: 171).

In the context of molecular evolution phenograms were reinterpreted as molecular phylogenetic trees and cladograms became molecular phylogenetic trees that do not represent the amount of evolutionary change within lineages. With the integration of practices of systematics with molecular evolution, phenograms and cladograms were no longer used to represent different forms of knowledge. Instead, both UPGMA-based trees and cladograms are used to represent evolutionary relationships between taxa.

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