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2. Tree and Network in Systematics, Stemmatics, and Linguistics: Structural Model Selection in Phylogeny Reconstruction

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Abstract

Phylogenetic reconstruction in general aims at estimating the most plausible tree or network based on character data of evolving objects. In evolutionary biology, textual stemmatics, and historical linguistics, researchers have independently and repetitively developed a set of rules for building phylogenetic trees from data on organisms, manuscripts, and languages, respectively. All these sciences have in common the basic features of historical sciences (“palaetiological sciences” by William Whewell 1847 / “historiographic sciences” by Avezier Tucker 2004). Estimating evolutionary history means searching for the best solution among possible alternative phylogenetic hypotheses. However, the best solution isn’t necessarily true in a historical sense because we can’t observe directly or experimentally the past evolutionary processes and its consequent patterns. All we can do is to find the best estimate as accurately as we can by comparing all possible trees or networks on the basis of an optimality criterion such as parsimony, likelihood, or Bayesian posterior probability. Historical reasoning (“tree-thinking” Robert J. O’Hara 1988) is comparable in nature; it has been recognized as “abductive” reasoning. Abduction is a form of non-deductive inference providing the best hypothesis for given data. An iconographical survey of historical development from ancient times to the present of phylogenetic diagrams reveals a wider array of various graphical tools (chain, tree, and network) for visualizing object-diversity and its spatiotemporal modification. These graphical tools could be used for selecting efficient structural models for estimating phylogenies and constructing classifications of evolving objects. Evolutionary biology, textual stemmatics, and historical linguistics share not only the basic characteristics of historical sciences but also those of data visualization and information graphics.

2.1. Introduction: Pattern and Process in Object Diversity

When “history” is referred to as any spatiotemporal transformation of various things (objects), we must estimate the history based on available data. For example, in recent

years, biologists estimate the phylogenetic relationships among organisms on the basis of the genetic sequence data of nucleotides and amino acids. The basic idea of descent with modification was made popular by Darwin (1859), Haeckel (1866), and other biologists in the 19th century. Modern biology since then has established the theory and methodology of reconstructing phylogeny using morphological and molecular characters. Descent with modification was usually depicted as the “tree of life”, whose conceptual history dates to the Middle Ages, much older than evolutionary thinking.

The task of estimating the phylogeny of organisms is quite different in its character from other sciences such as experimental physics and chemistry. Almost all events forming the lineage of biological evolution were completed millions of years ago, even hundreds of millions of years ago in some cases. Thus, not only direct observation is impossible, but also repeated experiments are impractical in evolutionary and phylogenetic biology. However, none of us would assert that evolutionary biology or phylogenetics are “pseudo-sciences.” These sciences are nothing but historical sciences different from physics and chemistry. While using a scientific method of their own, historical sciences and experimental sciences have shaped a loosely interconnected unity called “science” as a whole.

Moreover, the recognition that different sciences have different methodologies of their own can whittle away the merely apparent “wall” that isolates natural sciences from the humanities and social sciences. A preconception that there is a deep and wide groove separating the humanities and social sciences from natural sciences is seen widely. However, from the fact that science is not monolithic, and from its methodology we can notice that there was no barrier from the beginning between science and humanities.

In this paper, I discuss how to understand the diversity formed by spatiotemporally changing objects with special reference to the problem of phylogeny estimation in manuscripts, languages, and organisms. And I point out a historical fact that a common logic has been used independently from the centuries-old differences of these sciences. No matter what kinds of object were studied, almost the same methodology was independently established in order to reconstruct genealogical relationships among objects. Nevertheless, that was not noticed until very recently (Minaka 2006, 2016; Minaka and Sugiyama 2012; Lima 2014).

Problems of studying the patterns and processes of diverse objects are scattered in various fields. For example, the field of studying biodiversity is called biological systematics. How can we grasp the global biodiversity on the earth, and what principles of systematics can help us achieve the purpose?

2.2. Classification and Phylogeny in Biological Systematics

A renowned botanist, Walter Zimmermann of Germany in the first half of the 20th century, wrote a long article on botanical phylogenetics (Zimmermann 1931). Zimmermann stated clearly the reason why it is necessary to classify diverse objects for us human beings (Zimmermann 1931: 942). He pointed out that we cannot make groups (“*Wir müssen gruppieren*”) only because natural objects and their parts do not exist as

clearly demarcated groups (“*wohlabgegrenzte Gruppen*”) but as individuals as unique phenomena. Because it is impossible for human beings to grasp those objects one by one separately, he concluded that we need to order and systematize them for our economy of memory. It is worth noting in his view that biological classification and taxonomy can be viewed as one of “grouping sciences” (“*Gruppierungswissenschaften*”).

Zimmermann’s second question was how to make groups (“*Wie wollen wir gruppieren?*”). In this regard, he took the position that any classificatory system should be strictly consistent with a phylogenetic tree (see Figure 2-1). He advocated that the strictly phylogenetic system of a group of organisms can be constructed, if closely related subgroups (monophyletic taxa) are ordered hierarchically based on the phylogenetic tree estimated for the group.

After Zimmerman’s pioneering discussion there was a continuing dispute concerning the principles and methods of building classificatory systems. In particular, over 20 years throughout the late 1970s from the 1960s, a severe controversy has been fought among schools of systematists (Hull 1988; Minaka 1997; Yoon 2009). The focal point of the controversy at the time was the criterion for constructing classificatory systems of organisms. Traditional taxonomists use both logic and intuition for classification. For example, a famous paleontologist George Gaylord Simpson stated in his classical textbook, *Principles of Animal Taxonomy* (Simpson 1961), as follows:

Like many other sciences, taxonomy is really a combination of a science, most strictly

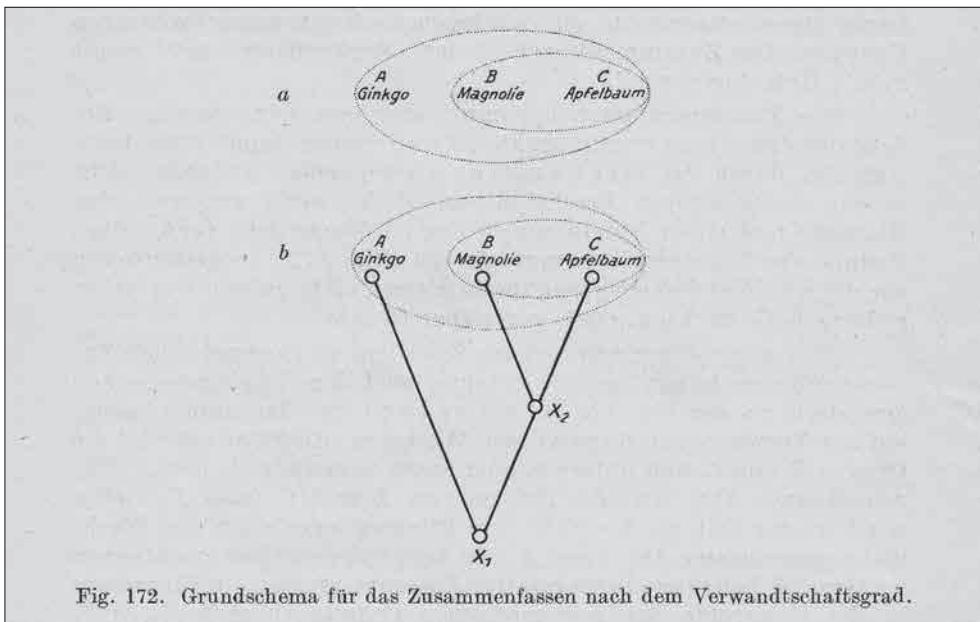


Figure 2-1 The relationship between classification (above) and phylogeny (below).
(Reproduced from Zimmermann 1931: 990).

speaking, and of an art. Its scientific side is concerned with reaching approximations, hopefully believed to be successively closer as the science progresses, toward understanding of relationships present in nature. One of the dictionary definitions of “art” is “human contrivance or ingenuity,” and taxonomy becomes largely artistic, in that sense, when applied to construction of classifications (Simpson 1961: 110).

Simpson’s view that biological classification cannot be constructed solely by pure logic has been accepted by many systematists. However, in opposition to Simpson and other evolutionary systematists, Willi Hennig, a German entomologist, insisted on the supremacy of the strictly phylogenetic system over other kinds of classificatory systems (Hennig 1950; 1957; 1966). From the end of the 1940s to the 1950s, Hennig clarified the logical relationship between phylogeny and classification, which reinforced and generalized the basic recognition that Zimmermann had developed earlier (Figure 2-2).

After Hennig’s important book, *Phylogenetic Systematics*, was translated into English (Hennig 1966), his theory landed in English-speaking countries with the result that the “cladistics revolution” spread over the systematics community during the following twenty years (Hull 1979; Schmitt 2013).

For Hennig, the German word “*System*” (“system”) implies something more fundamental than the German word “*Klassifikation*” (“classification”). Hennig aims at constructing the one and only “system” of organisms in order to comprehend biodiversity on the earth. The “system” is not merely “classification” for some practical use. In the first place, what is “system” for Hennig? He used a metaphor to illustrate the point:

Let me begin with an example. If an archaeologist discovers potsherds in a tomb, he might begin by ordering, or classifying, them in some way: according to their material (clay or metal), their color, their decorations, etc. Subsequently, he might attempt to reconstruct the original vessels (vases, urns, etc.), of which the potsherds are fragments. This reconstruction is another kind of ordering. One might call it a system, but one need not call it a classification. For another example, I refer to the rivers of Europe. These may be classified according to their navigability, water management, the conditions they offer for the settling of organisms, etc. But one might seek to determine the drainage (Danube, Rhine, Elbe, etc.) to which each belongs, in order to construct a different kind of system of rivers. Similarly, the construction of a cladogram in accordance with the principles of phylogenetic systematics results in a system rather different in principle from various kinds of possible classifications. Although my original perception of this distinction was somewhat unclear, I have nevertheless avoided speaking of phylogenetic “classification,” preferring instead phylogenetic “system” — but I have sometimes used “classification” under the influence of English usage (Hennig 1974: 281; 1975: 245–246 for English translation).

In the paragraph cited above, Hennig gave as examples of “system”, not as “classification”, the reconstruction of archeological objects and the determination of the drainage of rivers. There may exist many practical classifications each with a specific

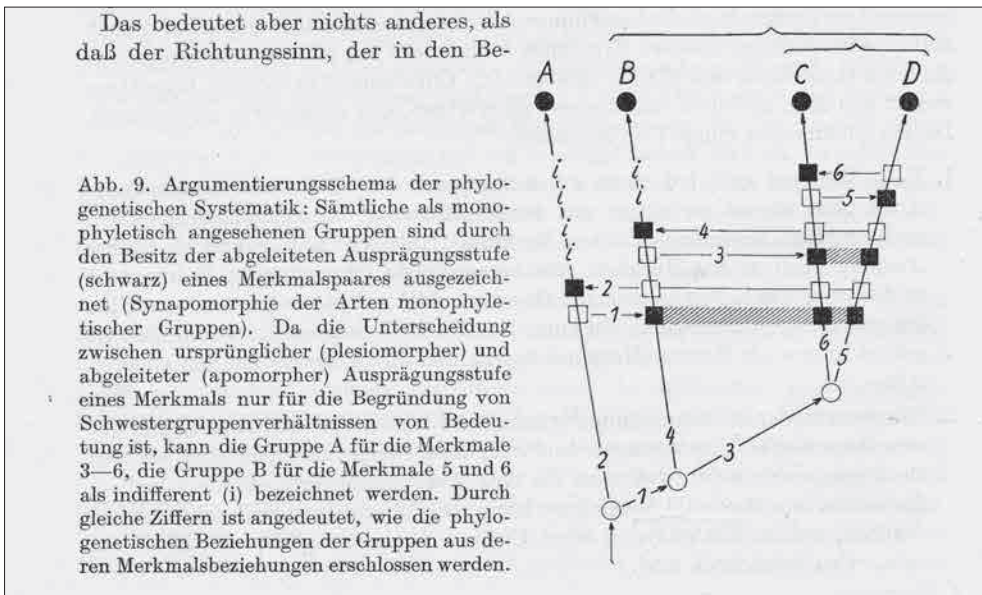
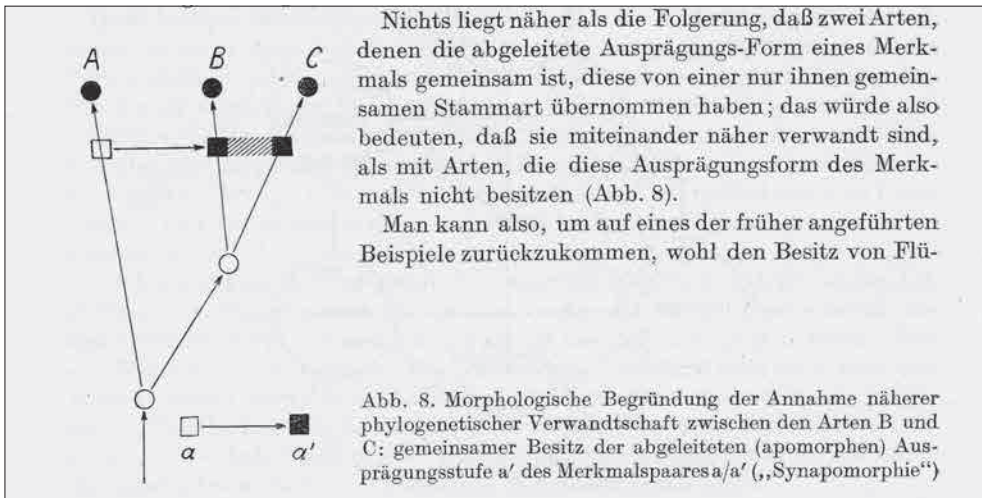


Figure 2-2 The argumentation scheme of Hennig’s phylogenetic systematics. Above: For a character with a primitive state (a) and a derived state (a’), organisms sharing the derived state (a’) form a monophyletic group. Below: A phylogenetic system can be constructed for a group of organisms by repeating this procedure for all characters. (Reproduced from Hennig 1957: 66, Figures 2-8 and 2-9).

purpose, but there may exist a unique and unitary “system” with a general purpose. His viewpoint is applied to biodiversity. Similarly, the construction of a cladogram in accordance with the principles of phylogenetic systematics results in a system rather different in principle from various kinds of possible classifications (Hennig 1974: 281–282; 1975: 245–246 for English translation).

Hennig claimed that the phylogenetic tree composed of all organisms, extant or extinct, on the earth is nothing other than “The Tree of Life” which is a unique phylogenetic system. This unique phylogenetic system is, according to Hennig’s view, a general reference system (“*allgemeines Bezugssystem*”: Hennig 1950; 1966) which should be located on top of all other special-purpose classificatory systems. From the standpoint of cladistics, systematic pattern means this general reference system represented as a phylogenetic diagram called “cladogram.” A cladogram is defined to be a branching diagram showing only sister-group relationships among organisms without any connotations about evolutionary rates, progressiveness, phenetic similarity, etc. Every branching point in a cladogram corresponds to a monophyletic group based on one or more shared derived character states.

The controversy over the principles of constructing classificatory systems began in the 1960s and was waged during the 1970s. During the 1980s, the focal point moved to how a systematic pattern can be defined and analyzed independently from the evolutionary framework. Among other things, whether a cladogram depicting a pattern (“being”) among organisms can be separated from any assumptions of evolutionary processes (“becoming”) was much discussed in this period.

Some cladists who claimed a strict consistency of phylogenetic relationships and the classificatory system insisted on a radical proposal of decoupling cladograms and cladistics from the idea of evolution itself. This “transformation” (Platnick 1979) formed a new cladistics school called “transformed cladistics” or “pattern cladistics” (Nelson and Platnick 1981). Transformed (pattern) cladistics is opposed to “phylogenetic cladistics,” which asserts that evolutionary assumptions are needed in cladistic theory and practice.

2.3. Generalized Pattern Cladistics as a Science of Trees and Networks

The theory of pattern cladistics (Nelson 1979) was established during the 1970s as a general system of tree diagrams, including cladograms and phylogenetic trees. Hull (1979) pointed out that those wider applications of cladistics to any evolving objects, necessarily require a temporal dimension:

In general, cladistic analysis can be used to discover the cladistic relations between any entities which change by means of modification through descent (Platnick 1979). As general as this notion of cladistic analysis is, it still retains a necessary temporal dimension. Transformation series must be established for characters, not just an abstract atemporal transformation series like the cardinal numbers or the periodic table, but a series of actual transformations in time. (Hull 1979: 418)

And Hull insisted that the transformation made cladistics split into the following two “schools”:

From the beginning, Gareth Nelson (1973) seems to have been developing two notions of cladistic analysis simultaneously, one limited to historically developed patterns (cladism

with a small ‘c’), the other a more general notion applicable to all patterns (Cladism with a large ‘C’). His method of component analysis is a general calculus for discerning and representing patterns of all sorts (Hull 1979: 418).

Pattern cladistics aims to discover and represent patterns of any kinds of objects, regardless of their origin (Williams and Ebach 2008). In this sense pattern cladistics can be regarded as being a part of discrete mathematics that studies the partial-order relationships whose structures are visualized as trees and networks (Minaka 1993; Davey and Priestley 2002).

This generalized version of pattern cladistics, or Nelson’s cladistic component analysis, as Hull called it “Cladism with a large ‘C’”, was not limited to biology. Discerning patterns of any kinds of object is the inferential basis for the discussion of causal processes which brought about those patterns.

Due to this generality pattern, cladistics can be widely applied not only to biological taxa but also to other nonbiological objects (Platnick and Cameron 1977). In fact, cladistics and related parsimony-based methods have been widely and independently used for phylogeny reconstruction not only for organisms but also for languages and manuscripts, archeological materials, historical styles, and other culture constructs (Hodson et al. 1971; Hoenigswald and Wiener 1987; Atkinson and Gray 2005; O’Brien and Lyman 2003; Lipo et al. 2006; Schmidt-Burkhardt 2005; Moretti 2005; Forster and Renfrew 2006; Nakao and Minaka 2012).

2.4. Phylogeny Estimation in Manuscript Stemmatics and Historical Linguistics

As discussed in the previous section, the severe controversy in biological systematics in the 1960s and 1970s was concerned with how to construct classificatory systems and to estimate phylogenetic relationships among organisms. Pattern cladistics which arose as a new school of systematics during this period had sufficient generality as to be used for objects other than organisms. At this point it is worth looking back on the history of historical linguistics and manuscript stemmatics (see Timpanaro 1971; 2005 for stemmatics, and Alter 1999 for linguistics for more details).

Methods for estimating genealogical relationships among languages in historical linguistics and among manuscripts in comparative philology have been mutually related in their historical development. Henry M. Hoenigswald (1973) pointed out succinctly the existence of a parallel connection between linguistics and stemmatics:

A number of languages descended separately from one ancestor (a number of manuscripts copied from one model) may be expected to share innovations (common errors) of a non-trivial sort only by accident. If accident can be excluded and if innovations (errors) can be independently recognized as such, subancestors (hyperarchetypes) and the ancestor (archetype) may be reconstructed and the resulting tree may be historically interpreted in terms of separation, migration, etc. (in terms of monastic history, of the history of writing

and printing, etc.). (Hoenigswald 1973: 25)

Systematizing solely based on shared innovations in linguistics and shared errors in stemmatics is in principle equivalent to the cladistic method which discovers monophyletic taxa using shared derived character-states (Hennig 1950, 1966; Baum and Smith 2013).

Procedures of manuscript stemmatics were originally established through revising and editing the Cristian Bible and the classics in Greek and Roman times (Timpanaro 2005). For example, the Biblical scholar, Johann Albrecht Bengel (1687–1752), wrote in 1734 about the “genealogical relationship” between manuscripts as follows:

“Manuscripts are closely related if they have the same ancient arrangements of text on the page, subscriptions, and other subsidiary features,” cited in Timpanaro (2005: 65). In addition, Bengel conjectured that it is possible to trace the genealogy of all manuscripts to their roots, which can be summarized as “*tabula genealogica*” (Timpanaro 2005: 65). Bengel discussed the estimation of relationships among manuscripts about a century before the appearance of evolutionary thinking in biology.

Carl Johan Schlyter (1795–1888) in Sweden drew for the first time this “*tabula*

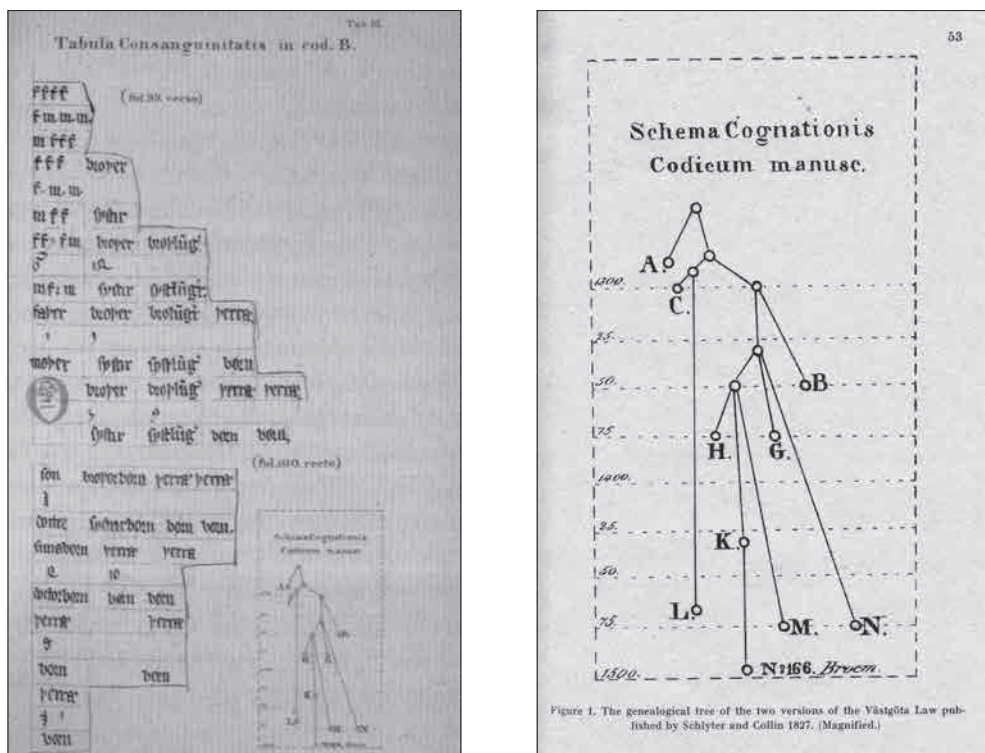


Figure 2-3 *Tabula consanguinitatis* (left) and genealogical tree (right: enlarged) of ancient Swedish legal manuscripts *Västgöta* (taken from Collin and Schlyter 1827). (Reproduced from Holm 1972 and Ginzburg 2004).

geneologica” of manuscripts in the form of a phylogenetic tree (Holm 1972; Ginzburg 2004). In 1827, Schlyter estimated manuscript stemma of the ancient Swedish legal texts *Västgöta* to show their genealogical relationships as a branching “tree” (Figure 2-3). His tree was the origin of the style of drawing a manuscript genealogy upside down, by placing the root (archetype) on top of the tree and hanging all descendants downward.

Schlyter drew his manuscript genealogy (“*schema cognationis codicum manuscriptorum*”) in Figure 2-3, right) based on the table of cognates (“*tabula consanguinitatis*”) in Figure 2-3, left). An absolute age scale is added to this genealogy. His *tabula consanguinitatis* can be associated with older forms called “*arbores consanguinitatis*” or “*arbores affinitatis*” which had been widely used since the Middle Ages in Europe. With reference to this graphical representation “tree (*arbor*)”, many iconographical studies accumulated in the past (Schadt 1982; Barsanti 1992; Klapisch-Zuber 2000, 2003; Minaka and Sugiyama 2012).

In 1831, a Latin scholar, Carl Gottlob Zumpt (1792–1849), coined the term “*stemma codicum*” for manuscript genealogy. In this era when the idea of biological evolution was not yet popular, comparative philologists had already established the phylogenetic theory of reconstructing manuscript relationships as a research program. Karl Lachmann (1793–1851), Classical scholar in the 19th century, compiled major methods and techniques of manuscript stemmatics. Since then the genealogical method of stemmatics has come to be called “Lachman’s method” (Timpanaro 1971; 2005).

Now let’s focus on how textual mutations (that is, transcription errors) in descendent manuscripts are used to estimate the stemma in Lachmann’s method. Paul Maas (1880–1964), a comparative philologist in Germany, published in 1927 a short but highly influential textbook on manuscript stemmatics, *Textkritik* (Maas 1950[1927]). His book summarized briefly the basic concepts and practical methods for reconstructing manuscript stemma.

Maas described in his book three categories of informative errors, distinct from uninformative errors, that can occur at any time only by chance (Maas 1937):

Significant errors (*errores significativi*): informative errors which cannot occur by chance.

Separative errors (*errores separativi*): informative errors which are specific to a particular manuscript.

Conjunctive errors (*errores coniunctivi*): informative errors which are shared by multiple manuscripts.

When the original ancestral text (prototype) contains no errors in principle, any errors occurring in descendent manuscripts can be considered to be derived character-states. However, among various kinds of errors, only conjunctive errors have evidential value for estimating the manuscript stemma. The reason is that shared derived similarities can discriminate between competing phylogenetic trees while the other similarities cannot.

This conceptual scheme (Figure 2-4) proposed by Maas indicates a definite correspondence with Hennig’s phylogenetic theory discussed in the previous section because separation errors are uniquely derived character-states called “autapomorphy”

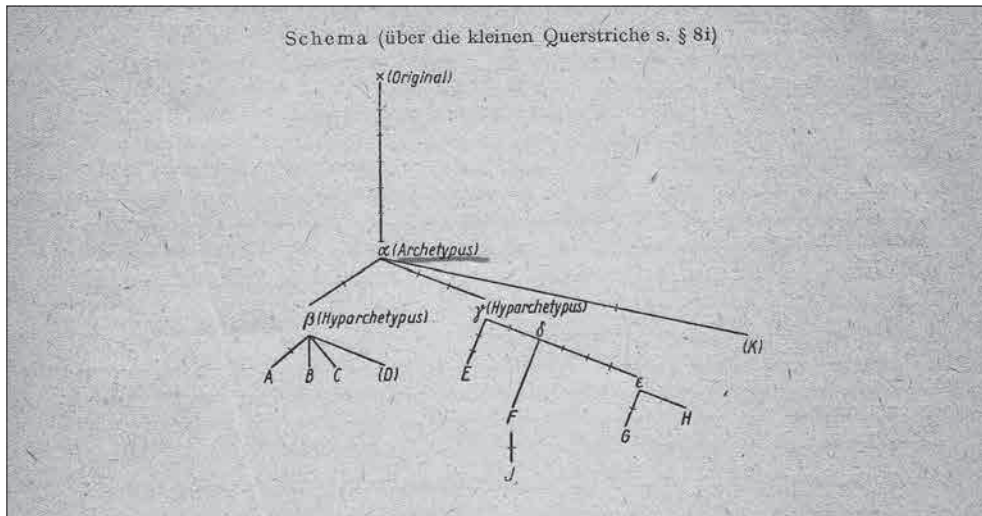


Figure 2-4 The argumentation scheme of manuscript stemmatics formulated by Paul Maas. (Reproduced from Maas 1950[1927], p. 7).

and conjunctive errors are shared derived character-states called “synapomorphy” in cladistic terminology. In this way, the methods for phylogeny reconstruction in manuscript stemmatics, historical linguistics, and biological systematics were independently established, with the result that they converged into the same methodology based on the principle of parsimony (Platnick and Cameron 1977; Cameron 1987; O’Hara 1996; Atkinson and Gray 2005).

On the other hand, Maas’s formulation of manuscript stemmatics is related to graph theory or “discrete mathematics” in our time. In fact, Maas was interested in the graph-theoretical properties of manuscript stemma and tried to enumerate all possible trees for a set of manuscripts (Figure 2-5).

Maas’s intellectual heritage was inherited by Henry M. Hoenigswald (1915–2003), a

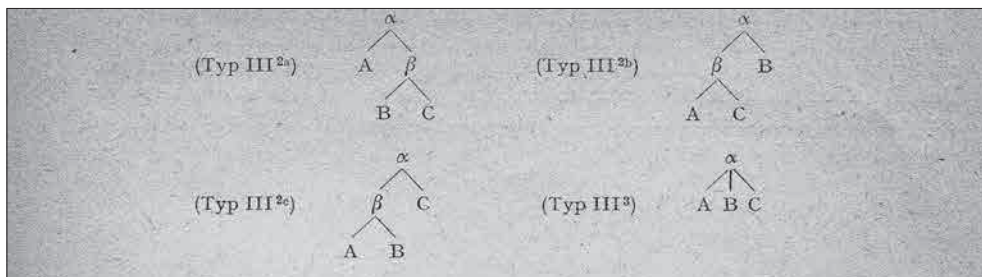


Figure 2-5 Enumeration and categorization of manuscript stemma. (Reproduced from Maas 1937).

comparative linguist, who published a theoretical work in which he developed a general graph theory of linguistic and stemmatic trees in detail (Hoenigswald 1973). These mathematical treatments of tree structures in phylogeny reconstruction found successors in pattern cladistics and molecular phylogenetics from the 1970s to the present (Semple and Steel 2003; Dress et al. 2012; Minaka 2017).

2.5. Conclusion: Abductive Inference in Systematics in Biology, Stemmatics, and Linguistics

The meaning of “ancestor” is different in manuscripts, languages, or organisms because the processes of evolution (transmission) from ancestor to descendent are quite different among these three kinds of object. A variety of “mutations” such as misspelled words or erroneously deleted sentences that could occur during handwriting by scribes would be transmitted from an ancestral manuscript to descendent ones. Similarly, another kind of “mutation” such as phonological shifts in words or morphological changes in sentences would also be inherited from a protolanguage to daughter languages. These shared “mutations” in stemmatics and linguistics are historical markers of lost routes of phylogenetic history.

The concept of shared derived similarity, that is, “synapomorphy” (Hennig 1966) can be equally applied to biology, stemmatics, and linguistics when our aim is to reconstruct phylogenetic history based on inherited similarities. From the point of synapomorphy there is no essential difference in the logic and methodology of estimating phylogenetic history. An example is the stemmatic study of *the Canterbury Tales* by Geoffrey Chaucer (1343? –1400). Phylogenetic analyses of descendent manuscripts, using the maximum parsimony method, have estimated the best tree and network. These were calculated by molecular phylogenetic computer software (Robinson and O’Hara 1992; Barbrook et al. 1998).

In the intellectual tradition of William Whewell’s “palaetiological sciences” (Whewell 1847; O’Hara 1988), Tucker (2004) proposed a new category “historiographic sciences” which is composed of those sciences that share the purpose of reconstructing phylogenetic relationships among objects and searching for common causes for historical processes. Historically speaking, theory, methodology, and conceptual systems for phylogeny estimation in stemmatics, linguistics, and biology showed considerable convergence (Atkinson and Gray 2005). The fact that these disciplines had independently established the same procedures for tree building confirms that they aim at the identical problem of historiographic sciences separately. The identical, common problem is “abduction” of past historical events (Sober 1988; Fitzhugh 2006). Historiographic abduction is to estimate the best systematic pattern based on the observed data at present. The goal of historiographic sciences is reconstructing genealogical traces based on observed data regardless of whether the objects under study are manuscript, language, or organism, etc. From the point of view of abduction in historiographic sciences, manuscript stemmatics and historical linguistics have tackled the common problem of how to estimate genealogy with high accuracy, given the limited amount of information

about the past.

The trends of thought and background knowledge have changed from one era to the next. For one example, Greg (1927) attempted to construct an axiomatic logical system of textual criticism based on the logical positivism of *Principia Mathematica*. However, Greg's logical system was not accepted by most contemporary philologists (Rosenblum 1998: Preface). For another example, Woodger (1937) and Gregg (1954) built an axiomatic system for biological taxonomy but they could find very few sympathizers around them. Strict logical systems in historiographic sciences were not sufficiently appreciated (Minaka 2016).

Sebastiano Timpanaro (2005) pointed out the parallel relationship of phylogenetic reconstruction methods in historical linguistics and comparative philology:

There is an undeniable affinity between the method with which the Classical philologist classifies manuscripts genealogically and reconstructs the reading of the archetype, and the method with which the linguist classifies languages and as far as possible reconstructs a lost mother language, for example, Indo-European. In both cases inherited elements must be distinguished from innovations, and the unitary anterior phase from which these have branched out must be hypothesized on the basis of various innovations. The fact that innovations are shared by certain manuscripts of the same text, or by certain languages of the same family, demonstrates that these are connected by a particularly close kinship, that they belong to a subgroup: a textual corruption too is an innovation compared to the previously transmitted text, just like a linguistic innovation. On the other hand, shared "conservations" have no classificatory value: what was already found in the original text or language can be preserved even in descendants that are quite different from one another (Timpanaro 2005: 119).

That is, shared innovations are evidence of monophyletic groups of manuscripts, languages, or organisms, although shared conservations provide no evidence of phylogenetic relationship. This means that the distinction between shared innovation and conservation were being made in philology and linguistics before Hennig (1966) coined a pair of new words, synapomorphy and symplesiomorphy, to label them. Moreover, it suggests that a universal historiographic method is feasible, despite the differences among various objects including manuscripts, languages, and organisms.

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