



Moving Past the Systematics Wars

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Abstract. It is time to escape the constraints of the Systematics Wars narrative and pursue new questions that are better positioned to establish the relevance of the field in this time period to broader issues in the history of biology and history of science. To date, the underlying assumptions of the Systematics Wars narrative have led historians to prioritize theory over practice and the conflicts of a few leading theorists over the less-polarized interactions of systematists at large. We show how shifting to a practice-oriented view of methodology, centered on the trajectory of mathematization in systematics, demonstrates problems with the common view that one camp (cladistics) straightforwardly “won” over the other (phenetics). In particular, we critique David Hull’s historical account in *Science as a Process* by demonstrating exactly the sort of intermediate level of positive sharing between phenetic and cladistic theories that undermines their mutually exclusive individuality as conceptual systems over time. It is misleading, or at least inadequate, to treat them simply as holistically opposed theories that can only interact by competition to the death. Looking to the future, we suggest that the concept of workflow provides an important new perspective on the history of mathematization and computerization in biology after World War II.

Keywords: David Hull, Mathematization, Cladistics, Numerical taxonomy, Workflow, Evolutionary epistemology

Introduction

“I used to think that we fought a lot in when I worked in population genetics,” wrote Joseph Felsenstein, “but in that field we used to sit side by side at meetings without growing red-faced, hissing at each other, or spreading scurrilous rumors” (Felsenstein, 2001, pp. 466–467). Another biologist, Paul Ehrlich, reported after a conference in the 1960s that it “went very well – one old-line systematist cried (the meeting would hardly have been a success without that!)” (Vernon, 2001, p. 327). Countless experiences of this sort were emblazoned on the memories of systematic biologists from the mid-1960s through the 1980s – the afterimages left from a series of explosive debates between competing theories of biological classification and phylogenetic inference.

The sheer intensity of these conflicts, commonly known as the “Systematics Wars,” has understandably led historians to focus on charting the course of the debates and uncovering the origins of each theory (Hull, 1988; Vernon, 1988; Scott-Ram, 1990; Williams and Forey, 2004; Rieppel, 2007, 2008; Jensen, 2009; Williams and Ebach, 2009; Hamilton, 2014). However, the passage of time has brought the adequacy of this conflict- and theory-centric framing into question: it provides only a partial and biased view of what systematic biologists actually *did* in this time period – the full range of empirical problems they addressed, the procedures they devised to overcome these problems, and the practices that became the normative basis for evaluating good science. Furthermore, the narrow focus of the Systematics Wars narrative undersells the importance of the history of systematics for the history of biology more broadly.

We argue that the Systematics Wars narrative depends on a competition-drives-progress model of science that obscures and distorts a fundamental and lasting transformation of the field during this time period: the introduction of mathematical methods into the heart of classification and phylogenetics (Hagen, 2001, 2003; Sterner, 2014; Sterner and Lidgard, 2014). In a previous study (Sterner and Lidgard, 2014), we contrasted Ernst Mayr’s attempt to reform standard practices in systematics using a qualitative formalism based on human judgment (Mayr, 1942) with numerical taxonomy’s effort to introduce a quantitative formalism based on automated procedures for computing classifications. Crucial differences between the two were the way they conceptualized the temporal sequence of steps in classification and how and why their systems should become standard practice. This was a historical turning point: mathematical methods were indispensable to

revolutionizing the workflow biologists used to produce classifications and phylogenies.

As we use it here, a workflow is a standardized sequence of tasks and procedures that scientists perform to achieve some goal. The term “work flow” first became common in business management after World War II, but its use as a single compound “workflow” entered a new phase of rapid growth around 1990 with the development of computers systems to aid the design and coordination of the many interdependent activities needed to run a complex business (Dourish, 2001). Scientists began paying serious attention to computational workflows in the 2000s as they struggled to build robust, automated “pipelines” for processing data such as genome sequences (Lüdascher et al., 2006, 2009). More broadly, workflows have similarities with experimental protocols and are linked to efforts in the early twentieth century to “rationalize” the movements of factory workers in order to increase efficiency. A key achievement of numerical taxonomy in this regard was to individuate and make explicit a number of methodological problems faced by systematists and organize them into a linear sequence of procedural steps (Sternler, 2014; Sternler and Lidgard, 2014). Figure 1 shows an early workflow diagram provided by Robert R. Sokal and Peter H. A. Sneath in their 1963 textbook *Principles of Numerical Taxonomy* (Sokal and Sneath, 1963).

Approaching the history of systematics from the perspective of workflow is a powerful alternative to treating scientific theories as abstract conceptual systems. Indeed, systematists’ theories about how to classify or infer evolutionary trees did not merely or even primarily aim to encapsulate representational knowledge about nature. Instead, they were first and foremost tools for governing how biologists did their work. In other words, they served as conceptual instruments for specifying, evaluating, and justifying normative claims about how systematists should go about generating and organizing knowledge about the history and diversity of life (cf. Suchman, 1993; Winograd, 1994; Shipman and Marshall 1999; Dourish, 2001). Systematists also quickly identified key elements in the workflow as critical research problems, such as the development of improved techniques for character coding or mathematical measures of similarity between specimens.

By taking the entirety of the systematists’ workflow as our guide to their practices, rather than their most contentious theoretical disputes, we uncover a more comprehensive view of the steady development of mathematical methods in the field. In order to illustrate the limitations of the Systematics Wars narrative, we present a new analysis of Hull’s

A FLOW CHART OF NUMERICAL TAXONOMY

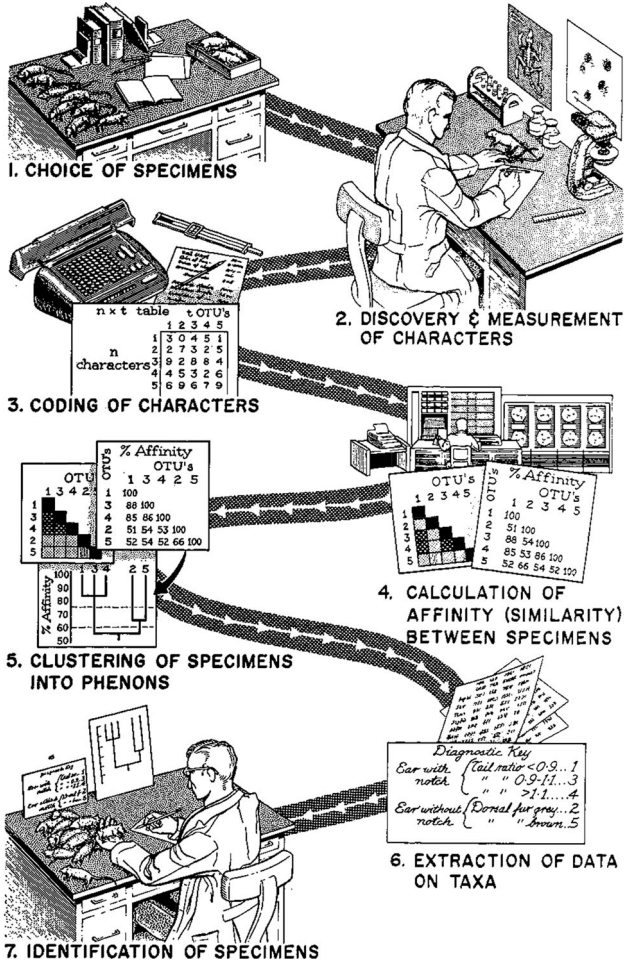


Figure 1. Diagram of the workflow for numerical taxonomy published in Sokal and Sneath's (1963) *Principles of Numerical Taxonomy*. Both cladistic and phenetic methods concerned themselves with all the steps identified here, although the most high profile debates centered on procedures between the coding of characters and the production of a dendrogram. Later innovations also introduced an iterative process to the workflow, so that the tree produced from one iteration would be used to produce a modified character matrix for a second iteration. See Section “[Workflow and Methodology](#)”

(1988) claim that two of the competing theories, phenetics and cladistics, formed independent historical lineages of ideas. This claim is pivotal to the empirical adequacy of Hull's broader argument about how science works, but it has received only limited attention in prior criticism (see Maynard-Smith, 1988; Farris, 1989; Craw, 1992; Wilkins,

1998; Hagen, 2001). Hull only examines the histories of the most contentious concepts for cladistics and phenetics, overlooking other cases in which cross-lineage mixture could and did occur more easily.

This result calls into question a number of assumptions contained within the Systematics Wars narrative that have led to a biased understanding of the history:

- (1) That it is obviously true that numerical taxonomy and cladistics were absolute mutually exclusive alternatives. Calling this assumption into question renders problematic the familiar claim that cladistics won and numerical taxonomy lost, since the two cannot be fully disentangled.
- (2) That studying the origins of concepts and their logical relationships provides an adequate empirical basis for explaining the development of methodology during this period. While important, the history of ideas becomes misleading when it is seduced by the drama of conflict into overlooking the very conditions that made the Systematics Wars possible: what did all parties to the debate take for granted as obvious? Why did some groups raise specific complaints but not others? What was the relative importance of structural differences in methodologies versus personal antagonisms in stirring the field to conflict? By undermining the total nature of the conflict between numerical taxonomy and cladistics, our results suggest alternative histories that raise different and new questions.
- (3) That tracking the fates of the “great men” of systematics tells us all we need to know about the reception of new methods into the field as a whole. As Hull put it, “If science were egalitarian, if the vast majority of scientists working in an area actually influence conceptual development in that area, then the recognition of conceptual historical entities would be a formidable task. Luckily for our purposes, everyone who studies science comes to just the opposite conclusion. A very few scientists at any one time account for the vast majority of change. Very little is lost by narrowing one’s attention to the contributions of the scientific elite” (Hull, 1982, p. 495). One reason these assumptions are especially dangerous in systematics is that their biases align to obscure alternatives: the highest-status figures in the field were also the most polarizing and the most forceful about theory and ideology.

To close, we turn to discuss how thinking in terms of workflows opens up a number of important but relatively unexplored topics related to the mathematization and computerization of systematics. In partic-

ular, we suggest several ways in which the history of systematics may hold distinctive insights for historians working on related issues in other fields of biology in the post-World War II era (Sepkoski and Ruse, 2009; Strasser, 2010; Leonelli and Ankeny, 2012; November, 2012; Sepkoski, 2012).

The Systematics Wars Narrative

David Hull originally coined the phrase “systematists at war” to refer to the aggressive, often personal battles waged between supporters of two methodologies, phenetics and cladistics, in the 1970s and 1980s (Hull, 1988). The term “Systematic Wars” in turn expresses a broader pattern in the history of systematics from around 1940 to the present: the apparent waxing and waning of several methodological theories, each claiming dominance over the field and attacking the perceived errors of its predecessors. In this section we briefly review this common view of the history. Table 1 summarizes some relevant terminology. Since there is sometimes dispute over what these terms mean and how they have changed over time (e.g., Williams and Ebach, 2009), we have included definitions from the glossaries of two textbooks published at about the same time (Kitching et al., 1998; Schuh, 2000).

The first contestant to plant its flag was the New Systematics (Huxley, 1940), which later became “evolutionary systematics” in the 1960s. Spearheaded by strong advocates such as ornithologist Ernst Mayr and paleontologist George Gaylord Simpson, this approach asserted the central importance of evolution, especially theories of speciation, for producing taxonomic classifications (Mayr, 1942, 1969; Simpson, 1961). Mayr, for example, argued that species were reproductively isolated populations produced by their divergence during a period of geographic separation. As a result, systematists had to study morphological variation across whole geographic ranges of populations in order to decide whether they formed discontinuous (non-interbreeding) units or whether they were still capable of exchanging genes at points of overlap (Mayr, 1942). In contrast with its competitors, evolutionary systematics has remained an openly “eclectic” approach in the sense that Mayr, for instance, sought to incorporate what he saw as the best of phenetic and cladistic methods within his overall viewpoint (Mayr, 1969).

Numerical taxonomy developed in the late 1950s in large part as a critical response to the New Systematics, arguing that reliance on

Table 1. Some key terminology in classification and phylogenetics.

Additive coding*	A method for representing <i>ordered multistate characters</i> as a <i>linked series of binary</i> characters. Cf. <i>non-additive coding</i>
Additive binary coding	A method of coding multistate characters that allows for representation of branching patterns through the use of multiple two-state variables
Character	A feature showing group-defining variation
Character state	One of the various conditions of a feature (character) observed across a group of taxa
Cladistics	Grouping by synapomorphy through the application of the parsimony criterion
Consensus tree	[The tree depicting] the collection of groups (components) that is contained exactly in all (most parsimonious) trees resulting from a phylogenetic analysis
Data matrix	Information in tabular form on characters for a set of taxa, with the rows representing the taxa and the columns representing the characters
Derived	Used in reference to character data for describing a relative condition, namely as opposed to primitive; the derived condition of a feature; apomorphic
Gap coding*	A method for recoding <i>continuous</i> characters (usually <i>morphometric</i> data) as <i>discrete</i> characters by the creation or recognition of <i>gaps</i>
Lineage	A terminal taxon or monophyletic group
Multistate character	A feature for which there are three or more conditions in a set of three or more taxa
Non-additive coding*	A method for representing <i>unordered multistate characters</i> as a <i>linked series of binary</i> characters. Cf. <i>additive coding</i>
Numerical taxonomy	The name originally attached to phenetics; the theory and practice of grouping by overall similarity with the attendant assumption of uniform rates of change; sometimes, any taxonomic approach that applies quantitative techniques
Parsimony	Simplicity of explanation; minimizing ad hoc hypotheses; the approach applied in cladistics whereby similarities are assumed to be homologous, in the absence of evidence to the contrary
Phenetics	The method(s) of classifying organisms whereby rank and relationship are determined on the basis of overall similarity (i.e., the sum of similarities and differences) and uniform rates of change are assumed
Phylogeny	The genealogical relationships among a set of taxa; sometimes, the process of evolutionary diversification
Taxon (taxa)	A grouping of organisms at any level in the systematic hierarchy
Tree	Generally, any branching diagram that specifies hierarchic relationships among taxa; sometimes, a branching diagram specifying ancestor–descendant relationships or patterns of speciation (after Nelson)
Synapomorphy	Shared, derived, group-defining trait
Systematics	The practice of recognizing taxa, determining hierarchic relationships among those taxa, and formally specifying those relationships; frequently used in a sense roughly equivalent to taxonomy
Taxonomy	The practice of recognizing and classifying organisms; frequently used in a sense equivalent to systematics

Table 1. continued

Type specimen	[Holotype] the unique specimen designated to represent the concept for a named species; the name bearer for a taxon of the species group
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All definitions save three are taken from the glossary of *Biological Systematics: Principles and Applications* (Schuh, 2000, pp. 217–226)

* Definitions from the glossary of *Cladistics: The Theory and Practice of Parsimony Analysis* (Kitching et al., 1998, pp. 199 and 207)

speculative claims about evolution leads to circular reasoning and undermines the empirical basis of classifications (Vernon, 1988, 2001). Although similar ways of thinking emerged independently in several places, we focus on the alliance eventually formed by Sokal and Sneath. Together, they published the extremely influential and controversial book *Principles of Numerical Taxonomy* in 1963, which advocated for basing classifications on estimates of the morphological similarity among populations (Sokal and Sneath, 1963). Given a varied collection of specimens, one was supposed to identify taxonomic units by finding clusters of similar organisms and progressively joining the clusters together to form higher levels in the taxonomic hierarchy (i.e., species, genera, families, etc.) While clustering based on similarity was the intellectual heart of numerical taxonomy, Sokal and Sneath also pursued a broader program of advancing numerical methods in systematics of all types. Camin and Sokal (1965), for example, contributed one of the first computational methods for inferring phylogenetic trees. For this reason, it is useful to reserve the term numerical taxonomy for this broader program and use another common name, “phenetics,” to refer to the narrower project of basing classifications on clustering using similarity measures.

In the 1970s phenetics found itself increasingly under attack from a new group, the phylogenetic systematists, who were also dubbed “cladists” by Mayr (1965). Cladists took their inspiration from the German entomologist Willi Hennig, who himself was drawing on deep German traditions in biology and philosophy that were little known to English-speaking systematists at the time (Rieppel, 2007, 2016; Williams and Ebach, 2008; Rieppel et al., 2012).¹ The driving force behind cladism was the recognition that evolutionarily related taxa could be grouped together based on sets of distinctive characters inherited from shared ancestors. Known as synapomorphies, these shared derived traits enabled cladists to build hierarchical classifications that reflected the

¹ See also Craw (1992) for a more global view of the origins and uptake of Hennig’s work.

temporal sequence of branches linking taxa in phylogenetic history. Although Sokal and Sneath sought to incorporate “numerical cladistics” under the big tent of numerical taxonomy, cladistics and phenetics did not end up coexisting peacefully. Staunch cladists such as James S. Farris and Mary Mickevich made forceful arguments in the mid-to-late 1970s that cladistic methods were better at achieving key goals of phenetics, such as robustness, than phenetic methods (Mickevich and Johnson, 1976; Farris, 1977).

Exactly what or who the name “pattern cladism” (or “transformed cladism”) designates is controversial, yet the idea of a split that emerged within cladism is now entrenched in the history itself (Rieppel, 2013). One problem is that this fourth camp was imputed by outsiders (Beatty, 1982; Hull, 1988) rather than announced and defended as such by its alleged members. The split within cladism supposedly reflected opposition by pattern cladists to using a priori evolutionary hypotheses in the construction of classifications, much as pheneticists had rejected the use of evolutionary theory in the New Systematics. Just as one could build a classification using phenetic similarity and then analyze it for correspondence to genealogical history, one could build a hierarchical tree using the parsimonious distribution of synapomorphies among taxonomic units and then analyze it in terms of evolutionary processes: “the pattern cladistic interpretation gave cladistics (and systematics in general) a chance to discover processes, thus highlighting the importance of uncovering patterns prior to invoking processes” (Williams and Ebach, 2008, p. 260). Because the name “pattern cladism” suffers from an especially high level of indeterminacy and disagreement, it would take us too far afield to describe its full contours here; instead, we direct the reader to (Beatty, 1982; Hull, 1988; Williams and Ebach, 2008; Vergara-Silva, 2009; Farris, 2012).

Although molecular phylogenetics began to develop at almost the same time as phenetics first gained attention, its rise to dominance in systematics had to wait until new technologies swamped the field with DNA sequences, starting in the late 1980s (Morgan, 1998; Hagen, 1999; Felsenstein, 2004; Strasser, 2011; Suárez-Díaz, 2013). Molecular data had the virtues of (eventually) being easy and cheap to acquire without deep expertise in the morphology or ecology of the taxa under study. Perhaps more importantly, biologists developed probabilistic models for processes of molecular evolution that enabled them to apply the full quantitative power of likelihood and Bayesian methods to phylogenetic inference. In many ways, molecular phylogenetics coexisted with the other theoretical approaches without being “of” them – its community

of researchers belonged as much to population genetics and molecular biology as to traditions within systematics. In this vein, the proper justification and scope of cladistic methods such as parsimony have remained a major point of contention between biologists using probabilistic models (e.g., Felsenstein, 1983) and those defending a falsificationist approach (e.g., Farris, 2008). The editors of the journal *Cladistics* have recently fanned the flames of this debate again by declaring that “phylogenetic data sets submitted to this journal should be analysed using parsimony” (The Editors, 2016, p. 1).

The Systematics Wars narrative succinctly captures two broad patterns of change in this time period. First, the value of evolutionary theory was a central point of contention (Hull, 2001). A second feature is a shift in emphasis over time away from taxonomy and toward phylogenetic inference (O’Hara, 1994; Felsenstein, 2004). For New Systematists such as Mayr, classification was an opportunity to study the process of speciation, and speciation was a central basis for naming and ranking taxonomic groups. As molecular phylogenetics and cladistics have matured, however, biologists who know little about taxonomy can now produce and use phylogenetic trees for many purposes without needing to go through the demanding process of naming new species or other taxa (cf. Pante et al., 2015).

Missing from this narrative is a clear sense of how systematists got from rarely using quantitative tools for classification or phylogenetics in the early twentieth century to mathematics being almost unavoidable today (Hagen, 2001, 2003). None of the camps distinguished themselves specifically by opposing the mathematization of systematics, although Williams and Ebach (2008) see the bulk of numerical methods as inconsistent with pattern cladism.² In fact, phenetics, cladistics, and molecular phylogenetics share certain key elements of their computational workflow in common, as we describe in more detail below (Hagen, 2001; Sterner, 2014). We use this common ground to argue that the progressive mathematization of systematics requires a more expansive historiographical approach than the Systematics Wars narrative.

The Competition-Drives-Progress Model

We begin by analyzing David Hull’s version of the Systematics Wars narrative as an exemplar of the competition-drives-progress model

² Also see Haber (2009) on the split between parsimony-based cladists and statistical phylogeneticists who used maximum likelihood or Bayesian inference methods.

(Hull, 1988). Hull went so far as to elevate the struggles among systematists into a general account of how science makes progress. He viewed scientific progress as an instance of evolutionary selection driven by competition between small, largely independent groups of closely allied researchers. In this way, Hull treated cultural evolution and biological evolution as forms of the same general process. Moreover, he sought to justify why the aggressive, personal attacks made across the warring camps were desirable because of how they accelerated scientific progress.

On Hull's view, selection is a general historical process – at work in both cultural and biological evolution – that acts on lineages composed of interactors and replicators. Interactors are individuals with an integrated identity over time, such as organisms or scientists, while replicators are units of information that are transmitted between interactors using some copying process, such as DNA replication or the communication of beliefs using printed research articles. According to Hull, replicators and interactors are logical individuals, i.e., spatiotemporally bounded historical objects without defining essences. Therefore, just as the organisms in a biological species cannot be demarcated by some unchanging, essential property of their respective genomes, there are no fixed, essential meanings to concepts. That is, a concept's defining properties can vary across an existing population and across generations in the lineage as well. Nonetheless, replication requires some degree of similarity between ancestor and descendant uses of a concept.

Interactors typically bundle together replicators and provide them with an interface to the environment. In some cases, replicators may be nested into a hierarchy of interactors: genes are contained within cells that exist inside organisms that are members of social groups. Similarly, concepts are nested within theories that are held by scientists who cooperate in social groups. Each concrete instance where a scientist uses a theory or one of its component parts contributes to the replicator's "inclusive conceptual fitness," so what happens to the interactors as a result of their engagement with the environment determines the fitness (i.e., survival and reproduction in a rough evolutionary sense) of the replicators. Without ongoing use, the lineage of replicators dies out – if two biologists independently came up with the concept of "operational taxonomic units," for instance, we would have two distinct conceptual lineages no matter how similar the meanings were, so long as each biologist remained within a separate tradition of use. The way that scientists give credit and attention to other scientists for their ideas is thus an essential mechanism for translating scientists' experiences with

using these ideas into fitness consequences. In other words, the evolutionary fate of a concept lineage depends on the attention and influence received by the scientists who carry and propagate it.

When Hull applies this account of selection to the history of systematics, he construes competing theories such as phenetics and cladistics as historical lineages composed of concepts and beliefs. “Phenetics,” for example, designates an historical individual that evolves over time rather than a kind of theory defined by a set of fixed properties. Thus molecular phylogenetics may use inference methods based on similarity measures between specimens, but uses of similarity methods do not necessarily count as phenetic unless the methods are historical descendants of conceptual lineages existing in phenetics at an earlier time. Without this historical link, the rise of molecular phylogenetics cannot contribute to the fitness of conceptual lineages in phenetic theory.

In addition, Hull argues that systematists in this time period are polarized into non-overlapping social groups, one corresponding to each competing theory lineage. Each social group works cooperatively to develop its shared theory, increase the recognition and influence given to its members, and criticize the work of other camps. The relative dominance of a group then reflects its ability to acquire credit for its work and influence the practices of other systematists. There is no logical requirement that concept lineages align with social groups in a field, but the organization of a field into competing social groups increases the potential for selection. “One contention of the present work is that the small research groups that periodically crop up are the most important focus of rapid, though usually abortive, change in science” (Hull, 1988, p. 112).

Hull’s construal offers a nuanced version of the competition-drives-progress model in that it recognizes the importance of internal cooperation within competing social groups. Nonetheless, competition is the primary force responsible for progress in Hull’s view. Addressing the fierce and often personal conflicts between systematists, Hull argues “not only that these scientists are behaving the way that all innovative scientists behave but also that this sort of behavior actually facilitates scientific development” (Hull, 1988, p. 26). The precise issue at hand, then, is whether this link between competition and progress is sufficient for the case of systematics. If yes, then it validates the adequacy of the Systematics Wars narrative. If not, then we have opened the door to alternative historical approaches.

Testing the Competition-Drives-Progress Model

As Hull acknowledged in a precursor paper to his book, “Real complications [for his account] are produced by a moderate amount of interlineage borrowing. It is too extensive to ignore and yet not so extensive that it simplifies matters by merging the two systems into one” (Hull, 1982, p. 497). Unfortunately, Hull never provides direct, organized evidence against this possibility, nor does he clearly specify what standards an adequate test would have to meet. This oversight shows up in two key places: defining what counts as “too extensive to ignore” and how to individuate “conceptual systems.”

First, though, we should note that Hull’s views have already received serious criticism along multiple dimensions. One issue is that he focuses on the actions of the researchers with the highest social status in the field and ignores factors affecting graduate students along with scientists not at top-tier institutions (Allen, 1991). Hull’s attempt to unite science and biology under the same model of selection processes has also met stiff resistance (Grantham, 1994, 2000; Sterelny, 1994; but see Wilkins, 1998; Renzi and Napolitano, 2011). Concepts-as-replicators are not responsible for building scientists-as-interactors in the way that genes are responsible for building organisms, for example. There is also a persistent gap between Hull’s abstract mechanism for science and his ability to describe its action and effects in his empirical case studies (Kitcher, 1988; Latour, 1990). Using evolution as a metaphor for describing cultural change (understood broadly to include scientific inquiry) is often illuminating as a tool for seeing historical events in a new way, but the comparison rarely advances to literal equivalence. As a result, the epistemic tools scientists have developed for evolutionary theory – things like quantitative models, type specimens, comparative methods, and so on – fail to carry over to cultural processes.

None of these criticisms, however, delve seriously into the claim that phenetic and cladistic theories formed independent lineages. Everyone agrees that prominent systematists fought bitterly along partisan lines during this time period, of course, but are the social contours of these fights enough to explain all the important methodological changes in those decades?

Since Hull does not explicitly state what he means by interlineage borrowing being “too extensive to ignore,” we suggest that hybridization meets this standard for a problem when concepts introduced to solve the problem in the context of one theory become commonly used by other systematists to solve the problem in the context of another theory. In

addition, the significance of hybridization is modulated by the importance of the problem: its necessity for the completion of the workflow, or more broadly, how regularly systematists found it relevant to their aims. The overall historical importance of hybridization will then be a function of the importance and number of methodological problems that exhibit extensive crossing over of ideas, regardless of whether the problems figure in disputes between adherents of rival theories.

In order to measure the extent of interlineage borrowing, we need some principled way of determining which concept lineages fall within each theory. Hull introduced the idea of a “conceptual type specimen” in order to address this issue:

One way to individuate conceptual systems in the face of all this heterogeneity is by selecting a particular token of a particular tenet at a moment in time as a conceptual type specimen, e.g. Nelson’s 1971 claim that the principle of dichotomy is essential to Hennig’s phylogenetics. In doing so, nothing is implied about the importance of this tenet, let alone whether it is or was actually essential... Just as ‘Nelson in 1971’ can fix the reference for ‘the American Museum cladists,’ ‘Nelson’s specification of dichotomy as essential in 1971’ can be used to fix the reference for ‘American Museum cladism’ (Hull, 1988, p. 511).

Similarly, Hull also stated, “If one wants to individuate a conceptual system, all one has to do is to select a particular token of a particular tenet and trace out its conceptual relations, both inferential and genealogical. When we trace out inferential relations, the only ones that count are those that were actually made” (Hull, 1988, p. 509).

As Hull indicates, simply picking one type specimen for “phenetics” and a different type specimen for “cladistics” is not sufficient to guarantee that these names designate different conceptual systems. In fact, the type method presupposes that there are distinct, cohesive individuals to pick out in the first place: “*Assuming that conceptual systems are sufficiently discrete to be manageable*, the question then arises how they are to be picked out and named. Once again, the type specimen method seems up to the task” (Hull, 1982, p. 496, emphasis added).

It is essential, then, that we actually “trace out” the causal connections between conceptual lineages associated with the type specimens to see if each is part of a distinct, cohesive whole. In order to do this, we need guidance from some theoretical notion of cohesion or integration appropriate to conceptual systems (Abrantes and El-Hani, 2009). Among other things, we need to know which conceptual relations are

relevant, since there are all sorts of heterogeneous causal connections between concept lineages, such as co-occurrence in sentences appearing in published papers or causing a scientist to reach a new insight.

Hull never fully specifies the appropriate sense of cohesion for conceptual systems. In fact, he recognizes this question as a major, open challenge for his work: “Specifying the relations that integrate distinct replication sequences into conceptual systems and distinguish different conceptual systems from each other remains the chief piece of unfinished business of the ‘new philosophy of science’” (Hull, 1982, p. 494). Nonetheless, cohesion clearly involves concepts that participate in chains of inference together, although this is neither a necessary or sufficient condition. “The relations that integrate the elements of a conceptual system into a system include but cannot be limited just to inferential relations” (Hull, 1982, p. 493).³

It should be clear at this point that Hull’s claim against moderate hybridization remains unproven because he has not provided a clear specification of how to test the claim that phenetics and cladistics are independent individuals or a standard of proof such a test would have to meet. We argue that the workflow for classification and phylogenetic inference we describe below provides a principled and independent basis for circumscribing the content of methodological theories that is consistent with Hull’s criteria. While Hull focused his attention on concepts involved in stages of the workflow where phenetic and cladistic theories diverged most sharply and contentiously, phenetic and cladistic theories in fact claimed authority over the entirety of the workflow. In cases where the proper procedure for a task was not directly and wholly derived from phenetic or cladistic theory, these theories still typically placed constraints on which procedures were acceptable. On this basis, we can recognize a conceptual lineage as part of a methodological theory if we observe systematists using tokens of the concept lineage to define or regulate procedures in the workflow.

³ For purposes of comparison, here is a related view from a paper by Robert Richards that Hull cites in his book: “The proper analogue of species is, I believe, the conceptual system, which may be a system of theoretical concepts, methodological prescriptions, or general aims. The gene pool constituting such a species is, as it were, the theory’s individual ideas, which are united into genotypes or genomic individuals by the bonds of logical compatibility and implication and the ties of empirical relevance” (Richards, 1981, pp. 57–58).

Workflow and Methodology

Tracking the workflow of classification and phylogenetic inference over time provides an alternative basis for organizing the history of systematics (Griesemer, 2007; Sterner and Lidgard, 2014). It gives us a more principled basis for enumerating and tracking methodological debates, which in turns allows us to critically examine the adequacy of the competition-drives-progress model. Most importantly, we will show that there are problems of central importance to the workflow, though not to the dominance battles, which exhibit hybridization of conceptual lineages across theories.

The shared, underlying aim of all the competing theories we discussed above was to regulate and standardize how systematists produced classifications and phylogenetic trees. From this perspective, the value of each theory originated in how it provided tools for tracking what systematists did and evaluating the results. For example, Mayr brought his theory of speciation to bear on many aspects of classification: in order to detect patterns of divergence produced by geographic isolation, systematists must track the variation of traits from many specimens sampled in multiple regions, and morphological difference served as a proxy for the likelihood of reproductive isolation (Mayr, 1942). Classifying a population as a species, therefore, required multiple strictures on how systematists collected specimens, selected traits for study, and assigned ranks to taxa, among other tasks.

Sokal and Sneath located these strictures in a recommended sequence of operations for the production of classifications (Sokal and Sneath, 1963; Sneath and Sokal, 1973). The foundation of their linearization of the workflow (Figure 1) was their insertion of automated mathematical procedures into the middle of the classification process. This transformation is clearly signaled in steps 3–5 of Figure 1. Prior to step 3, the taxonomist starts from qualitative knowledge about the specimens and characters that will serve as input to the classification. In order for the mathematical procedures to be applied, this qualitative knowledge must be translated into a numerical matrix according to guidelines imposed by the relevant methodological theory.

With the character matrix in hand, a computer program operates on the data to calculate the similarity or difference between each pair of specimens according to their character values. These “distances” between specimens are then used to cluster specimens into groups, producing the branching tree diagram shown in step 5. If the methods applied in the workflow were successful, then the way that specimens

clustered together should reflect overall relationships of morphology between the actual populations of organisms from which these specimens came. The binary tree that was output by the computational procedures could therefore be used to perform various tasks, such as ranking taxa in the Linnaean classification system or producing diagnostic keys.

Later developments complicated the linearity of the workflow by introducing iterative procedures as well as the choice of procedures as new cladistic methods became available. A number of systematists sought to introduce a limited form of non-linearity into the workflow process, typically in the context of character weighting where the output of the workflow is modified and used as input for another iteration (Farris, 1969; Legendre, 1975; Hogeweg, 1976; Wheeler, 1986). Allowing feedback between results, data, and procedures reintroduces some of the flexibility that earlier systematists believed to be crucial when they described classification as an art dependent on expert judgment (Hagen, 2001; Sterner, 2014). However, the sequence of calculations in the numerical workflow process remained explicit and standardized in a way that earlier practices were not.

Cladistic methods also expanded the possibilities of the workflow by introducing a considerable number of new types of procedures and hence pathways of analysis (e.g., Camin and Sokal, 1965; Kluge and Farris, 1969; Le Quesne, 1982). However, these procedures did not alter key structural features of the original workflow: specimen and character selection still led to the production of a character matrix, which was then processed into a branching binary tree, which in turn was used as the basis for various other activities. For our purposes here, we will bracket the historical question of how precisely this basic workflow structure came to be shared across different numerical methodologies – it is more a matter of historical coincidence and contingency than a necessity. Either way, we can use the workflow as a reasonably comprehensive framework for representing the development of methodology for classification and phylogenetics after the introduction of numerical taxonomy.

Segmentation of classification and phylogenetic inference into a temporal sequence of discrete tasks provides a new way of partitioning the published methodological literature. Instead of situating research articles according to their support or opposition to the competing theories, we can categorize articles by the methodological problems they address. Methodological problems are individuated by their place in the workflow: given some step in the workflow, a systematist must decide

how to manipulate the output of the prior step in order to produce the correct input for the following task. This decision becomes subject to methodology when it has implications for the quality of the final output. Examples of methodological problems specific to phenetics are the choice of a similarity/distance measure and the choice of a clustering algorithm, while examples from cladistics include how to polarize characters as ancestral or derived, how to measure character compatibility, and the choice of method for inferring a cladogram (e.g., Farris's (1970) Wagner tree method or Camin and Sokal's (1965) parsimony approach). Methodological problems that are common to both camps include: which characters to select, how to code characters into the matrix, how to weight characters, how to evaluate the quality of a dendrogram,⁴ how to produce consensus trees, and how to produce diagnostic keys.⁵ Each of these methodological problems has an extended history of multiple published research articles devoted to finding the best solution to the corresponding procedural decision.

Evidence for Hybridization

We now turn to examine the history of two methodological problems, both of which are located in parts of the workflow shared by phenetic and cladistic methods. The first problem, character coding, lies at the start of the workflow prior to the character matrix. The second case, consensus trees, lies at the end of the workflow after the dendrogram is generated, where systematists sometimes seek to compare multiple dendrograms. Such multiples might result from a single analysis (e.g., equally parsimonious trees with different branch configurations) or from analyses conducted with different data or methods. Both problems are of great practical importance to classification and phylogenetic inference. Character coding is the essential step where biologists translate trait characteristics or measurements for individual specimens into computer-readable data, and consensus trees provide the most common and basic approach to comparing multiple trees. Although neither problem became the locus for high-stakes debates between phenetics and cladistics, we'll see below that leading theorists from both

⁴ A dendrogram is a minimal term for a binary branching tree with specimens at its tips that leaves unspecified what meaning we assign to each branching event, internal nodes, and branch lengths.

⁵ To be clear, the fact that competing theories share a problem does not imply any agreement about solutions.

sides spent considerable energy developing new solutions for both methods.

Character Coding

The problem of character coding addresses the task of translating character measurements into a numerical format acceptable to downstream computation. For example, we might translate the presence or absence of a horn on the head of an animal into an entry of ‘1’ or ‘0’ respectively. A more complex case would be a trait that has multiple, qualitatively distinct states, such as the color of petals in a flower. White, pink, red, or blue petals are not strictly ordered states. We might say that pink is intermediary to white and red (especially if the trait is Mendelian), but there is no way to place blue on that spectrum. If we arbitrarily assign the values of 0, 1, 2, and 3 to the four colors as listed, then some computer algorithms treat this as implying that blue and white are more different than blue and red because the former pair are further apart in numerical order. We can evade this particular issue by translating the single character into four characters (white or not, pink or not, etc.), but this can end up adding more weight to petal color in the overall data set because it now corresponds to four traits instead of one. Bad character coding can turn an otherwise good data set into garbage, and that means “garbage in, garbage out” for the rest of the calculation (Mishler, 2005).

Many of the most common techniques for character coding were already described in Sokal and Sneath’s (1963) *Principles of Numerical Taxonomy*, including multistate and additive binary coding along with character normalization. The published literature on coding is largely fragmented through the 1960s and 1970s, focusing on specialized issues with particular coding techniques. Starting in the mid-1970s, a stream of new research emerged on the “gap coding” problem of transforming continuously varying data into discrete states (Archie, 1985; De Bivort et al., 2010). Given a frequency distribution of trait values on a continuous variable (e.g., length or height), this new work sought to use statistical reasoning to decide when clumps of values could be treated as discrete units (Almeida and Bisby, 1984; Archie, 1985). At the same time, gap coding received harsh criticism for introducing artifacts into the data and lacking a sound basis in biology (Felsenstein, 1988).

Even as the Systematics Wars reached their peak in the 1980s, phenetics and cladistics continued to share techniques for complex cases, including additive coding and gap coding (Sokal and Sneath, 1963;

Archie, 1985; Pimentel and Riggins, 1987). We can see evidence for this hybridization on two levels: theoretical developments and application of theories to producing actual classifications and phylogenies. On the theoretical level, it's clear that several coding methods readily crossed among theories. For example, two pivotal papers in the development of cladistics cited Sokal and Sneath (1963) as an influence or direct source for additive and non-additive coding methods: Farris et al.'s (1970) "A Numerical Approach to Phylogenetic Systematics" and Mickevich and Johnson's (1976) "Congruence Between Morphological and Allozyme Data in Evolutionary Inference and Character Evolution." Farris et al. directly cite (Sokal and Sneath, 1963) for their non-additive coding technique, and they state that "our 'additive coding' is equivalent to that of Sokal and Sneath except for the interpretation of the ordering relation used to define the binary coding" (1970, p. 181). Mickevich and Johnson also straightforwardly cite Sokal and Sneath for additive coding: "The codes for each character were transformed to additive binary coding (Sokal and Sneath, 1963)" (Mickevich and Johnson, 1976).

The case of gap coding is particularly interesting because authors often explicitly treat the method as neutral to phenetics and cladistics. In a highly influential review, for example, James W. Archie wrote that a key aim of his paper was "to further develop two new approaches for coding information from variable characters into a form useful for either phylogenetic (cladistic) or phenetic data analysis" (Archie, 1985, p. 327). Another contributor to gap coding, Frank A. Bisby (Almeida and Bisby, 1984), identified with the taximetric tradition that aligned with the more inclusive sense of numerical taxonomy rather than phenetics in particular (Bisby, 1970). In another case, Nick Goldman published a paper in the journal *Cladistics* about the use of Archie's (1985) methods for cladistic inference but wrote in the acknowledgments that he "should like to thank ... Bob Cadwalladr for encouraging me to remove all occurrences of the word 'cladistics' from the paper" (Goldman, 1988, p. 69).⁶

Moving to consider applications of coding methods, we can find multiple examples of all three coding techniques being used for both phenetic and cladistic analyses. We collected papers that applied these coding methods to real morphological data (not fictional or simulated)

⁶ Technically, he does use it once in the main text of the paper: In the introduction he writes, "If quantitative data are to be used in cladistic analysis, recently questioned by Pimentel and Riggins (1987) and Cranston and Humphries (1988), then Archie's (1985) method is generally applicable" (Goldman, 1988, p. 59).

in order to produce classifications or phylogenies.⁷ We found 55 papers using additive coding, 34 using non-additive coding, and 41 using gap coding. Additive coding was the most balanced between phenetics and cladistics, but all three sets included at least five instances of each method. Note, however, that the samples are not representative since the proportion of papers using phenetics or cladistics changes dramatically over time,⁸ so it would be a mistake to draw conclusions about the relative frequency of use. Similarly, the sample is not exhaustive because authors are not always careful to describe their coding techniques and moreover usually do so only in the main texts, which therefore requires the paper to be accessible to full-text search. Nonetheless, these results provide us with clear evidence for the adoption of each technique within both phenetic and cladistic methodologies. In particular, it is important to emphasize that the initial introduction of a technique in the context of one theory (e.g., additive coding in phenetics or gap coding in cladistics) did not prevent the technique from crossing over into the other theory.

Consensus Trees

Meanwhile, at the other end of the workflow, systematists were grappling with how to reconcile multiple conflicting dendrograms. These conflicts might arise from a cladistic analysis resulting in several or many equally parsimonious trees or from using different data sets or different analytical procedures (e.g., measures of similarity or coding methods). Either way, taxonomists had to address the disagreements in order to produce a final, best tree. Furthermore, measuring how much two or more trees disagreed was important to evaluating the stability of computational methods and settling whether phenetics or cladistics offered better results in this regard.

We can split this problem of comparing trees into two parts: the consensus tree problem that focuses on finding a single tree that best embodies the structural information shared by a set of input trees and

⁷ We searched for papers using Google Scholar (advanced search) and JSTOR (advanced search) and by looking at reference lists of other papers cited in our results. We performed the searches in May 2016 with the following search terms: “additive coding”, “additive” AND “coding”, “nonadditive coding”, “non-additive coding”, “nonadditive” AND “coding”, “non-additive” AND “coding”, “gap coding”, and “gap” AND “coding”. Full tables with evidentiary data for numbers of papers reported in this section are available from an online repository, <https://repository.asu.edu/collections/282>.

⁸ See Hull’s study of papers in *Systematic Zoology* for an example Hull (1988).

the problem of measuring congruence, which aims to produce a numerical index for the similarity or distance between trees. To our knowledge, Edward N. Adams III (1972) was the first to pose and provide solutions to the problem of consensus trees in systematics. The issue then lay dormant in the published literature for several years until James B. McGuire published two articles linking the problem of choosing a consensus tree to Arrow's famous impossibility theorem in economics, which provides a set of basic conditions under which it is impossible to aggregate individual preferences to arrive at a single optimal choice (McGuire and Thompson, 1978; McGuire, 1979). This formal analogy provided an initial set of general principles for evaluating algorithms for consensus trees.

Attention to the problem grew rapidly starting in 1979, inspired in part by the ongoing debate between pheneticists and cladists over measuring the stability of their trees (Hull, 1988). As William Day wrote in 1985, "Subsequently [to (Adams, 1972)] there has been an amazing proliferation of consensus methods... a proliferation stimulated by confusions, disagreements, and uncertainties concerning what consensus methods depict and what consensus indices measure" (Day, 1985, p. 215). Of the new methods systematists developed, "the most commonly used is strict consensus, mainly on the grounds that it is the most conservative" (Barrett et al., 1991, p. 487), while Adams' consensus method has also been popular (Wilkinson, 1994). In brief, the strict consensus method looks at trees as nested hierarchies of sets, and it selects only those nested sets that are present in all the trees considered, while the Adams method looks at trees as a set of overlapping three-node branchings, and it selects only those branchings shared by all input trees (Adams, 1986).

As with the character coding problem, hybridization occurred at both the levels of theory and application for consensus trees. The contentious history of strict consensus trees exemplifies this point. Sokal and Rohlf introduced the name "strict consensus tree" (Sokal and Rohlf, 1981, p. 312) in an attempt to clarify the methods used by another paper in the larger debate over whether phenetics or cladistics led to more stable dendrograms: "Schuh and Polhemus (1980, p. 13) imply that the consensus trees featured in their Figure 24 are Adams' (1972) consensus trees. This is not so. The trees given are what we prefer to call strict consensus trees, since they consist of just those subsets of OTU's ('informative components,' Nelson, 1979) that are common to both trees being compared" (Sokal and Rohlf, 1981, p. 312).

This quote is quite rich in implications for tracing out causal connections between concept tokens. Adams originally positioned his 1972 paper as addressing the results of phenetic methods developed in numerical taxonomy.⁹ Schuh and Polhemus, writing in favor of cladistics, then say that they applied one of Adams' algorithms to compare the stability of results produced by phenetic and cladistic methods. Sokal and Sneath then restate what they take Schuh and Polhemus to have done, coining the term "strict consensus." In quick succession, Schuh and Farris published a new paper (Schuh and Farris, 1981) where they substitute the name "Nelson trees" for strict consensus trees based on the methods laid out by (Nelson, 1979), which Sokal and Sneath also cited (but not for the method itself). As summarized by Nixon and Carpenter (1996, p. 306), "Subsequently, cladists commonly used the term Nelson consensus tree, proposed by the cladists Schuh and Farris, rather than the term strict consensus tree, which had been proposed by pheneticists. But the latter term also came into common use, and both were used interchangeably."¹⁰ Moreover, Mickevich and Norman Platnick later recommended the use of Adams trees over Nelson trees: "Similarly, for a consensus estimate, the best fit criterion requires us to choose a method which combines all, rather than some, of the taxonomic statements found in common; hence, the Adams consensus can be preferred over a Nelson consensus" (Mickevich and Platnick, 1989, p. 46). We can therefore see crossing-over of concepts at several points: from Adams to Schuh and Polhemus, from them to Sokal and Sneath, and among the understandings of systematists in the years since the split between strict and Nelson trees.¹¹

Turning to consider applications of Adams trees more broadly, we collected 52 papers applying Adams consensus methods to real morphological data.¹² We found seven papers using Adams' methods in

⁹ Strictly speaking, 1972 is too early for Adams to have chosen between phenetics and cladistics as (putatively) distinct conceptual systems because cladistics had yet to fully emerge at that point. However, the point remains that his methods were originally introduced in the context of phenetic theory and then later crossed over to be used in cladistics—a type of causal connection between concept tokens that Hull explicitly recognizes as legitimate.

¹⁰ Also see Nixon and Carpenter for a discussion of further debates among cladists about whether the any of the methods Nelson proposed in his 1979 paper are actually equivalent to strict consensus.

¹¹ One could also argue that this exercise is a *reductio ad absurdum* of Hull's use of type specimens as a way of individuating conceptual systems.

¹² We used Google Scholar (advanced search) for the phrase "adams consensus" and JSTOR (advanced search) for the terms "adams consensus" and "adams" AND "consensus" in June 2016.

phenetic analyses, and fifty papers used them in cladistic analyses. Again, these numbers should not be used to estimate relative frequencies of use by each theory, but they demonstrate their multiple uses in both contexts.

As an aside, it's interesting to point out that many of the contributions to consensus tree methods came from mathematicians or computer scientists who were outsiders to the fight between phenetics and cladistics. Adams published his first paper while located in a computer science department, for example, while another major class of methods (majority-rule consensus) was introduced by two researchers working in the mathematics department at Bowling Green State University (McMorris and Neumann, 1983). This points to interesting cross-disciplinary interactions among systematists and other disciplines that we would miss by tracking only the most elite and polarizing of systematists.

Summary

These examples exhibit sufficient hybridization to undermine the independence Hull posits between theory lineages. We presented evidence from two important methodological problems on two different levels: theoretical innovation and application to real data. In both cases, the published literature shows hybridization occurring in multiple cases for multiple solutions to each problem. More broadly, the examples also show that systematists made methodological progress in ways that depended on positive sharing of ideas between otherwise polarized social groups. If one chose the first appearance of any of the methods we discussed as a type specimen, one would find that phenetics and cladistics were not distinct theories. There is enough moderate inter-lineage borrowing to pose “real complications” for Hull’s account of phenetics and cladistics as independent historical individuals competing for dominance.

Seeing Systematics Anew: Mathematization as a New Problem Agenda

Recognizing and tracing the history of shared elements in the computational workflows of phenetic and cladistic theories has proved to be crucial for uncovering the constraints of the conflict- and theory-centric Systematics Wars narrative. Our goal in this section is to expand on this result to raise new questions for future research in the history of systematics that will advance its importance to the history of biology and

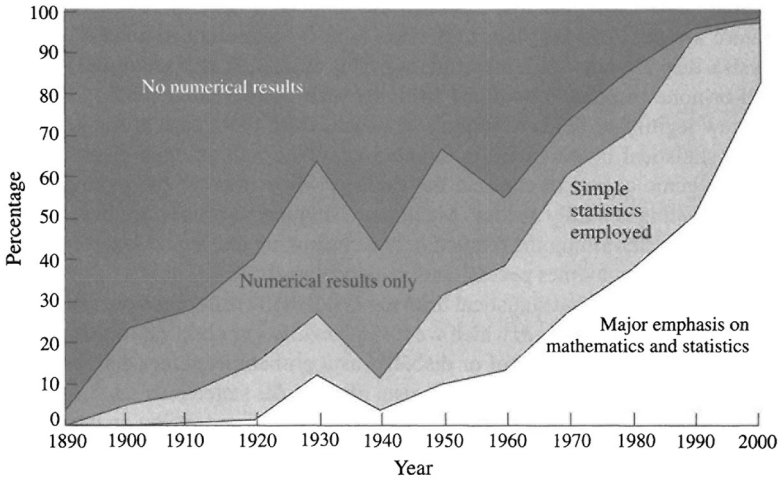


FIGURE 1.1 Proportions of articles involving numerical and statistical work in decennial issues of *The American Naturalist*.

Figure 2. A quantitative survey by Sokal and Rohlf (2012) of numerical and statistical methods in decennial issues of *The American Naturalist*. Unfortunately no definitions are provided for the classificatory categories they used

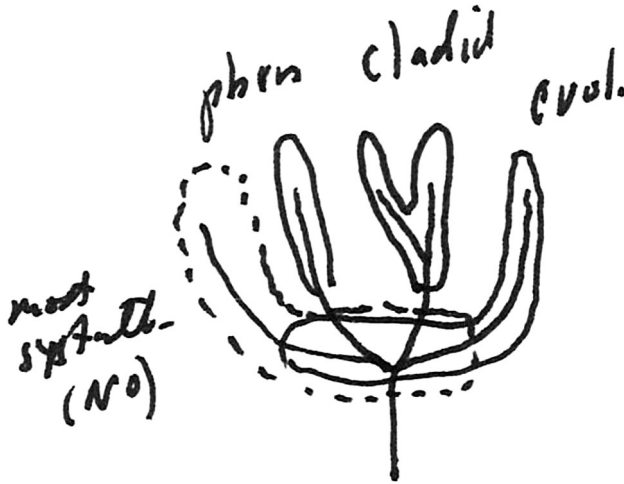


Figure 3. Marginalia from David Hull's personal copy of (Scott-Ram, 1990). The figure depicts the three major methodological theories of the 1960s through 1980s: phenetics ("phen"), cladistics ("cladist"), and evolutionary systematics ("evol."). Hull then raises and rejects the idea that most systematists took an entirely different path

of mathematization more broadly. We describe a conceptual framework for articulating and comparing historical cases of mathematization and use the framework to connect the history of systematics to parallel

transformations in other fields in the life sciences at the same time. The framework also enables us to address broader questions about how one should approach the mathematization of science beyond systematics.

We characterize mathematization as “making math indispensable,” a slogan that is not meant as a definition in the sense of necessary and sufficient conditions (Sternier and Lidgard, 2014). Rather, the slogan provides an abstract template that must be interpreted within a particular historical situation in order to specify a fully concrete meaning for mathematization. In other words, the point of the slogan is to provoke a common set of questions, and its value lies precisely in the recurring structure of the issues it raises across cases. For example:

- What is being mathematized?
- Who makes math indispensable?
- When and where does it become indispensable?
- Indispensable for what?
- What does it mean to be indispensable?
- What sort of work is involved in making math indispensable?
- What is “math”?
- How is math distinct from whatever is being mathematized?¹³

Despite its abstractness, the framework is not empty of content. Most importantly, it emphasizes how mathematization is an inherently normative and institutional activity by requiring us to make explicit the work that particular people have to do to change pre-existing practices. An essential feature of making math indispensable is that it requires changing how people judge success and failure in their own work. With this framework in hand, we can consider important aspects of mathematization in systematics that raise new historical questions about the field.

When and where does math become indispensable? At this point, we still have only limited, coarse-grained information about when and where mathematical methods spread into subfields of systematics (Sneath and Sokal, 1973; Duncan and Baum, 1981; Goodfellow et al., 1985; Hull, 1988). Figure 2 breaks down the use of mathematics into several categories based on a survey of *The American Naturalist* over 100 years (Sokal and Rohlf, 2012).¹⁴ Would a similar analysis for

¹³ The process of mathematization can also lead to changes in the meaning of mathematics, so math is not generally something isolated and immune to influence.

¹⁴ Unfortunately, Sokal and Rohlf do not give explicit definitions of the categories they use so the figure can only provide the broadest of outlines.

Systematic Zoology, *Taxon*, or the *Journal of General Microbiology* also show consistent growth in the use of math after 1940?

At stake in studying the reception of mathematical methods is another major tenet of Hull's theory-centric approach. "A very few scientists at any one time account for the vast majority of change. Very little is lost by narrowing one's attention to the contributions of the scientific elite" (Hull, 1982, p. 496). In other words, Hull expects that the "masses" more or less track the elite over time: "I argue that in the early stages of conceptual change, science exhibits the demic structure described by Wright. Later, as the views involved become more widely assimilated, Fisherian mass selection takes over" (Hull, 1988, p. 231). Figure 3 illustrates the question with a piece of marginalia written by Hull in the front pages of his copy of Scott-Ram (1990).

Another key aspect of the reception of mathematical methods is the importance of scientists' material situation, including the availability of key resources such as computers. We know very little about the ways systematists propagated knowledge about how to use computational tools, such as common practices for packaging and distributing computer software. One starting point is the journal *Kansas Geological Survey Computer Contribution*, which offered a venue for publishing descriptions of algorithms and actual computer code along with a clearinghouse for purchasing scientists' software on magnetic computer tapes. In addition, the quality of these resources, along with the availability of computers to run the code on, may have had a substantive impact on the early popularity and perception of various procedures for classification and phylogenetics.

What does it mean to be indispensable? With the publication of *Principles of Numerical Taxonomy*, Sokal and Sneath (1963) initiated a contentious and still ongoing debate in the field about the relative epistemic value of mechanical objectivity (in this case, computational reasoning) and trained judgment (implicit expert knowledge about taxa).¹⁵ As a result, they and other systematists advocating for mathematization put the very meaning of a "good" classification or phylogeny up for debate (Sterner and Lidgard, 2014). The history of methodology in the field is therefore ripe for treatment from the perspective of historical epistemology.

For example, a growing body of work has explored how logical positivism provided crucial conceptual resources and authority to the

¹⁵ See Daston and Galison (2007) for discussion of mechanical objectivity and trained judgment. Also see Suárez-Díaz and Anaya-Muñoz (2008) about objectivity in molecular phylogenetics.

articulation of new logics of classification (Vernon, 1988; Rieppel, 2007, 2009, 2016; Nicholson and Gawne, 2013; though see Cain, 2000). Sneath, for instance, took inspiration from John Stuart Lennox Gilmour's work on taxonomic philosophy, and Gilmour drew explicitly from logical positivism in formulating his view of concepts and scientific reasoning (Gilmour, 1940; Vernon, 1988), though little has been written on Gilmour's contribution in this regard (but see Varma, 2013). Perhaps more surprising is the influence that logical positivism had on Hennig, including Carnap's phenomenology and Woodger's set-theoretic axioms for biology (Rieppel, 2006, 2007, 2009, 2011, 2016; Nicholson and Gawne, 2013). There is also, of course, Karl Popper – a critic of the Vienna Circle who nonetheless shared important ideas in common with the logical positivists – who had a lasting influence on phylogenetic and pattern cladism (Rieppel, 2003; Helfenbein and DeSalle, 2005; Vergara-Silva, 2009). This line of historical inquiry has the potential to force a re-estimation of the historical relationship between logical positivism and biology and perhaps rehabilitate Woodger's reputation as an influential philosopher of biology (Hofer, 2013).

What is being mathematized? We can distinguish two general and historically recurring answers to this question: the things that people do (their practices), and what those activities are about. As an example of the second category, historian Alexandre Koyré has argued that Galileo's discovery of the law of uniform acceleration for falling bodies depended on his first adopting the worldview that “nature is mathematical” (Koyré, 1978). By contrast, numerical taxonomists were primarily oriented toward changing how systematists reason rather than advancing a mathematical theory of species and speciation.

In order to further unpack the worldview that “nature is mathematical,” we can distinguish two forms the claim may take. On the one hand, it may mean that natural phenomena are best defined as following a real mathematical pattern of behavior. For instance, we might believe that there are classical genes that truly follow Mendelian inheritance patterns, or that physical bodies in free fall accelerate according to an inverse-square law. On the other hand, “nature is mathematical” may refer to the causes of phenomena having a mathematical nature. Examples include the view that motion is caused by the size and geometric shape of fundamental atomic particles, that the size of a biological population is a cause of evolutionary drift, or that the curvature of space–time causes gravity.

In his discussion of “the statistical frame of mind in systematics,” Hagen shows that Sokal and Rohlf, at least, adopted the view that

nature is mathematical (Hagen, 2003). As they wrote in their 1965 edition of *Biometry*, “The biological processes under study are largely concerned with populations and as such operate under statistical laws of probability. Thus the statistical approach to systematics is consonant with the essential nature of the subject matter” (Sokal and Rohlf, 1969, p. 383). Hagen has argued that the rise of a mathematical worldview corresponded to a generational shift in attitudes, from George Gaylord Simpson’s belief that statistics offered isolated tools for testing hypotheses about the distributions of traits in populations to Sokal’s more expansive views.

What is the history of mathematical natures in systematics from the Modern Synthesis onwards? There seems to have been rapid turnover in the ontological grounds for classification and phylogenetics: population genetics and speciation for evolutionary systematics, the genotype-phenotype map for phenetics, the tree of life for phylogenetic cladistics (Vergara-Silva, 2009), and the molecular clock for molecular phylogenetics (and what about pattern cladistics?). Which ontologies were most influential for the attitudes systematists adopted about mathematical realism, or should we look to other sources of change such as pedagogy? Is Hagen’s suggestion of a generational shift in views sufficient to explain the apparent increase in realist views after the 1950s? The rise of statistical methods in comparative phylogenetics and phylogeography could also expand the scope of this question beyond classical taxonomy and phylogenetics.

Who makes math indispensable? Mathematization often leads to changes in social identities as new roles close and open up within the community. The ‘who-question’ is thus linked to the community’s broader moral and political economy. Bruno Strasser, for example, has documented Margaret Dayhoff’s struggles with winning support and recognition for her work in building the *Atlas of Protein Sequence and Structure* from the 1960s onward (Strasser, 2011). Building the sequence database was an activity of collecting and comparing more familiar to the tradition of natural history in biology than the tradition of experiment upheld by geneticists and molecular biologists. Indeed, experimenters saw little intellectual value in the work that Dayhoff did, despite her careful validation of published protein sequences against experimental results and the value of her database for theoretical inferences about molecular evolution. Someone like Dayhoff had to generate financial support and cooperation for the work of collecting and sharing the data without much recognition for its scientific value and without using the data herself in a way that threatened the rewards

of experimenters. In other words, “there was an essential contradiction in the requirements for a sequence database: the collector had to be a recognized figure in the field of DNA sequences yet not display any personal interest in the data it contained” (Strasser, 2011, p. 68). The social role of a database organizer was novel to the context of molecular genetics and required fraught negotiations in order to win sustained support in the political economy of the field (e.g., funding from the National Institutes of Health) while respecting existing norms about sharing and using data.

The analogous challenges faced by builders of taxonomic databases have not yet received serious attention from historians, though see Pullan et al. (2000) and Agar (2006). However, we also want to point out another type of role that is more central to the development of methodology in systematics: scientists who specialize in building and maintaining software packages for use by other scientists who specialize in the study of particular taxa (Sterner, 2014). In the case of systematics, it appears that the scientists who helped write, manage, and distribute these packages were also often leading theorists in the field: Sokal and NTSYS, Farris and Hennig86, David Swofford and PAUP, and David and Wayne Maddison and MacClade. Understanding how these efforts fit within the moral and political economy of systematics would be a major advance in explaining how the field adopted mathematical methods.

Conclusion

It is time to escape the limitations of the Systematics Wars narrative and pursue new questions that are better positioned to establish the relevance of the field in this time period to broader issues in the history of biology and history of science. To date, the underlying assumptions of the Systematics Wars narrative have led historians to prioritize theory over practice and the conflicts of a few leading theorists over the less-polarized interactions of systematists at large.¹⁶ We have shown how shifting to a practice-oriented view of methodology, centered on the trajectory of mathematization in systematics, demonstrates the problems with the common view that one camp (cladistics) unproblematically “won” over the other (phenetics). In particular, we critiqued David Hull’s historical account in *Science as a Process* by demonstrating exactly the sort of intermediate level of positive sharing between phenetic

¹⁶ See our discussion of character coding and consensus trees above.

and cladistic theories to undermine their distinct individuality as conceptual systems over time. As a result, it is biased and thus misleading to treat them as holistically opposed theories that can only interact by competition to the death.

Looking to the future, we suggest that systematics provides important new perspectives on the history of mathematization and computerization in biology after World War II (Sepkoski and Ruse, 2009; Strasser and de Chadarevian, 2011; García-Sancho, 2012; Leonelli and Ankeny, 2012; November, 2012; Sepkoski, 2012; Strasser, 2012). More broadly, we have shown how computational workflows provide a powerful way of articulating and tracking the organization and development of knowledge in systematics: systematists quickly associated particular procedures such as character coding and mathematical objects such as similarity measures with major research problems that shaped methodological work for decades.

Tracking mathematization in terms of workflow also has interesting implications for the historiography of mathematical practices. Workflows are not merely a standardized sequence of calculations, they are also means for segmenting work according to a division of labor, coordinating the results of independent groups, and establishing the jurisdiction of methodologists over a distinctive set of tasks or problems (Bowers et al., 1995; Bardram, 1997; Dourish, 2001; Gerson, 2008; Sterner, 2014). Moreover, the ability of scientists to disseminate or adopt a workflow is strongly influenced by the technologies available to implement it as a practice. Workflows are therefore a crucial nexus linking the intellectual history of methodology, the social history of practices, and the material history of technology. In this vein, we suggest that workflows provide an often-overlooked answer to why computer technology matters for the history of mathematization: the widespread availability of computing technologies marks an important new social mechanism for instituting the indispensability of mathematics across a community.

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