The Systematics Association Special Volume Series 67

Milestones in Systematics

Edited by
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London

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CRC PRESS
Boca Raton London New York Washington, D.C.

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The Systematics Association Special Volume Series

Series Editor

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This edition published in the Taylor & Francis e-Library, 2005.

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Cover Illustration

The illustration depicted on the cover is of the Chironomid *Zelandochlus latipalpis* Brundin, the "ice-worm," taken from Lars Brundin's 1966 monograph (*Kungliga Svenska Vetenkskapsakademiens Handlingar, fjärde serien,* 4 (11):Fig. 35, reproduced with permission). Brundin's monograph was the impetus for much of the cladistic revolution, particularly with respect to progress in biogeography and as a major inspiration for the "reform" of palaeontology. Brundin's influence can be found in Chapters 6, 7 and 10. His influence on the development of systematics and biogeography has yet to be fully explored.

Library of Congress Cataloging-in-Publication Data

Milestones in systematics / edited by David M. Williams, Peter L. Foley
p. cm. (Systematics Association special volume; no. 67)
Essays from a symposium held within the 3rd Systematics Association Biennial Meeting, September 2001.
Includes bibliographical references and index. (p.).
ISBN 0-415-28032-X
1. Biology--Classification--History--Congresses. I. Williams, David M. (David Malcolm), 1940- II. Forey, Peter L. III. Series.
QH83.M64 2004
578′.01'2—dc22 2003065587

International Standard Book Number 0-415-28032-X
Library of Congress Card Number 2003065587

ISBN 0-203-64303-8 Master e-book ISBN

ISBN 0-203-67603-3 (Adobe eReader Format)

Introduction

Peter Forey and David Williams

This collection of essays arose out of a symposium under the same title of this book, held within the 3rd Systematics Association Biennial Meeting (September 2001). As organizers we tried to invite contributors who had first-hand experience of the changes in systematic practice that were taking place during the last third of the twentieth century. This period was pivotal for the position in which we now find ourselves. Systematic methodologies were being scrutinized mainly through the meaning of relationship and how that meaning was to be expressed in classification — the vehicle reflecting our understanding of the order in the natural world. The concept of relationship is so basic to biology that there has been constant upheaval and realignments of ideas, so to single out authors active during the past 30 years may seem eclectic. However, these authors do provide a link with the more distant past and they are a part of that history, ostensibly better equipped to document the contemporary background than authors one hundred years from now. At the same time, our authors also approached their subject with their own reading of history so we cannot claim objectivity.

The first two chapters come nearest to this endeavor since they are written by historians of science, skilled in the art of unprejudiced commentary. Mary (Polly) Winsor (Chapter 1) has some rather penetrating statements on scientists writing history, claiming that some do so to influence the future. Her case is compelling even though it may sound uncomfortable to some and is exemplified by the writings of Ernst Mayr and Peter Sneath who, she claims, set up Darwin and Adanson, respectively, as forefathers of their own views.

In general, systematists have not been good at organizing themselves to speak with one voice, which is seen today as counterproductive to securing the financial underpinning of the discipline. This is true. There have always been deep divisions in philosophical stances, objectives and methods in trying to make sense of the order of life. Richard Blackwelder's account of the formation of the Society of Systematic Zoology (SSZ) in 1947, ostensibly in opposition to the Society for the Study of Evolution, has always been viewed as just another instance of an ideological tiff. Joe Cain's fascinating retelling of events (Chapter 2) leading up to the formation of the SSZ draws on previously ignored documentation and suggests a more complex history, steeped in postwar reconstruction of scientific dialogue. He suggests that Blackwelder's account is distorted by his dislike of the evolutionary systematics championed by Ernst Mayr.

In the early days of spirited debate between cladists and the then traditional taxonomists, Walter Bock was one of the first to argue the case for evolutionary taxonomy from a philosophical point of view. Part of those early arguments concerned Karl Popper's distinction between science (theories established that could be falsified through some test) and nonscience (theories that could not generate tests leading to potential falsification). Cladists had claimed that evolutionary taxonomy fell into the latter category, although none claimed that it was unscientific in the more general sense of that word. In Chapter 3 Bock returns to this subject in distinguishing between nomological deductive explanations (those arrived at through Popperian science) and historical narrative explanations (instances of singular events such as those documented in phylogeny reconstruction). His thesis is that historical narrative explanations, once proposed, are corroborated by more evidence rather than falsified. Nevertheless, the formulation of those historical narratives must of necessity involve nomological deductive explanations such as several facets of evolutionary theory.

The influence of Popper's ideas on the demarcation of science from nonscience continued to wax and wane throughout the past 25 years, at one time dropping out of sight altogether only to be recently resurrected, this time in defense of statistical methods of phylogeny reconstruction such as maximum likelihood. Olivier Rieppel, a previous champion of the more usual hypothetico-deductive understanding of the application of Popper's ideas, presents a general attack on falsification as applied to systematics, damning its use in both camps, hypothetico-deductive and statistical (Chapter 4). Rieppel's arguments are complex but repay a careful read. If, as is suggested, congruence might be a questionable enterprise, then what, if anything, might there be left for the systematist with which to evaluate their data? It is also evident that statistical methods are not applicable to the falsification arguments either. Rieppel presented suggestions for the future elsewhere, but the issues he raises here are of general concern, not least that it might be surmised that Willi Hennig, the father of cladistic analysis, may indeed have had some sympathy for Rieppel's general conclusions.

The method of phylogenetic reconstruction proposed by Willi Hennig and known as phylogenetic systematics is rather different from the cladistic methods in use today. Hennig formulated his ideas before the era of computer-generated trees and the strict application of parsimony algorithms. He suggested that characters be polarized into primitive (plesiomorphic) and derived (apomorphic) states before analysis; he did not believe in character weighting in the sense that it is applied these days and he was probably unaware of such things as unrooted networks and the possibilities of finding the root by some outgroup criterion. Johann-Wolfgang Wägele (Chapter 5), in describing the transmutation of Hennig's method, suggests that we might be better served by developing some of Hennig's original ideas to improve our methods of phylogeny reconstruction. Most importantly he suggests that considerably more attention be paid to the identification, description and codification of characters before entering them into the computer. He calls this crucial stage character analysis (a term more usually reserved for the computational stage in most cladistic analyses). Wägele is a morphologist who appreciates the richness of morphological variability and proposes that characters can be polarized, assessed and weighed by their quality and discusses ways in which this might be done.

Gary Nelson, one of our contributors who played a dominant role in the cladistic revolution, addresses the concept of ancestry in systematics (Chapter 6). He recounts that the difficulties posed by trying to recognize ancestors were started by paleontologists at the turn of the twentieth century and are continued today in the oft-quoted contention that dinosaurs are ancestral birds — a view, he argues, that is entirely mistaken. He has more to say about optimization, as used by modern computerized parsimony analysis, finding that it falls far short of what systematists should be doing — enquiring about relationships. Alarmingly, he identifies that current computer programs fail to find relationships (nodes on cladograms) where they should be found and finds them where they should not. If this happens, then the addition of more data might simply lead to a path of least distortion rather than a path to enlightenment.

Peter Forey (Chapter 7) covers some of the same ground as Nelson, tracing the paleontologists' quest for ancestors at the end of the nineteenth century and its unhelpful influence on systematics, with the establishment of grade groups and the preoccupation with time. Two strands of evolutionary theory (adaptation and genealogy) caused difficulties for the paleontological contribution to phylogeny reconstruction, which became uncritical of the evidence and generous with evolutionary scenarios. This approach came under attack by cladists who questioned the use of time in phylogeny reconstruction as well as the ability to recognize ancestors, two uniquely paleontological contributions. Recently, both time and ancestors have resurfaced in the latest discussions of phylogeny reconstruction.

A.W.F. Edwards recounts the early days of computer algorithms used to reconstruct phylogenetic relationships (Chapter 8). He was in the 1960s circle of those debating the use of parsimony analysis and the theoretical justification for its implementation. He argued that the most plausible estimate of an evolutionary tree is that which invokes the minimum amount of evolution. Naturally this approach was not accepted by all since "plausible" and "amount of evolution" are constrained by particular models of evolution. The algorithms developed by Edwards and contemporaneous workers needed to address these uncertainties. Edwards' chapter is interesting because similar discussions of model parameters surround the use of current algorithms used to reconstruct phylogeny. As an aside it is interesting to note that in these early days (1964) computing power restricted analyses to just four taxa!

David Williams (Chapter 9) traces the history of the concept of homology, the most fundamental concept in comparative biology, at the heart of the meaning of relationship. No wonder that, with the exception of the species, it has been the most discussed word in biology. He reaches back to the middle of the nineteenth century when Richard Owen was one of the first to clearly articulate the meaning of homology and to distinguish it from other kinds of relationships (e.g., analogy). After Darwin, Ray Lankester translated the idea of homology to historical continuity (evolution) while George Mivart resurrected the embryological spin so that at the turn of the nineteenth century ideas of homology multiplied and became entangled with ideas of pattern and process. This led to a plethora of terms that were used in subtly different ways by different authors. Williams identifies a second milestone in the 1970s. Here, the distinction between transformational (process) homology and taxic (pattern) homology was made clear and led to the third milestone, identified by Williams as the concept of homology as a relation between groups. As he says, this last is yet to have its full impact.

Homology has been applied not just to morphological features but to molecular data, behavioral data and many other kinds of information that can be applied to comparative biology. It remains a little surprising, then, that the concept of biogeographic homology has been little explored, in spite of the resurrection of biogeography as an analytical science in the late 1970s and 1980s. Chris Humphries (Chapter 10) continues his exploration of Leon Croizat's dictum that "Earth and Life evolved together," captured in the revised threefold parallelism, "space, time, form." Humphries examines much new historical material, again showing that the notion of a stable Earth was challenged on many occasions, resisted almost wholly because of prevailing trends, rather than careful assessment of the available data. Darwin's natural selection, as Humphries points out, was essentially an ecological theory concerning the origin of life and had little to do with historical development of the Earth those same organisms inhabited. Humphries reviews the methods for analytical biogeography, especially those developed in the past 30 years. Surprisingly, almost all researchers neglect the concept of biogeographical homology save those who deal directly with taxon cladograms. Some noted 25 years ago that biogeography was in its infancy. Humphries' chapter suggests that rather than reaching maturity, childhood is still some way off.

Peter Holland (Chapter 11) documents the revival of the link between studies of evolution and embryology, colloquially known as evo-devo. These two endeavors had drifted apart during the first half of the twentieth century, each searching for answers to different questions: evolutionary biology became concerned with gene frequencies, selection coefficients, etc., while embryology became less of a comparative discipline and concentrated on experimentation in a few tame lab animals. The renewed link has been made through the intermediary of molecular biology and phylogenetics, new techniques in tracing cell lineages as well as the manifestation and understanding of gene action. These techniques have allowed broad comparisons to be made between many species. Systematics is central to evo-devo because it provides the patterns of morphological variation to be explained, articulates the questions to be asked as well as directing the selection of species to be investigated. In turn, patterns of development that were key to systematics in the nineteenth century are becoming known in ever finer detail, such that our conjectures of homology may be more tightly constrained.

One area in which we feel some regret is the absence of a chapter dealing with the rise and development of molecular systematics, which was almost exponential in the last quarter of the twentieth century. While the subject was addressed during the symposium, perhaps it is too soon to assess a history that has not yet had time to get old. Nevertheless, its history is intermingled with the development of the molecular clock, events that have been captured in a recent essay by Morgan (1998). Hillis et al. (1996) provide some historical details pertinent to the practical techniques that have made molecular systematics routine enquiry, and Page and Holmes (1998) cover many of the analytical techniques used in inferring phylogeny from various kinds of molecular data.

Finally, we express our thanks to all of our colleagues who refereed the contributions; we hold them in no way responsible for the final outcome.

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Editors

David Williams is a researcher of diatoms — freshwater, marine, and fossil, at The Natural History Museum, London. His primary interests are in the systematics, evolution, and biogeography of freshwater diatoms. Diatoms, a group of photosynthetic eukaryotes, have often been recognized as a ubiquitous group of organisms, without any discernable geographic differentiation. Williams has endeavored to penetrate this myth, and has contributed to the beginning of serious diatom biogeography. His other interests are the history, theory and practice of systematics, classification, and biogeography, studies that help to expose other myths — some harmless, others not. He has co-authored two books on cladistic methods in systematics and co-edited a book on phylogenetic methods.

Peter Forey is a researcher in fossil fishes at the Natural History Museum, London, where he undertakes research into the anatomy and relationships of fishes, in particular coelacanths and primitive teleost fishes. While most of his research is specimen based, there is inevitably a theoretical component concerned with how relationships are discovered and how the results are expressed in diagrams and classifications. Within the field of paleontology there is division between those who advocate that the "present is the key to the past," and those who believe that the "past is the key to the present." Forey sides with the former, and explores ways in which the fossil record is best able to supplement our explanations of present diversity. He has contributed to and edited several volumes of essays concerned with such diverse subjects as the theory and practice of cladistics, the relationship between systematics and conservation, and the kinds of observations that can usefully reveal the paths of evolution.

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Chapter 1

Setting Up Milestones: Sneath on Adanson and Mayr on Darwin

Mary P. Winsor

Abstract

History is written by people, and whether those people are historians, scientists, or philosophers makes a difference in what they want from the past. Usually, scientists hope to foretell or even influence the future, a motive uncongenial to historians. Two instances of biologists setting up historical figures as milestones, heroic forerunners of their own views, exemplify important issues about the writing of history. In 1957 Peter Sneath, a founder of numerical taxonomy, identified Michel Adanson as his precursor, proposing the term *Adansonian* for principles Sneath advocated. Sneath did not realize that statements about Adanson by previous scientists, including Francis Bather and Georges Cuvier, misrepresented his methods. Sneath's historical interpretation was immediately challenged by botanists who had paid close attention to Adanson's writings. With co-author Robert Sokal, Sneath appealed to historians of science to adjudicate the question, but none responded. In 1957 Ernst Mayr announced that Charles Darwin had replaced typological thinking by population thinking. Mayr's claim about the dominance of typology acquired new lustre when melded with Karl Popper's coinage, "essentialism." Mayr's historical interpretation reflected 20th-century concerns but was supported by scant historical evidence. The example of Adanson undermines Mayr's claim, but here too historians failed to supply an effective evaluation. Both stories warn that scientists must take responsibility for their own history.

> Several recent occurrences indicate a revival of interest in systematic biology and the broad problems of classification … . [Their effect is] to disturb our confidence in the concepts with which we have worked so long and to make us wonder whether any System at all can be based on the Theory of Descent. What, we fearfully enquire, is to be the future of Biological Classification? Is the Linnean nomenclature breaking down? (Bather, 1927:lxii–lxiii)

Although sounding so modern, these words date back to 1927, when a distinguished British Museum palaeontologist, Francis Bather, addressed his colleagues on the subject of the past, present, and future of systematics. Many systematists still believe, as he did, that investigating history illuminates fundamental issues about systematics, issues that are central to choices being made about future taxonomic practice. "To foretell the future," Bather declared, "it is necessary to understand the past" (p. lxiii).

Scientists' interest in the past is usually, perhaps always, intimately tied up with their interest in the future. Science in its innermost nature is heavily oriented toward the future.

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Unanswered questions cry out for action, debates demand resolution on the basis of new evidence rather than mere rhetoric, and more research is needed. Arthur Cain was very clear, in his several historical articles of the late 1950s and early 1960s, that his motive for doing history was to reorient present thinking in hopes of a better future (Winsor, 2001). When he said in 1958, "I think that we are about to see a considerable revision of the whole basis of taxonomic theory" (Cain, 1959b:241), he was pointing to the infant field of numerical taxonomy arising from his own work with Harrison and the work of Sokal, Michener, and Sneath.

At that time Cain was pleased to discover, as he then thought, that Linnaeus's understanding of nature was hopelessly bound up with inappropriate Aristotelian logic. Cain's superficial smattering of philosophy dazzled biologists and historians alike, and no philosopher troubled to chastise him. Forty years later Cain in his retirement began to make more careful readings of Linnaeus, but by then he had quite given up on the idea that investigations into the past were useful guides to the future (Winsor, 2001).

Peter Sneath's excursion into history was likewise part of his effort to shape the future of taxonomic theory and practice. Searching for a rationally based systematics, he recognized a kindred spirit when he read John Gilmour's essay "Taxonomy and Philosophy" in the Systematics Association volume *The New Systematics* (Gilmour, 1940; Winsor, 2000). The first item in Gilmour's list of references was Bather's address, which Sneath looked up and found very useful. There (Bather, 1927: lxx) Sneath read about an eighteenth-century botanist, Michel Adanson, who had, in Bather's words, "set to work to tabulate all possible characters, basing a classification on each. Then, setting his 65 classifications side by side, he found certain groupings to occur most frequently, and those he took as his families." This sounded like some kind of mechanical tabulation, so it immediately resonated with Sneath, who at that time was tabulating similarities between strains of bacteria (Vernon, 1988, 2001). How could Sneath have guessed that his guide, Bather, had himself been misled about what Adanson's method was? Adanson's own two-volume *Familles des Plantes*, though hard to interpret, can give the impression of fitting Bather's description, for it contains tables of his 65 artificial classifications as well as his 58 natural families. In fact, however, Sneath was about to step on an old landmine, laid during a long-forgotten war.

By the time of Adanson's death in 1806, Georges Cuvier had established himself at the center of French biology, and, as Secretary of the Institute, it was up to him to write the naturalist's obituary (Outram, 1978:162). An important part of Cuvier's claim to fame was his new and supposedly rational approach to systematics, an approach distinctly at odds with the raw empiricism Adanson had espoused. Cuvier's bias is revealed in his comment that Adanson's method produced an estimate of affinity "independent of the rational, physiological knowledge of the influence of organs ..." (Cuvier, 1807:282), in other words, knowledge of the kind required by Cuvier's principle of the subordination of characters. Adanson had clearly argued in favor of a natural classification, but to him that simply meant one that takes into account all features of organisms, in contrast to an artificial method, which uses only a few features.

Adanson said that he had constructed several artificial classifications in his early youth, but later decided that none would ever mirror nature because the features important for some groups were not the important ones for other groups. He nevertheless continued to make one-character systems, while also seeking nature's own groups. The result of his search was 58 natural families, given in detail in Vol. 2 of *Familles des Plantes*, published in 1763. In Vol. 1 (not actually published until the following year [Stafleu, 1963:238—239]), Adanson sketched his artificial systems, followed by a table that measured the "degree of goodness" of each, in comparison with the 58 natural families. This exercise was designed to show how far each of the 65 fell short, and it also suggested which characters were less bad than others.

Adanson did explain how he had arrived at his 58 natural families:

> First I made a complete description of each plant, putting into the description each of its parts in separate articles, in all its details; and to the extent that some new species appeared that had a relationship to ones I had described, I described them on the side, not mentioning the resemblances but only noting their differences. It was by the totality of these compared descriptions that I perceived that plants naturally arranged themselves under classes or families which were neither systematic nor arbitrary, not being based on one or a few parts that can only change within certain limits, but on all parts … . (Adanson, 1763–1764:clviij)[1]

Probably Cuvier, who did all his work with notorious speed, was really unconscious of how inadequate was his comprehension of Adanson. The atmosphere Adanson had breathed as a student of Bernard de Jussieu in the 1740s, when Linnaeus's artificial classes and orders were the subject of passionate debate among botanists, was a thing of the past when the young zoologist Cuvier was a student of C. F. Kielmeyer in the 1780s. After another quarter of a century, the mature Cuvier began by reporting what Adanson had done.

> Considering each organ by itself, he made a system of division based on its different modifications. He arranged in this system all the organisms known. Repeating the process for each of a great many organs, he constructed a number of such systems, all of them artificial and each based on a single organ chosen arbitrarily.

Then Cuvier went on to offer a speculative account of what a reasonable man could possibly do with such a large number of artificial systems, an account any trusting reader would wrongly imagine to be based on something Adanson had said.

> It is evident that entities which are classed together in every one of these systems are exceedingly close to one another, since they resemble each other in all their organs. The relationship is less when the entities are placed in different classes by some of the systems. And finally, the most distant are those entities which are not grouped into the same class by any of these systems. This method thus gives a precise estimate of the degree of affinity between the organisms … . (Cuvier, 1807:282)[2]

[1] "Je faisois d'abord une description entière de chaque Plante, en metant dans autant d'articles séparés, chacune de ses parties, dans tous ses détails; & à mesure qu'il se présentoit de nouveles Espèces qui avoient du raport à celles déja décrites, je les décrivois à côté, en suprimant toutes les ressemblances, & en notant seulement leurs diférences. Ce fut par l'ensemble de ces descriptions comparées que je m'aperçus que les Plantes se ranjoient naturelement d'elles-mêmes sous des Classes ou Familles, qui ne pouvoient être systématiquès ni arbitrères, n'étant pas fondées sur 1 ou quelques parties qui dussent chanjer à de certaines limites, mais sur toutes les parties … ." Adanson believed that French spelling should be made more phonetic, which did nothing to make his text more attractive to his contemporaries.

[2] "Considérant chaque organe isolément, il forma de ses différentes modifications un système de division dans lequel il rangea tous les êtres connus. Répétant la même opération par rapport à beaucoup d'organes, il construisit ainsi un nombre de systèmes, tous artificiels, et fondés chancun sur un seul organe arbitrairement choisi. Il est évident que les êtres qu'aucun de ces systèmes ne séparerait, seraient infiniment voisins, puisqu'ils se ressembleraient par tous leurs organes; la parenté serait un peu moindre dans ceux que quelques systèmes ne rassembleraient pas dans les mêmes classes; enfin, les plus éloigns de tous seraient ceux qui ne se rapprocheraient dans aucun système. Cette méthode donnerait donc une estimation précise du degré d'affinité des êtres … ." The translation is Sneath's (1965:482).

Yet Adanson said no such thing. He never explained exactly what use he made of his 65 artificial systems while seeking his natural families. The closest he came were these two statements:

> [After finding that none of my artificial systems worked] I only used them in the search for the natural method, in which they all helped me greatly.[3]

> [Among the advantages of my set of artificial systems is:] Taken together, they give all existing or observed relations among all the parts of plants, relations from which our 58 families are formed. (Adanson, 1763–1764:cciij)[4]

Adanson never pointed to any entities "classed together in every one" of his 65 systems. His testimony that he had perceived how plants naturally arranged themselves, after he had written as full a description as he could, suggests that his artificial systems were useful to him as a data bank, a kind of index in which he could look up whether a given character was found in a particular plant. We must assume that by the time he was writing his book, every species he knew had been entered in its proper place within each of his 65 systems, but he did not put into print this complete catalog because, he said, with 1615 genera, it would have taken too much space. What he gave instead was, in each artificial system, the names of his natural families, distributed among the several sections. This was enough for him to then compute the extent to which his natural families are broken up or left intact by each system, but obviously he cannot have portrayed his systems in this way until he had decided upon his natural families (Nelson, 1979:16–17).

Cuvier's student Augustin-Pyramus de Candolle repeated Cuvier's interpretation in his 1813 *Théorie Élémentaire de la Botanique*, adding the information, not mentioned by Cuvier, that the number of Adanson's artificial systems was 65. de Candolle had the wit to recognize how unlikely it was that anyone could really have done what Cuvier claimed, so he added that Adanson had probably formed his families "as much by means of feeling his way as by his own method" (de Candolle 1813: 71).[5] de Candolle's reservation as to its practicality did not call into question Cuvier's version of the method itself, however. As the years rolled by, Cuvier's name acquired the luster of immortal fame, while eighteenth-century theoretical disputes dropped further beneath the horizon. For many later writers, including Bather, the lucid historical section of de Candolle's widely reprinted textbook was the source for their mention of Adanson.

To Sneath it looked obvious that a person whose method was to make 65 different classifications, each based on a different character, and then to combine them, must be giving equal weight to each character. Indeed de Candolle had made the same assumption. In 1957 Sneath proposed that a classification "based on giving every feature equal weight … may conveniently be called 'Adansonian'" (Sneath, 1957:196, 1958). This interpretation was fully endorsed by Arthur Cain (1959a), who was misled by the same sources (Bather and de Candolle) and for the same reasons (he too thought taxonomy needed to become more objective). The founding textbook of numerical taxonomy that Sneath co-authored with Robert Sokal relayed this mistaken view of Adanson and expanded the scope of the term *Adansonian* (Sokal and Sneath, 1963:50).

When Sneath was invited to speak at a well-funded conference at the Hunt Botanical Library in Pittsburgh, he was so far from recognizing the ticking bomb set by Cuvier that

[3] "… je ne les emploiai que pour la recherche de la Métode naturele, à laquele leur ensemble m'aida beaucoup."

[4] "Leur ensemble done tous les raports existans ou observés entre toutes les parties des plantes, raports d'où se sont formées nos 58 Familles."

[5] "… qu'il a peut-être formées, autant par voie de tâtonnement, que par sa propre méthode …"

he said (in August 1963) "What were the main features of Adanson's method? One cannot do better than quote from Cuvier's *Éloge* …" (Sneath, 1965:482). Yet in the meanwhile Sneath had been studying Adanson's own works, the earlier work on the molluscs of Senegal as well as the botanical volumes, so how could he still accept Cuvier's version as sound? Part of the reason is doubtless Adanson's own lack of clarity; Sneath was a microbiologist, and Adanson's examples are hard even for a malacologist or botanist to penetrate, because so many taxon names have changed. Perhaps also, Sneath imagined that Cuvier, a contemporary of Adanson's though 42 years his junior, was more likely to understand Adanson's intent than a twentieth-century reader could. It must also be admitted that Sneath's interest in having a colourful precursor for his new scientific enterprise may have dulled his critical faculties. Sneath had a much sharper conception than de Candolle had had of the practical impossibility of the method Cuvier described, yet still it did not occur to him, any more than it had to de Candolle, that the problem might lie with Cuvier, not with Adanson. After quoting Cuvier, Sneath said,

> [Adanson] then apparently counted the number of times that a pair of entities fell together in the subdivision. In effect this procedure counts the number of disagreements in the characters used to make the divisions, and if carried out systematically would have yielded a table of the comparisons between each organism and every other, which would have been, in effect a similarity matrix. Whether Adanson ever proceeded in this systematic way is very doubtful: the number of pairwise comparisons between the 1615 genera in the *Familles des plantes* total over a million. It is more likely that he counted the disagreement for some of the comparisons only, but did enough to obtain a fair idea of the salient relations between the organisms. (Sneath, 1965:483)

The number "over a million" shows that Sneath had really not given close attention to the statement he quoted from Cuvier, much less to Adanson's statements. Sneath's figure comes from making one act of comparison between each of the 1,615 genera and all the others, which is 1,615 squared, minus the self-comparisons and minus the duplicates (1,615 x 1,614)/2 = 1,303,305. However, the method described by Cuvier would have required Adanson to also ask, for each pair being compared, whether or not it is found united in each of his 65 artificial systems. This extra step, without even wondering how the answer to that question could generate the natural families, forces the 1,303,305 to be multiplied by 65, so even being conservative, Sneath should have said "over 84 million" (for 84,714,825). Actually, neither number would be so terrible if one had set up the data such that comparisons could be made at a glance. One comparison every 5 seconds, working an 8-hour day, resting on Sundays, would allow one to cruise through the task set by Sneath in less than 9 months and finish the task described by Cuvier in 47 years, not fun but feasible.

The explosion Sneath met with in Pittsburgh was an explosion of historical information. Jean-Paul Nicholas, financed out of the deep pockets of Roy Arthur Hunt to make a full-time study of the manuscripts Hunt had purchased from Adanson's heirs, traced his life in minute detail (Nicholas, 1963). Frans Stafleu, the Dutch botanist and historian of botany, had gone through Adanson's *Familles des Plantes* with a fine-toothed comb and went to great lengths in the published version of his Pittsburgh lecture to contradict all of Sneath's historical claims (Stafleu, 1963:195, 201). The proceedings of the Hunt conference were promptly published, soon followed by a reprinting of Adanson's *Familles des Plantes* with a preface in which Stafleu insisted that any taxonomy using

> the unbiased inductive method … has always been Adansonian. To use the term Adansonian for numerical taxonomy alone is not conducive to a better understanding of the latter subject. Adanson was anything but a computer avant la-lettre, and a study of his systems and basic statements reveals that he did not rest content with equal weighting. (Stafleu, 1966:x)

Stimulated by the publication of the proceedings of the Pittsburgh conference, several other botanists, unsympathetic to numerical taxonomy, weighed in with complaints against Sneath and Sokal's "wish to adorn their movement with a historical figure: poor Adanson" (Jacobs, 1966:55). B. L. Burtt of the Edinburgh Botanical Garden seized on Sneath's admission that to really do the matrix implied by Cuvier would require over a million comparisons (Burtt, 1966). Michel Guédès, botanist at the Muséum National d'Histoire Naturelle, Paris compiled a thorough review and published it in a historical journal. It was he who first identified Cuvier as the source of the mistake (Guédès, 1967).

Sokal and Sneath now faced a dilemma. The botanists cited above had put more time into reading Adanson than this zoologist and this microbiologist were willing to devote to the issue, but to simply drop Adanson from their account would be too much like admitting their opponents' case, which was not only bad strategy but not what they felt. Unsure of just how strong a case might be made for or against calling their approach Adansonian, they chose to keep him in the story but with less emphasis. In the 1973 revision of their textbook, rather than repeating their 1963 statement that "numerical taxonomy is based on the ideas first put forward by Adanson" (p. 50), they made the weaker claim that the principles of numerical taxonomy "embody concepts that can be traced to Michel Adanson" (Sneath and Sokal, 1973:5). If you press hard for the meaning of either statement, you find yourself asking things such as, for a later idea to be "based on" an earlier one, does the later author have to be familiar with the earlier author, or is it enough if the later author has come upon a similar idea independently? Are ideas like living things, which must maintain an unbroken chain of reproduction to maintain their identity, or do they enjoy some kind of ideal existence, like mathematical relations, so that different people may call to mind the same idea?

Sokal and Sneath also toned down their 1963 statement that an idea, like the equal weighting of characters, "may be called Adansonian," wording that seems to give permission and perhaps encourages that usage; however, in 1973 they just say that such ideas are "frequently called neo-Adansonian," which seems to report usage without judging it. The difference between the euphonious *Adansonian* and the longer *neo-Adansonian* is fraught with — what? politics? rhetoric? optics?

In their second edition, Sokal and Sneath retreat to pretended neutrality on the question of whether Sneath "is wrong in proclaiming Adanson to be the father of numerical taxonomy" (Sneath and Sokal, 1973:23). As if to wash their hands of the whole question, they declared,

> We prefer to let historians of science pursue this argument. For although it was — and remains — important to trace the roots of the historical origins of an idea in science, the development of numerical taxonomy has so far outpaced the early primitive ideas on this subject that to have to rely on Adanson's views for a validation of modern numerical phenetics seems as irrelevant as to rely on Mendel's writings for a validation of the findings of the molecular geneticists. (Sneath and Sokal, 1973:23–24)

Their defensiveness is obvious, for surely no one who used the term *Adansonian* pretended that the views of that dead botanist certified the validity of numerical taxonomy.

These remarkable statements seem to me to point to some significant issues concerning the status of history in relation to science. Sokal and Sneath said:

1. History is important.
2. Old views cannot validate current science.
3. Historians of science rather than scientists should sort history out.

I believe the apparent inconsistency between issue 1 and 2 can be explained by a careful consideration of what history is and how the present relates to the past. I believe that both statements are deeply true and I intend to address this topic explicitly elsewhere. Here, I shall address only issue 3. Sokal and Sneath seem to assume the existence of an unbiased higher court populated by "historians of science." They imply that the critics of their view of Adanson, who were biologists by profession rather than historians, had an axe to grind and were finding fault with Sneath's references to Adanson as a way of questioning the soundness of numerical taxonomy itself. That concern about objectivity is valid, though of course it also points to the possibility that their own interest in Adanson was likewise liable to be biased.

The point that interests me, as a professional historian of science, is the fact that I and my fellow historians of science responded to this direct appeal for our judgement with stony silence. (The only non-biologist who offered a judgement, as far as I know, was Réjane Bernier [1984], but that was almost 20 years later, and her professional home is philosophy rather than history.) The guild to which we historians belong has membership rules that strongly discourage, indeed practically forbid us, from accepting such an invitation. We are taught from our first days of graduate school that when we do history, we must view past events in their own context. We could take up questions such as What did Adanson actually say? What did he do? What was he probably thinking? Who read his work and what did they think of it? We are carefully taught, though, to avoid pronouncing on questions of the form, "Of what modern branch of biology was Adanson the forefather?" These professional rules are exactly parallel to what graduate students in research science learn, that a biologist can report on what kinds of organisms live in a particular place, and how they interact with one another, and even what their ancestors may have looked like, but the pressing question of whether the property owner has the moral or legal right to pave the place over is beyond the realm of pure or basic science. The professional training of most historians of science pledges us to do pure history. When scientists have serious disagreements, acting as referee is the last thing the historian wants to do. This is not to say that the scientists' appeal to our expertise is unreasonable, nor that our tendency to stay aloof is a virtue, only to say that the structure of academic disciplines has had this effect.

You may be inclined to doubt the accuracy of my portrayal, because you are thinking of several people who write the history of biology who have no hesitation at taking part in current debates, among whom are Michael Ghiselin, David Hull, and Marc Ereshefsky (Ghiselin, 1997). These, however, are people who do history without being members of our guild. Ghiselin is a biologist; Hull and Ereshefsky are philosophers.[6] The distinction between a philosopher and a historian is just as real as that between a mouse and a finch. The fact that we both talk about the past (which the philosophers do only some of the time, historians

[6] I am oversimplifying a bit. David Hull, when a student in a program in history and philosophy of science, did do some graduate work in the history of science and sees himself as interdisciplinary, saying that "historians think I do philosophy, scientists think I do philosophy, while philosophers think I do science" (personal communication, October 2001). He also testifies, however, that even in programs like Indiana's, students either identified themselves as historians or philosophers, not as hybrids (Hull, 2002).

full time) should not lead you into mistaking one kind for the other any more than the fact that both finch and mouse eat seeds. The guild to which philosophers belong does not forbid them from becoming involved in scientists' quarrels, although their professional rewards depend upon them returning from that excursion with some spoils that their fellow philosophers will think worthwhile. Perhaps you consider my ecological analogy far-fetched, because when animals use a resource they consume it, whereas when people look at historical material, the material remains available (indeed may become even more available through quotation and reprinting). Yet the professional demand that a publication must say something new means that if a historical event is well described, it becomes unavailable to another historian looking for an original topic. There may even be a process analogous to character displacement, for when historians of science emerged as a distinct new species, in the late 1950s, they defined their questions so as to be distinct from the questions of priority, precursors, and guidance for the future that scientists had always addressed through history.

A more sophisticated analysis of such guild distinctions than my ecological analogy is Elihu Gerson's application of the sociological concept of social worlds (Gerson, 1983). Scholarly research, even though one experiences it as the very lonely reading of an old book no one else has looked at, is truly a social activity, because one carries into the library one's expectations of the reactions of one's peers, to whom any significant findings must be communicated. Unfortunately the consequence is often that workers in each discipline respond only to the work of their peers working within the same discipline instead of giving appropriate attention to all relevant publications. For example, writings on Adanson by biologists, even such scholarly ones as Stafleu, Guédès, and Nelson, have been ignored by some later philosophers (Tort, 1989).

Biologist Ernst Mayr has never been content to leave anything he cares about to the historians to settle. Indeed he has been eloquent in support of biologists' right to do their own historical research and to make their own claims about the past. When professional historians, in reviewing his book *The Growth of Biological Thought*, criticized Mayr's Whiggishness; that is, his willingness to focus only on those past developments that led up to the modern state of things, he vigorously defended his style of history (Mayr, 1990). Yet that monumental book, and his hundreds of historical statements in his other books and articles and lectures, have not been enough to make him into a historian in the judgement of the inner elite of my discipline, any more than Hull's presidency of the Society for Systematic Zoology made him into a zoologist. The subject matter is one thing, but the guild is quite another.

At first, Mayr added history to his exposition of biology even more cautiously than Sneath had done, although his excursions into the past were just as clearly linked to the vision Mayr cherished for the future of systematics as Sneath's would later be to his own vision. Mayr barely mentioned pre-twentieth-century authors in his landmark 1942 book *Systematics and the Origin of Species*. Step by small step, however, in the 1950s he began to develop a historical narrative to add authority to his biological arguments about species (Junker, 1996). There was a very short historical section in the textbook he co-authored with Gorton Linsley and Robert Usinger in 1953 (Mayr et al., 1953). The next year he was invited to a celebration of Karl Jordan's 94th birthday, and for that occasion he reviewed Jordan's publications of the late nineteenth century (Mayr, 1955). In 1955, Mayr organized a symposium on the species question for the American Association for the Advancement of Science (AAAS), and he opened the day with a historical review (Mayr, 1957) that was based on previous surveys of the species question by German biologists.

It was quite clear that Mayr hoped that history would yield something to assist biologists in their current struggles to understand species. At first the historical material seemed to offer no outstanding forefathers. Karl Jordan was the closest thing to a noble precursor of Mayr's view of species, but Jordan would never be well known outside of entomology. Mayr had to contend with the problem that the most attractive and apparently central hero in the history of the evolutionary view of species, Charles Darwin, seemed to belong to the wrong camp. The view of the biological species Mayr was pushing featured its status as a real natural entity, something more substantial than a man-made category, more than a set of individuals. It was a population, "held together by a supraindividualistic bond" (Mayr, 1957:8); the geneticists who thought of taxonomists as mere stamp collectors had missed this central fact of evolutionary biology. Species are not categories, they are real entities, the subjects of the verb *evolve*. Linnaeus, in spite of being a creationist, was a positive landmark from Mayr's viewpoint, because he had believed in the objective existence of species, whereas Darwin, in spite of his virtues as an evolutionist, had said things about species that made them dangerously subjective. Mayr said at the 1955 AAAS symposium,

> In Darwin, as the idea of evolution became firmly fixed in his mind, so grew his conviction that this should make it impossible to delimit species. He finally regarded species as something purely arbitrary and subjective. "I look at the term species as one arbitrarily given for the sake of convenience to a set of individuals closely resembling each other, and that it does not essentially differ from the term variety which is given to less distinct and more fluctuating forms … .The amount of difference is one very important criterion in settling whether two forms should be ranked as species or variety." And finally he came to the conclusion that "In determining whether a form should be ranked as a species or a variety, the opinion of naturalists having sound judgment and wide experience seems the only guide to follow" (Darwin, 1859). (Mayr, 1957:4)

This subjective view of species, which a philosopher would call nominalist, was one of the dragons Mayr was determined to slay. It was an attitude still very common among many biologists, who regarded taxonomists as librarians of a kind, who erected classifications of their own invention for the sake of convenient retrieval of information. Mayr felt it was necessary to contradict this nominalist view if systematists were to be promoted from their lowly position of servants up to the status of real scientists.

There was at the same time a second dragon standing in the way of this promotion of systematics. Herbarium and museum taxonomists, although many or most believed the taxa they named had some kind of substantial reality, were vague or worse when it came to articulating that reality. At the species level, where they should have cared about the reproductive dynamics that Darwin had discussed and the breeding networks geneticists such as Theodosius Dobzhansky described as a gene pool, herbarium and museum taxonomists limited their attention to characters preserved in their dead specimens, that is, morphological characters, explicitly declaring out of bounds features of living organisms such as breeding habits, that is, biological characters. They had an elaborate system of voucher specimens they called "types," which the more enlightened taxonomists often had to remind their dimmer associates did not need to be typical of the species for which they were the name bearers. With respect to the higher categories, some taxonomists were frankly nominalist, declaring all groups above species arbitrary, but among the antinominalists there were some, most of whom were anti-Darwinians, who advocated idealistic theories about abstract archetypes, heirs of the nineteenth-century science of morphology. Mayr lumped together all these unconnected, misguided beliefs to make one coherent enemy, which he named "typology" or "typological thinking."

In his 1955 AAAS paper, Mayr's historical section identified the real species of local naturalists as the Linnaean stream, which had flowed through time distinct from the nominalist stream flowing from Darwin. Then, leaving history, Mayr proposed a classification of current species concepts, in which the typological species concept was introduced as a possible mistake to be avoided. Although in his discussion the name of an ancient Greek is prominent, Mayr was alluding to a timeless logical position rather than proposing a concrete historical development.

> *The Typological Species Concept.* This is the simplest and most widely held species concept. Here it merely means "kind of." … This simple concept of everyday life was incorporated in a more sophisticated manner in the philosophy of Plato. Here, however, the word *eidos* (*species*, in its Latin translation) acquired a double meaning that survives in the two modern words "species" and "idea" both of which are derived from it. According to Plato's thinking objects are merely manifestations, "shadows," of the *eidos*. By transfer, the individuals of a species, being merely shadows of the same type, do not stand in any special relation to each other, as far as a typologist is concerned. Naturalists of the "idealistic" school endeavor to penetrate through all the modifications and variations of a species in order to find the "typical" or "essential" attributes. Typological thinking finds it easy to reconcile the observed variability of the individuals of a species with the dogma of the constancy of species because the variability does not affect the essence of the *eidos*, which is absolute and constant. Since the *eidos* is an abstraction derived from individual sense impressions, and a product of the human mind, according to this school, its members feel justified in regarding a species "a figment of the imagination," an idea. Variation, under this concept, is merely an imperfect manifestation of the idea implicit in each species. If the degree of variation is too great to be ascribed to the imperfections of our sense organs, more than one *eidos* must be involved. Thus species status is determined by degrees of morphological difference. The two aspects of the typological species concept, subjectivity and definition by degree of difference, therefore depend on each other and are logical correlates.
>
> The application of the typological species concept to practical taxonomy results in the morphological defined species … . (Mayr, 1957:11–12)

Mayr's portrayal of Plato was somewhat inaccurate. The Platonic *eidos* was not a product of human thinking; rather, human intuition allows us to recognize the really existing *eidos*. Species, far from being figments of the imagination, are more real than individuals. The imperfections of our sense organs have nothing to do with variability for a Platonist. Contrary to Mayr's polemic, no biologist would contend that the individuals of a species "do not stand in any special relation to each other," for they have always been understood to be related as blood relatives. The bonds of reproduction that link all members of a biological species together has been recognized from time immemorial. Plato's student Aristotle discussed it at length, and from the first days of the revival of natural history in the Renaissance, the idea was commonplace that what the naturalist was doing when characterizing a species by its morphology, that is, its outward form, was seeking marks by which blood relatives could be recognized. Mayr was creating an ugly category from which all museum workers would want to distance themselves.

Immediately after sketching the typological species concept, Mayr admitted that few people believed in it: "Most systematists found this typological-morphological concept inadequate and have rejected it," (1957:12). The whole exercise would be odd indeed if this were a disinterested historical narrative. When we recall its context, introducing a symposium he had organized, a symposium that was part of his two-pronged efforts to get systematists to adopt the biological species concept and nonsystematists to accord them more respect, it makes perfect sense that Mayr would conjure up the typological dragon, branded with the name of a long-dead philosopher.

Mayr's dragon of typology has been breathing flames so frighteningly for close to 50 years now, that it may be surprising to recognize it as a specter of his own creation. His 1942 *Systematics and the Origin of Species* had criticized the morphological concept of species without anywhere alluding to typological thinking. That is, he criticized the practice of taxonomists who limited their attention to physical features without identifying them as followers of the wrong philosophy. Likewise, the authors contributing to the 1940 collection *The New Systematics* (Huxley, 1940) seemed unaware of this dangerous mode of thought, and so was G. C. Robson, whose 1928 book *The Species Problem* focused on naturalists and ignored philosophers and other nonscientists (Robson, 1928). Bather had been oblivious to the problem in 1927, when he said, "… I propose to pass by the old logical methods of classification, because they have no practical bearing on the arrangement of any natural objects, least of all those endowed with life" (lxiv). Darwin, while writing his most famous book, put concentrated effort into surveying the views of fellow naturalists about the nature of species and the nature of classification, and though he found that many of them harbored vague and inconsistent concepts, including "God's plan," the Platonic *eidos* was not an idea Darwin felt he needed to slay.

Mayr had been interested in Greek philosophy in his youth[7] and had heard that Plato was the enemy of empirical science. He learned from his teacher Erwin Stresemann that idealism had diverted ornithology from its healthy progress. In the 1930s and 1940s he was concentrating fully on the demanding job of being a museum taxonomist. Arthur O. Lovejoy's 1936 book *The Great Chain of Being* may not have come to Mayr's attention until its 1960 reprinting (Lovejoy, 1960). This book, which he greatly admired (Mayr, 1976:254), encouraged Mayr to view the history of thought as a long story of persistent themes, and one of the themes identified by Lovejoy was Plato's rationalism, the conviction that the world was put together in such a way that reason could penetrate it. Lovejoy argued that people, and generations of people, can be following assumptions or habits of thought of which they are unconscious, and such ideas can be general and vague.

Viewing the history of concepts in terms of grand themes allowed Mayr to give his story the hero it had lacked. As a promoter of systematics, the situation he found himself in was a competitive one, as he explained in the opening sentences of *Systematics and the Origin of Species*.

> The rise of genetics during the first thirty years of this century had a rather unfortunate effect on the prestige of systematics. The spectacular success of experimental work in unraveling the principles of inheritance and the obvious applicability of these results in explaining evolution have tended to push systematics into the background. There was a tendency among laboratory workers to think rather contemptuously of the museum man, who spent his time counting hairs or drawing bristles, and whose final aim seemed to be merely the correct naming of his specimens. (Mayr, 1942:3)

As he later put it, "a peculiar myth" had arisen, to the effect that "mathematical population genetics is the source of population thinking" (Mayr, 1976:307). His reading of the early papers of Karl Jordan had made clear that this distinguished old taxonomist had recognized the importance of the wide range of variability in natural populations in 1905. Mayr also knew that many taxonomists, "counting hairs or drawing bristles," still regarded

[7] E. Mayr letter to Karl Popper, 13 February 1978 (Harvard University Archives, Mayr Papers, Box 26, file 1297).

such variability as an inconvenience to be suppressed rather than an opportunity to investigate evolutionary processes, and he had to admit that Jordan had been far in advance of his peers. It was strategically essential that Mayr give taxonomists rather than geneticists priority for the central evolutionary concept of the variable population.

Mayr's needs and ideas came together in 1957, when he was invited to speak to the Anthropological Society of Washington, DC, as one in a series of lectures commemorating the centenary of the publication of Darwin's *Origin*. In preparation Mayr reread Darwin's classic work, and realized that he, no less than Jordan, could be credited with appreciating the uniqueness of each individual in a population. In this context Darwin's nominalism on the species question was a detail that could be ignored. On this public occasion Mayr had larger fish to fry. In Washington, in October 1957, Mayr declared that besides the theory of evolution by natural selection, another of Darwin's great achievements, "equally important but almost consistently overlooked" was that he had "replaced typological thinking by population thinking" (Mayr, 1959:2).

> Typological thinking no doubt had its roots in the earliest efforts of primitive man to classify the bewildering diversity of nature into categories. The *eidos* of Plato is the formal philosophical codification of this form of thinking. According to it there are a limited number of fixed, unchangeable 'ideas' underlying the observed variability, with the *eidos* (idea) being the only thing that is fixed and real while the observed variability has no more reality that the shadows of an object on a cave wall, as it is stated in Plato's allegory. The discontinuities between these natural 'ideas' (types), it was believed, account for the frequency of gaps in nature. Most of the great philosophers of the 17th, 18th, and 19th centuries were influenced by the idealistic philosophy of Plato, and the thinking of this school dominated the thinking of the period … . The assumptions of population thinking are diametrically opposed to those of the typologist. (Mayr, 1959:2, 1976:27)

Previously Mayr's bits of history only described taxonomists, or biologists, but here Mayr (1959) seemed to be talking about everyone. From this grand perspective, Darwin was the white knight. From this perspective, the enemy was not a particular sort of biologist, but the philosopher Plato and all later philosophers who had been unable to free themselves from his influence.

Mayr would later (1976:26) identify his Washington lecture as "the first presentation of the contrast between essentialist and population thinking, the first full articulation of this revolutionary change in the philosophy of biology," but he did not use the word *essentialism* in 1957. Accepting this philosophical term as the equivalent of the biologists' word *typology*, which he did in 1968 (Mayr, 1968:430), represented Mayr's cautious acceptance of the arguments of a young philosopher of science named David Hull. As a graduate student Hull had taken a course taught by Karl Popper, already celebrated as the author of *The Open Society and its Enemies* (Popper, 1945) and *The Logic of Scientific Discovery* (Popper, 1959). In 1944 Popper coined the term *essentialism* for the stance opposite to nominalism, because the traditional philosophers' label for the Platonic view, where the *eidos* or universals were held to be real, was *realism*, yet to nonphilosophers this seemed counter-intuitive (Popper, 1944:94). Although there were things about Popper and his thought that Hull did not like, he fully agreed with Popper's powerful argument that "every discipline as long as it used the Aristotelian method of definition has remained arrested in a state of empty verbiage and barren scholasticism" (Popper, 1950:206 quoted in Hull, 1965:314). Hull's student paper, demonstrating Popper's thesis with a fresh example, was published in 1965 as "The Effect